NOAA Technical Memorandum
NOS MEMD 9

LOOE KEY
NATIONAL MARINE SANCTUARY

A PRELIMINARY INVESTIGATION OF UPWELLING AS A SOURCE OF NUTRIENTS TO LOOE KEY NATIONAL MARINE SANCTUARY

Washington, D.C.
August 1987

U.S. DEPARTMENT OF COMMERCE / National Oceanic and Atmospheric Administration / Marine and Estuarine Management Division

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National Oceanic and
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National Ocean Service

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Marine and Estuarine Management Division

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NOTICE

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ABSTRACT

Recent studies demonstrating the importance of upwelling to the Great Barrier Reef ecosystem as well as the productivity of the outer southeastern U.S. continental shelf suggested the need for an assessment of the importance of upwelled nutrients to Looe Key Marine Sanctuary. The present study provides one year (October 1984 to October 1985) time series of temperature and nutrients (NH_4^+, NO_3^-, NO_2^-, PO_4^{3-}), with bihourly and 7-10 day resolution, respectively. During fall and winter, the water column was not stratified with respect to nutrients or temperature, and NO_3^- and PO_4^{3-} concentrations were at low or undetectable concentrations while NH_4^+ was relatively elevated. During late spring and summer, the water column was stratified and nutrient concentrations were consistently opposite that of winter, i.e. NO_3^- and PO_4^{3-} were elevated while NH_4^+ was low. An upwelling event in late July resulted in a $10^{\circ}C$ drop in temperature as well as the lowest recorded yearly temperature ($20^{\circ}C$). These data suggest that upwelling occurs during spring and summer months at Looe Key and may be related to seasonal changes in the volume transport of the Florida Current and the seasonal appearance of a counter current west of the Pourtales Terrace. This research increases our understanding of how oceanographic processes affect nutrient flux within Looe Key Marine Sanctuary -- information that is basic to management decisions attempting to preserve this sanctuary in a natural state.

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PREFACE

We acknowledge the valuable assistance of Roger Bewig for providing nutrient analysis and Patrick Pitts for thermograph maintenance and data analysis and plotting during the course of this study. Mary Samuel drafted the figures and Julie O'Connell typed the report. We especially thank Mr. Billy Causey and his staff for logistical support in many aspects of this study. This is Contribution No. 491 from the Harbor Branch Foundation, Inc.

INTRODUCTION

Importance of Upwelling to Looe Key Marine Sanctuary

Tropical coral reefs rank as some of the most productive natural ecosystems known (Lewis, 1977) and are outstanding as ecological anomalies in the oligotrophic surface waters of intertropical seas. Much attention has centered on the relationship between nutrient dynamics and productivity of tropical coral reefs because of the sharp contrast between the characteristically high productivities and standing crops of coral reefs and the typically clear, nutrient-poor unproductive water which surrounds them.

Most studies of coral reef metabolism have concerned inorganic nutrient cycling within the coral reef ecosystem (e.g. Pomeroy *et al.*, 1974). Central to all reef ecology theories is the coral-zooxanthellae symbiosis which constitutes Darwin's (1933) "myriad of tiny architects". Studies by Pomeroy and Kuenzler (1969) and Pilson and Betzer (1973) show this relationship is very efficient in conserving inorganic phosphorous through tight phosphorous retention and recycling. Coral reefs are also thought to derive much of their required inorganic nitrogen from *in situ* N fixation (Wiebe *et al.*, 1975; Capone *et al.*, 1977). These studies, and others, have perpetuated the view that coral reefs are, in large part, independent of their oligotrophic environment and thus have the ability to evolve and flourish in otherwise nutrient-poor waters.

As a corollary to this nutritional autonomy, ecologists tend to study coral reefs as independant systems and ignore the influence of the surrounding ocean. Such an approach is reasonable for the short time scales on which many coral reef studies are conducted, i.e., studies of nutrient kinetics and primary production. However, such an approach may not be valid when one considers the biogenesis of coral reef systems over geologic time. The obvious and inevitable flux of nutrients to and from coral reefs forces one to consider allocthanous sources of dissolved and particulate nutrients which might promote localized reef development over geologic time scales.

The importance of upwelling to the development of coral reefs was first suggested by Orr (1933). Nutrients derived from upwelling could be used directly by reef forming calcareous and frondose algae as well as coral-associated zooxanthellae. Elevated levels of particulate organic matter resulting from enhanced phytoplankton productivity could be assimilated directly by reef filter and suspension feeders, including corals, and could be transferred to the benthos by fish. Recent studies by Andrews and Gentian (1982) documented the importance of intermittent upwellings to the Great Barrier Reef ecosystem and point out that the world distribution of coral reefs show a marked concentration along the cyclonic side of major tropical current systems which are probable sites for upwelling. Thus, coral reef development may in fact represent an ecological response to intermittent tropical upwelling.

Upwelling of cold water onto the continental shelf of Florida was first reported by Green (1944), who suggested that anomalously low water temperatures occurred during June, July and August along an approximately 600 km section of coastline centered at about latitude 29°N. This study was followed by a more complete investigation by Taylor and Stewart (1957), which described upwelling somewhat more preceisely in space and time and suggested that the process occurred in response to seasonal variation in coastal winds. Atkinson (1977) proposed that Gulf Stream meanders force the intrusions, while Lemming (1980) found that both windstress and the

Florida Current played a role in driving the upwellings. Blanton *et al.* (1981) have described another mechanism, also in response to the Gulf Stream; here, upwelling occurs when absolute vorticity is conserved in a current moving along a shelf with diverging isobaths. In this connection, Smith (1982, 1983) found upwelling in mid-shelf waters along a section of the Florida east coast where the angle between the 20m and 50m isobaths was 30^{o}. Examination of bathymetry indicates a similar situation on the continental shelf south of Looe Key Marine Sanctuary—the Portaules Terrace—and suggests a strong likelihood that the Florida Current, in combination with wind forcing may result in periodic upwelling adjacent to Looe Key.

Classically, nutrient and temperature distributions are used to trace upwellings. Along the southeastern U.S. shelf, upwelling source water is a mixture of water masses dominated by nutrient enriched North Atlantic Central water but can also include continental shelf water, Gulf Stream surface water, Subtropical Underwater and Antarctic Intermediate water (Yoder *et al.*, 1983). Because of the elevated nutrient levels in upwelled water, intrusions along the southeastern U.S. shelf initiate phytoplankton blooms (Dunstan and Atkinson, 1976; Yoder *et al.*,1983) which results in increased abundance of zooplankton (Atkinson *et al.*, 1978) and fish (Atkinson and Targett, 1983). With respect to coral reef metabolism, an important characteristic of upwelled water is that NO_3^- and PO_4^{3-} are linearly related to temperature below *ca* $21^{o}C$. As the temperature of freshly upwelled water ranges from about 15 to $22^{o}C$, this corresponds to about 15 and 0 μM NO_3^-, and 0.10 and 1.0 μM PO_4^{3-}, respectively (Yoder, personal communication). Observations by one of us (B.L.) at Looe Key during summer of 1984 indicated that, at times, strong thermoclines and nutrient stratification existed within the coral reef spur and groove zone, suggesting that upwelling was occurring and responsible for the colder, nutrient-rich bottom water (Littler _et al._, 1985). We hypothesized that PO_4^{3-} in upwelled water was particularly important to metabolism of the Looe Key coral reefs as recent studies have demonstrated a primary role for this nutrient in limiting algal growth in these waters (Lapointe and Miller, submitted).

The question of whether or not upwelling is seasonal in nature at Looe Key also needed to be addressed. Previous summer studies (e.g. Green, 1944; Taylor and Stewart, 1957) of upwellings along Florida's east coast invoked a "seasonal" label to the upwelling phenomena, even though, to date, there are no data that suggested upwelling is restricted to summer months. Upwelling would be best defined during summer because of greater thermal contrasts between the subsurface water moving up the continental slope and the inner continental shelf water it is replacing. Conceivably, the "seasonal" label has persisted because of the dominance of studies during summer when weather is more conducive to field work. By measuring both temperature and nutrients, both Atkinson _et al._(1978) and Yoder _et al._(1983) have documented Gulf Stream intrusions during fall, winter, and spring months between Cape Canaveral, Fl., and Cape Hatteras, N.C., suggesting that upwellings are not seasonal but occur throughout the year. Importantly, we predict nutrient data will be more useful indicators of upwelling than temperature during winter months because of more nearly isothermal temperatures of shelf and upwelled waters.

Climatological Setting of Looe Key Marine Sanctuary

In terms of causes and effects, the local temporal variability in nutrients and temperature at Looe Key should be thought of as a response to larger-scale features of the regional circulation, as well as to local air-sea interactive processes involving meso-scale weather patterns having spatial scales on the order of tens to hundreds of kilometers. Thus, it is appropriate to include background information describing the regional setting and therefore a perspective for the results of this study.

The Lower Keys of Florida have a distinctly tropical climate, with enough of a seasonal variation in precipitation to be classified by Critchfield (1974) as "Wet-and-Dry Tropics". This label reflects the decidedly lower precipitation characteristic of winter months. The five-month period from December through April receives less than 25% of the total annual rainfall. Mean monthly accumulation during that time of year is less than 4.5 cm (NOAA 1977). This is low compared with the September (maximum) value of 16.7 cm, and the average annual total of 96.5 cm. The annual air temperature curve is typically of a tropical climate. The average range in air temperature is less than 8°C (approximately 14°F). Monthly mean values for January and July are 21.1°C and 28.8°C—the minimum and maximum, respectively. Incoming solar radiation over the course of a year is perhaps the dominant factor controlling the very long-period variation in both air and water temperatures. Mean daily solar radiation at the Miami International Airport varies from 349 cal/cm^2 in January to 553 cal/cm^2 (Keyes 1974); slightly increased cloud cover reduces midsummer values to 532 cal/cm^2 for both June and July.

Wind data collected at Key West show all prevailing directions within the easterly quadrant (northeast to southeast), but headings slightly north of east predominate from October through January, while headings south of east are recorded from February through September (NOAA 1977). The 28-year average wind speed at the Key West Airport is 5.0 m/s (11.2 miles/hour); values above the mean occur from October through April.

Oceanographic Setting of Looe Key Marine Sanctuary

Background information of an oceanographic nature focuses logically upon two aspects of the circulation in particular: The effect of the Florida Current (sometimes mislabeled the Gulf Stream in this area) and the importance of direct exchanges of water through the Keys, between the Florida Straits and Florida Bay in the extreme eastern Gulf of Mexico. The circulation at Looe Key has not been described in detail, but some published studies, and some of the grey literature contain information which is especially relevant within the context of this study.

The Florida Current, from its origin southwest of Key West downstream to the waters off Miami, has received a considerable amount of attention, especially in terms of the dynamics of sharply curving cyclonic flow (Chew 1974, 1980). A study by Chew (1979) in particular predicted regions of upwelling and downwelling in a meandering surface flow with a succession of cyclonic and anticyclonic turns. These features might be advected along with the mean flow, and thus affect a given area only temporarily, however, the application to the present study is worthy of note. The Florida Current makes a cyclonic turn of approximately 120^{o} between latitudes 24^{o} and 27^{o}N. This occurs over substantially greater spatial scales, of course, but Chew's arguments could be applied to suggest a large area of quasi-steady upwelling.

In the immediate vicinity of Looe Key, a meso-scale feature of the general circulation in the form of a cyclonic gyre has been hypothesized for the western Florida Straits between Key West and Long Key—over the Pourtales Terrace. This feature may be somewhat ephemeral in nature, occurring only when the Florida Current is well east of the Lower Keys. Such a condition exists, in turn, when the Loop Current, connecting the Yucatan Channel with the Straits of Florida, penetrates deep into the northern Gulf of Mexico (Fig. 1a). At such times, the Florida Current at its origin has a more southerly heading, and the streamlines extend well to the east before turning northward. The flow past Looe Key under these conditions is west-southwesterly and may be thought of as a nearshore counter current (Brooks and Niiler, 1975). Alternately, when the Loop Current does not penetrate into the northern Gulf of Mexico (Fig.1b), but rather veers sharply eastward along the north coast of Cuba, the streamlines in the vicinity of Key West have an easterly heading, or even slightly north of east, and the Florida Current affects the Lower Keys directly. At these times, there is no room for a nearshore counter-current to exist, and the flow at Looe Key is toward the east-northeast. Satellite data support this general interpretation, but the available information is inadequate to determine the relative frequencies of occurrence of these two conditions.

The concept of seasonality in the position of the Loop Current, as well as in the strength of the Florida Current, is one which has sparked lively debate for well over a decade. Leipper (1970), Cochrane (1972) and Maul (1977) have presented data suggesting an annual periodicity in the Loop Current, with maximum penetration into the Gulf of Mexico in summer months. Hurlburt and Thompson (1980) have called into question the sufficiency of the available observational evidence, but at the same time they presented results of a modeling study which indicated an "almost annual" periodicity, even in the absence of an annual variability in the inflow through the Yucatan Channel. This is an important finding, because the annual signal in time series of Florida Current volume transport has been shown to be weak (Niiler and Richardson 1973). A summary of available findings suggests a midsummer maximum in volume transport, with an annual range of approximately 9×10^6 m^3/sec and a multi-annual mean of about 29×10^6 m^3/sec. Within the context of the present study, a working hypothesis would therefore include a west-southwesterly countercurrent at Looe Key in summer months, with the Florida Current at its furthest offshore position, and a probable maximum in Florida Current volume transport at that time.

On a smaller scale, but of no less importance to the circulation and hydrography at Looe Key, is the matter of exchange of water between the Florida Straits and Florida Bay, utilizing the gaps between the Keys. This issue has not been addressed directly, but a study by Ichiye et al. (1973) provides estimates of the magnitude and direction of Ekman (wind-driven) transport in each of eleven 2^ox2^o sectors—one of which is centered over Florida Bay. Results obtained for the Florida Bay sector are consistent with the speed and direction of monthly mean surface winds, as noted above: Transport vectors reach a maximum in winter months, but in all months the calculations suggest a net transport from the Florida Straits into Florida Bay. It is probable that individual wind events, as well as periodic tidal exchanges, move water back and forth over a wide range of time scales between the northwest and southeast sides of the Keys. Tidal excursions have not been estimated, however, and deviations from climatological means have not been quantified for this purpose. This remains a topic of further study.

A series of eight hydrographic cruises along the Keys, as well as in Florida Bay, were made over a nine-month period in 1960 and 1961 (Ichiya et al., 1973). Eight stations were reoccupied, and data were averaged both in space and in time. Results identify in a general way the seasonal cycles in temperature and salinity, and thus are relevant to the Looe Key work in the sense that the T-S cycles in the shallow waters of Florida Bay should approximate closely the T-S cycles in the shallow nearshore waters immediately southeast of the Lower Keys which move across the reef during half of each tidal cycle and during wind events such as frontal passages. The relatively large, 12^{o}C temperature range (Fig. 2) may reflect an uncharacteristically severe winter in 1960-61; midsummer maximum temperatures in excess of 30^{o}C are normal, however with only one survey between early June and early September, it is probable that the annual maximum has been underestimated somewhat. The relatively restricted salinity range is consistent with the lack of any direct dilution by freshwater run-off, and with the fact that the Florida mainland is downstream in terms of the prevailing Ekman transport. Highest salinities are recorded in late spring and early summer months as a result of the seasonal minimum in the annual precipitation cycle.

Scope of The Present Study

To give a preliminary assessment of the importance of upwelling to Looe Key Marine Sanctuary this study provides a time series of nutrient and thermograph data collected at four and two stations, respectively, over a one year period from 9 October 1984 to 12 October 1985. The primary objectives of this study were to identify and characterize upwelling events by utilizing their nutrient and thermal signatures. Specifically, we sought to answer the following questions:

(1) Is upwelling occurring within Looe Key Marine Sanctuary, and, in particular, within the coral spur and groove zone?

(2) What is the time-dependency of upwelling at Looe Key? Is it correlated with wind forcing and/or Florida Current meanders? Is upwelling seasonal in nature?

(3) What levels of nutrients (i.e. NO_3^- and PO_4^{3-}) and temperature occur during upwelling events?

METHODS

Study Area

Looe Key (24°N, 81°24'W) was established as a National Marine Sanctuary in 1981 and is located 12.9 km southwest of Big Pine Key, Monroe County, Florida (Fig. 3). Within the 18.2-km^2 Sanctuary lies an inner "core" area (Fig 4) of about 1.7 km^2 that includes rich seagrass, coral and macroalgal dominated assemblages. Corals, seagrasses, and macroalgae of this core area have been inventoried and mapped during excellent previous studies by J.L. Wheaton and W.C. Jaap (NOAA Report, Chap. 6, in draft), J.C. Zieman (NOAA Report, in draft), and M. Littler *et al.* (NOAA Report, in draft).

To address the above questions regarding the importance of upwelled nutrients to this "core" area at Looe Key Marine Sanctuary, four permanent seawater sampling stations were chosen along a north-south transect that extended from the BACK REEF to the DEEP REEF habitats through the "core" area (Fig. 4). Station 1 was located on the DEEP REEF (30m); Station 2 was located on the FORE REEF (10m); Station 3 was located on the REEF CREST; and Station 4 was located on the boundary of the REEF FLAT and BACK REEF (Fig 4).

Measurement of Dissolved Inorganic Nutrients

At approximately 7-10 day intervals between October 1984 and October 1985, replicate Niskin casts were used to collect seawater samples for nutrient and temperature determinations at Stations 1 to 4. Although our original proposal suggested sampling at only Station 1 and 2, the additional Stations 3 and 4 were added to better understand potential sources of nutrients to the core area, i.e. Hawk Channel vs. the Straits of Florida. Station 1 was sampled at three depths—bottom, midwater, surface; Station 2 was sampled at two depths--bottom, surface; Station 3 was sampled on the surface (2m) and Station 4 was sampled at midwater (4m). Seawater temperature of the samples was measured on shipboard immediately with a laboratory mercury thermometer. Seawater samples for nutrient analysis were taken in acid-washed Nalgene bottles and held on ice until filtered (0.45μ) and frozen upon return to the Harbor Branch Foundation laboratory on Summerland Key. Subsequently, the samples were thawed and analyzed for NH_4^+, NO_3^-, NO_2^-, and PO_4^{3-} by the methods outlined in Strickland and Parsons (1977).

Thermograph Deployment and Data Analysis

During each of three deployment periods, ENDECO, Inc. Type 109 film recording thermographs were deployed at Stations 1 and 2 to record water temperatures. Values were time-averaged over two-hour sampling periods. Thermographs were housed in, and protected by 10" diameter PVC pipes which were oriented vertically and embedded in concrete-filled "tire anchors". Pipes were completely open at the bottom; a small hole in the PVC end cap covering the pipe allowed water to move through the pipe and past the temperature sensor. The thermographs therefore recorded ambient temperatures outside the pipe accurately. The accuracy of the thermographs is 0.2^{o}C, according to instrument specifications. Comparison of air temperatures recorded simultaneously by pairs of thermographs during pre- and post-deployment periods suggests that in the reading and digitization process, data from properly calibrated thermographs have a precision on the order of $0.5^{o}C$.

A quick, although qualitative representation of the time series is provided by an anolog plot of temperature vs. time. Plots have been constructed individually for each of the three deployments, and results will be presented and discussed in that order.

Time series analysis of digitized water temperature records enabled temperature variations over a wide range of time scales to be quantified and compared. Tidal-period variations in temperature were singled out using the National Ocean Service least squares harmonic analysis computer program. The diurnal cycle was characterized using both harmonic analysis and a Buys-Ballots averaging technique that computed the mean of all temperatures recorded from 0000 to 0200, all those recorded between 0200 and 0400, etc.

An important question whenever two or more stations are involved in a study is whether the second, or any of the additional stations is providing redundant information. To explore this possibility, temperature differences were calculated from the Station 1 and 2 records obtained during the third deployment. Elementary statistics, especially the standard deviation of the differences, provide an indication of whether or not the same population is being sampled. There remains the possibility that an acceptable similarity in the two records exists over particular time scales of interest. To determine this, spectral analysis provided a coherence spectrum from the two 167-day time series from the third deployment period. Results included a phase spectrum, indicating the phase lag or lead of temperature variations at one location relative to those at the other.

RESULTS

Dissolved Inorganic Nutrients

A total of 532 seawater samples were analyzed for dissolved inorganic nutrients (NH_4^+, NO_3^-, NO_2^-, PO_4^{3-}) during the one year time series. These data, as well as temperature data of the seawater samples used for nutrient analysis are reported in Table 1 (Appendix A). To illustrate seasonal patterns in nutrient concentrations at Looe Key, nutrient data for each particular nutrient and sampling location were averaged for each month. Because of logistical problems (i.e. adverse weather, boat failure, etc.) in sampling seawater regularly at Looe Key, the number of samplings per month varied from a minimum of 2 to a maximum of 5. Thus, the monthly values shown in Figs 1-7 (Appendix I) represent means $\pm$ 1 standard deviation where $4<N<10$.

Concentrations of the two biologically important nitrogenous nutrients measured at Looe Key—NH_4^+ and NO_3^-—were generally low and followed different but distinct seasonal patterns. Concentrations of NH_4^+ were consistently about twofold higher during winter months compared to summer months at most stations (See Appendix A, Figs. 1-7). Overall, concentrations of NH_4^+ ranged from undetectable (< 0.10 μM) to the yearly high of 1.60 μM (1-10-85; See Appendix A, Table 1). In contrast to this pattern for NH_4^+, concentrations of NO_3^-, the source of "new" nitrogen possibly resulting from upwelling, were highest during late spring and summer months at all stations (See Appendix A, Figs. 1 to 7). Concentrations of NO_3^- ranged from undetectable (< 0.05 μM) to 1.80 μM (5-1-85; See Appendix A, Table 1). With few exceptions, the seasonal variation in concentrations of NH_4^+ and NO_3^- was greater than the observed station to station variation on any particular sampling day.

During late spring and summer when NO_3^- concentrations were elevated, the highest NO_3^- concentrations consistently occurred at the deepest station (Station 1-B) suggesting that upwelling was occuring (Appendix A, Table 1). For example, a plot of NO_3^- distribution on 5-1-85, when NO_3^- concentrations were stratified in the water column, clearly show that deep water appears to be, at least at certain times, a source of elevated NO_3^-(Fig. 5). Such a stratified pattern of NO_3^- distribution did not exist during any of the winter samplings (e.g. Fig. 6).

Although not as striking, concentrations of PO_4^{3-} also followed a seasonal trend similar to that of NO_3^-, i.e. higher concentrations occurring during late spring-summer compared to fall-winter. Concentrations of PO_4^{3-} ranged from undetectable (<0.03 μM) to 0.49 μM during the year study at all stations (Appendix A, Table 1). As with NO_3^-, the highest concentrations of PO_4^{3-} during late spring and summer also generally occurred at the deep station (Station 1-B). For example, a plot of PO_4^{3-} distribution on 5-1-85 shows that deep water also appeared to be a source of elevated PO_4^{3-} (Fig. 7). This stratified pattern of PO_4^{3-} distribution during summer did not exist during the samplings in winter months (e.g. Fig. 8).

Temperature profiles of the water column during the nutrient samplings also indicated a distinct seasonal pattern in thermal structure. For example, during summer months, the water column at stations 1 and 2 showed a distinct stratification with a 2.5^{o}C difference in temperature between surface and bottom water at certain times (Appendix A, Table 1; e.g. Fig. 9). In contrast, during winter months, the water column at stations 1 and 2 were thermally unstratified as suggested by homogenous temperature distributions (e.g. Fig 10). Because temperature decreased and nutrients increased with increasing depth during the spring and summer stratification, concentrations of NO_3^- and PO_4^{3-} during samplings were inversely and significantly ($r^2 \geq 0.90$) correlated with temperature.

Thermograph Records

First Deployment Period

The first deployment period commenced on October 4, 1984, for both Stations 1 and 2. The record from Station 2 ended 45 days later, on November 20th; the record from Station 1 continued an additional 55 days, covering a total of 100 days, as result of difficulty in relocating the outer station. The first deployment therefore provides information on the fall cooling segment of the annual cycle, when water temperatures might be expected to decrease at a relatively rapid rate. Results in the form of a composite of the two analog plots are shown in Figure 11.

At Station 2 (upper plot), the record is comprised of two rather distinct segments which are offset vertically by approximately 2°C. During the first 31 days, temperatures were relatively stable and remained generally within the range of 28-29°C. Beginning around the end of the first week in November, temperatures decreased abruptly and remained within the range of 26-27°C through the end of the deployment. Neither the tidal-period variation in temperature nor the diurnal cycle is of much significance at this time of year. In all cases, amplitudes were 0.3°C or less. Low-frequency, meteorological forcing is not pronounced either. Quasi-periodic temperature variations over time scales on the order of several days appear to be a degree or less in magnitude.

At Station 1, the longer record provides a better indication of how this segment fits into the annual cycle. Again, the first month of this 100-day record can be characterized by relatively stable bottom temperatures between 28^{o} and $29^{o}C$—nearly identical to the range recorded nearer the reef. Following the abrupt decrease, however, there is an unsteady but continuous decrease in temperature over the next two months. Bottom temperatures decreased a total of $1.2^{o}C$, or just over a tenth of a degree per week. Within the last week of this record, a second step-like decrease occurred which lowered the temperature an additional 1.5^{o}. The record terminates in early January, when one would expect the lowest temperatures of the year to occur.

Second Deployment Period

Results from the second deployment are restricted to the time series from Station 2 as a result of a faulty film magazine in the thermograph positioned at Station 1. Temporal variations in temperature recorded at the shallower station are shown in Figure 12. This time period included the last of the fall cooling, the midwinter minimum and the first of the spring warming. The plot reveals considerable thermal activity, when compared with data obtained from the same location during the first deployment period.

Figure 12 contains temperature variations over a broad range of time scales, but warming and cooling events occurring over periods of several days are particularly noteworthy—probably reflecting the quasi-periodic frontal passages. Temperature variations on the order of $2^{o}C$ occur throughout the plot, generally in the form of transient perturbations from the seasonal norm. In contrast to this, the shorter period, tidal or diurnal warming and cooling cycles remain small, raising and lowering temperatures about a half a degree. Ignoring one brief period when the bottom temperature dipped to $22^{o}C$, the winter minimum at this location reached approximately 23°C before a quasi-steady warming commenced in late February.

During the third week in March, spring warming was halted abruptly when the bottom temperature decreased 2°C. It is not known whether this event was associated with a shoreward upwelling of water from the Florida Straits, or with a south-southeastward flow of water out of Florida Bay. In any case, the warming trend resumed immediately, and by the end of the record temperatures just seaward of the reef were just over 25°C.

Third Deployment Period

The final deployment covered the late spring, summer and early fall components of the annual cycle. The two records differ slightly in length. The Station 1 thermograph was replaced just over three weeks later as a result of difficulty in station relocation. Even the shorter record was 147 days in length, however. The extended time period over thich the two time series overlapped makes this deployment suitable for the analysis necessary and sufficient to quantify similarities and differences.

Data from Station 2 are shown in the upper part of Figure 13. The first half of the record contains a continuation of the gradual warming that had started some two months earlier. The rise in bottom temperatures continue through mid summer, when the annual maximum of just over 30°C is reached. A prominent feature in the plot is the approximately 3° decrease recorded near the end of July. This feature persists only a few days, then temperatures recover to value at or just above 30°C. During late summer months, a subtle though distinct feature in the plot is the decrease in range of the high frequency temperature variations. Day-to-day fluctuations are characteristically on the order of a half a degree.

During the final two months of the record, an irregular cooling begins as temperatures decrease from the annual maximum. There is some indication of a step-like pattern, with periods of relatively rapid cooling interspersed with relatively stable periods of little or no additional cooling. This is what one would expect in response to meteorological forcing, when cooling occurs as frontal passages alternate maritime and continental air masses over the Keys.

The lower part of Figure 13 is basically similar to the pattern described above for the shallower station, but many of the individual features appear in exaggerated form. Throughout most of the record, the high-frequency temperature fluctuations vary between 1-2°C. Only during the final four weeks do they decrease to approximately one-half degree—comparable to the pattern recorded at Station 2. Temperature profiles are not available in this study, but it is probable that Station 1 was located at the top of the seasonal thermocline. If so, then internal wave activity of variations in the cross-shelf component of the current could explain short-term bottom temperature variations of a degree or two.

Particularly prominent is the transient decrease in temperature that is recorded in the middle of the deployment period. Bottom temperatures had risen to approximately 29°C by mid July. The drop in temperature, though intermittent and occurring over a period of nearly four days, decreased temperatures to 20.5°C. For comparison, the lowest temperatures recorded at that level during the first deployment (early January, 1985) were only 23°C. It is ironic that what may have been the coldest water of the year (30-meter depth temperatures from mid January to early May are not available) was recorded in mid summer—coinciding with the warmest air temperatures and nearly the most intense incoming solar radiation.

DISCUSSION

Results of both the nutrient sampling and thermograph record from this study provide the first hard evidence that upwelling occurs along the Florida coral reef tract and in particular, Looe Key Marine Sanctuary. The occurrence of upwelling appears to be restricted primarily to the late spring-summer period although its actual biological effects could persist throughout the year due to highly effective nutrient recycling characteristic of coral reef systems (Pomeroy and Kuenzler, 1966; Pilson and Betzer, 1973). The spring-summer upwelling period can be characterized by a stratified water column (even at 30m depth) both in terms of nutrients and temperature, as well as overall higher concentrations of NO_3^- and PO_4^{3-} compared to the low and often undetectable concentrations found during fall and winter. Furthermore, anomolously cold water can occur during the spring-summer period, such as in our study when the coldest temperatures recorded for the year occurred during July.

Hydrographic Processes and Upwelling at Looe Key

The nature of the upwelling observed at Looe Key does not appear to be of the intense "frontal transgression" type, where upwelling consists of relatively short pulses of cold (i.e. <20°C) water with characteristically high nutrient concentrations. Rather, the upwellings appear to be "frontal meanders" that consist of longer time scale pulses of moderately cool water with moderate nutrient concentrations. For example, the highest concentrations of NO_3^- and PO_4^{3-} observed during our study were 1.80 uM and 0.40 uM, respectively. While these concentrations lie roughly in the middle of the range reported for these nutrients in other coral reef systems (Pilson and Betzer, 1973; Smith and Jokiel, 1975; Marsh, 1977), they are lower than the concentrations reported for frontal transgressions;

Atkinson *et al.* (1984) reported NO_3^- concentrations ranging from 5 to 10 uM for cold (15 to 20°C) upwelled water at 30m in the South Atlantic Bight during a frontal transgression.

Although speculation at this point, several features of the Florida Current and bathymetry adjacent to Looe Key appear noteworthy as possible mechanisms forcing intrusions at Looe Key. First, recent studies of the volume transport of the Florida Current indicate that a seasonal maximum occurs during early summer (June) with minimum values occurring during fall and winter (Lee *et al.*, 1985) that may affect local circulation in the Looe Key environs. As noted previously, Ichiye *et al.* (1973) reported the Florida Current was well east of the lower Keys during summer, 1961. If this was the case in 1985, it could have led to the formation of a well-defined counter current during summer. Neither the dynamics of the counter current nor its seasonality is well-known, and it may well be that the counter current is actually part of the hypothesized gyre (See Introduction) that forms during summer months over the Pourtales Terrace. Inasmuch as our observed seasonal variation in nutrients at Looe Key parallel these seasonal changes in volume transport in the Florida Current, a cause and effect situation is clearly suggested.

Second, the Pourtales Terrace itself may serve as a topographic bottom feature that persistently propagates upwelled water that is entrained into the summer gyre or counter current. The Poutales Terrace is a large submerged terrace (about the size of Long Island) on the continental shelf that marks the southern extremity of the Floridian Plateau. The topography of the eastern terrace, which intersects the Florida Current, is characterized by bottom features that include knolls and highs that are aligned with elongate valleys and troughs (Jordan *et* al., 1964). This produces an extensive area of diverging isobaths adjacent to the continental shelf edge, a situation that can promote persistent, localized upwelling (Blanton et al., 1981). A similar ridge and trough bottom feature occurs at the "Charleston Bump" off the South Carolina coast where a dome-shaped volume of cold, upwelled water often occurs immediately downstream of the feature (Bane, 1983). Both the Pourtales Terrace and the Charleston Bump areas are unique in the southern Atlantic Bight for their geology; both areas have sediments with high phosphorite contents (Manheim et al., 1980) which is well known to form primarily in oceanic upwelling areas (Bentor, 1980). Clearly, this long term geologic evidence suggests upwelling must occur on the Pourtales Terrace (or downstream) and could result in elevated nutrient water being entrained and diluted with Florida Current surface water and continental shelf water. This would result in the mild or dilute upwelling situation observed at Looe Key during spring and summer of 1985.

Biological Considerations of Seasonal Upwelling at Looe Key

Upwelling has previously been observed on coral reef systems of the world ocean (Andrews and Gentian, 1982; Glynn and Stewart, 1973; Glynn, 1977; Birkeland, 1977) and its effects on coral reef development have been considered from both a positive and negative standpoint. Inhibition of coral growth is attributed to reduced temperatures associated with upwelling (Glynn and Stewart, 1973; Glynn, 1977) due to suppression of coral growth rate *per se* by low temperatures (Shinn, 1966; Weber et al., 1975). However, Dodge and Vaisnus (1975) found that coral growth in Bermuda bears an inverse relationship to temperature, presumably because of increased nutrient supply with intrusions of cooler, upwelled waters. More recent studies on the Great Barrier Reef (Andrews and Gentian, 1982) have also implied a nutritional importance to upwelling for sustaining coral reef development. Inasmuch as temperatures were sufficiently ameliorated during the mild summer upwelling in the present study (i.e. >20^{o}C), the increased nutrient flux associated with upwelling may play a key role to the extensive development of coral spur and groove systems at Looe Key.

For example, Marzalek et al. (1977) point out that that the most extensive coral reef development (in terms of area) in the Keys occurs along the northern reef tract off Key Largo which is consistently flushed with low nutrient, oceanic waters of the Florida Current. Maul (1977), in a one year study of the Florida Current migration, observed that when the Florida Current was at its southernmost extreme off the coast of Cuba (summer), Florida Bay water was advected south through the lower Keys, apparently visible in LANDSAT images and ship track data. Marzalek et al. (1977) considered this situation detrimental to coral reef development in the lower Keys, although this view ignores the fact that Looe Key represents the best developed spur and groove habitat along the entire reef tract (Shinn, 1963). Considering that spur and groove development at Looe Key is due to construction rather than erosion (Shinn et al., 1981), development of the Looe Key FORE REEF may be closely coupled to mild summer upwellings which could enhance coral growth and spur and groove development by ameliorating severe nutrient limitation that might otherwise occur. This may explain, in part, why such extensive spur and groove development occurs at Looe Key but not in the northern reef tract off Key Largo. Clearly, a comparison of the Key Largo and Looe Key reefs with respect to sumertime upwelling is needed to adequately address this hypothesis.

Our findings of seasonal upwelling at Looe Key are particularly noteworthy as they suggest an important ecological mechanism for allocthonous nutrient input that undoubtedly has important effects on seasonal metabolism of the reef system. Previous studies at Looe Key during summer 1984 by one of us (B.L.) found benthic macroalgae in the BACK REEF habitat to be well nourished and abundant (compared to winter 1984) which was also correlated with a stratified water column as found in the present study (Littler et al, in draft). The seasonal pattern of nutrient supply and macroalgal biomass suggested that residual macroalgal biomass may support organic nutrient demands of reef metabolism during fall and winter when low nutrient, blue-water conditions prevail at Looe Key (Littler et al., in draft). Our present findings of summertime upwelling also explain the phytoplankton blooms that often occur at Looe Key during summer which results in green water and reduced visibility compared to the blue water conditions prevalent during winter months. The ability of the reef system to directly assimilate dissolved nutrients and/or organic matter resulting from short-term, summertime upwellings and efficiently recycle these "new" nutrients explains why highly productive reefs, such as Looe Key, can thrive in what often appear to be nutrient depauperate waters. Our study clearly suggests the potential importance of short-term nutrient supply events to Looe Key and suggest future studies are needed to determine how different reef components (e.g. corals, macroalgae, etc.) respond to the seasonal variation in nutrient supply to the reef.

However, it should be noted that elevated nutrient concentrations can themselves be detrimental to coral reef development. Kinsey and Davies (1979) found that phosphate enrichment to 2 uM caused greater than 50% suppression of reef calcification and suggested that this was the reason for poor coral growth on reefs adjacent to upwellings (e.g. Glynn, 1977). This inhibition is due to blockage of carbonate crystal formation in the presence of high phosphate (Simkiss, 1964). Considering that the mild upwellings that occurred at Looe Key during summer 1984 produced phosphate concentrations that were five-fold lower than those in the experiments of Kinsey and Domm (1974), the elevated phosphate concentrations observed at Looe Key were probably not detrimental to coral growth and in the long run, were most likely stimulatory. It is clear, however, that Looe Key would be most susceptible to phosphate pollution and resultant coral toxicity during summer months when anthropogenic phosphate inputs, coupled with upwelled phosphate, could result in concentrations sufficient to reduce coral growth rates. Recent observations by one of us (B.L.) indicated that whereas elevated nitrogen occurs during summer months in nearshore waters of the Keys due to groundwater nutrient input of NO_3^- during the wet season, PO_4^{3-} is present at elevated but relatively low stoichiometric concentrations compared to the elevated groundwater nitrogen, due possibly to adsorption of PO_4^{3-} in carbonate soils and bedrock of the Keys. However, in view of the current rapid development of the lower Florida Keys, the relative contribution of terriginous nutrients compared to upwelled nutrients needs to be determined to help predict the impact of development on the ecology of Looe Key.

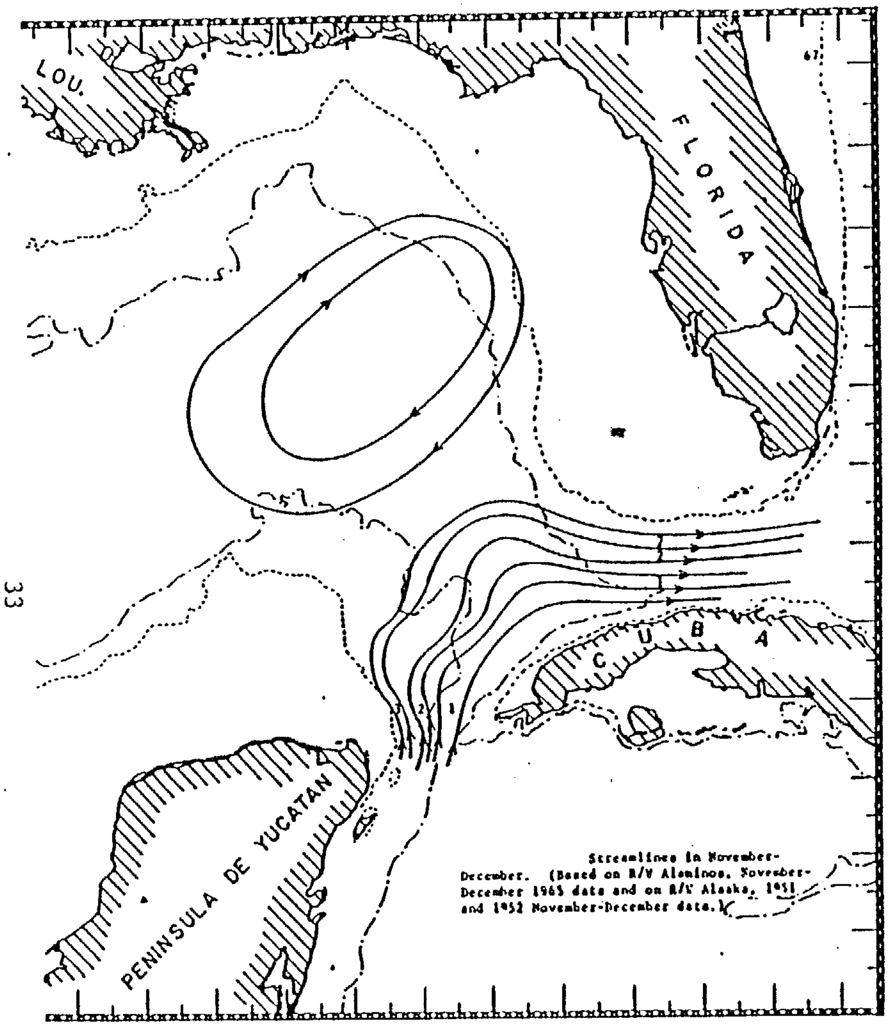

Figure 1b.

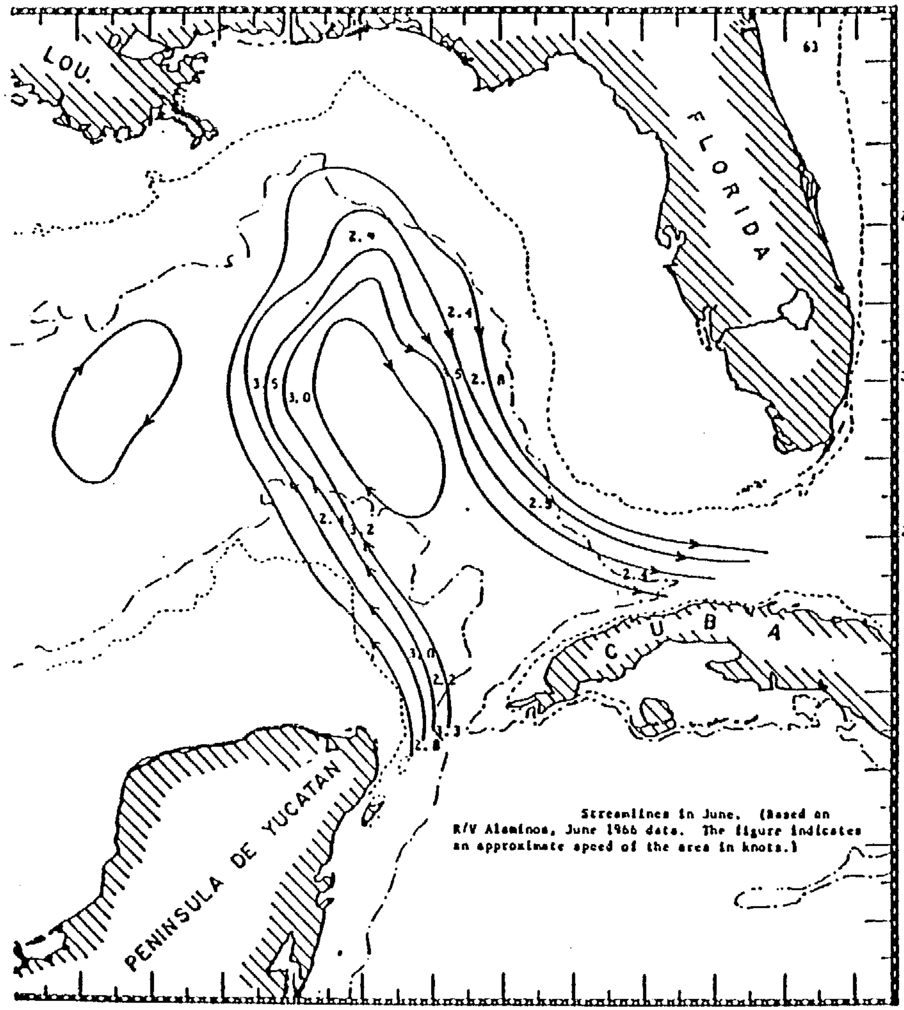

Figure 1a.

Figure 1. A – Loop Current streamlines, showing deep penetration into the Gulf of Mexico (after Ichiye, et al., 1973). B – Loop Current streamlines, showing sharp veering after entering the Gulf of Mexico (after Ichiye, et al., 1973).

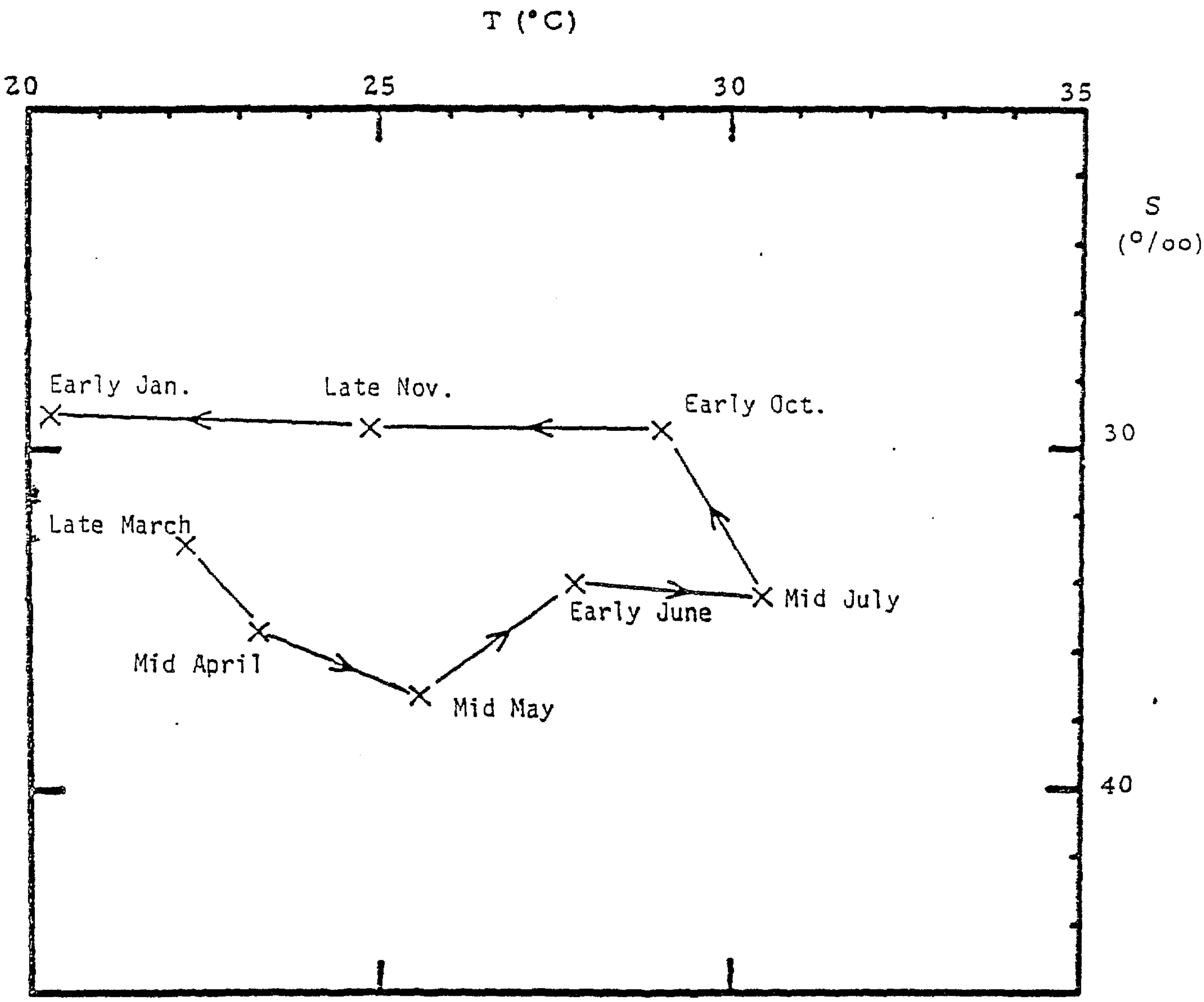

Figure 2. Temperature-salinity (T-S) plot of hydrographic data from Florida Bay, March 1960 to January 1961. Plotted points reflect a temporal averaging over a diurnal cycle, and a spatial averaging involving eight sampling stations.

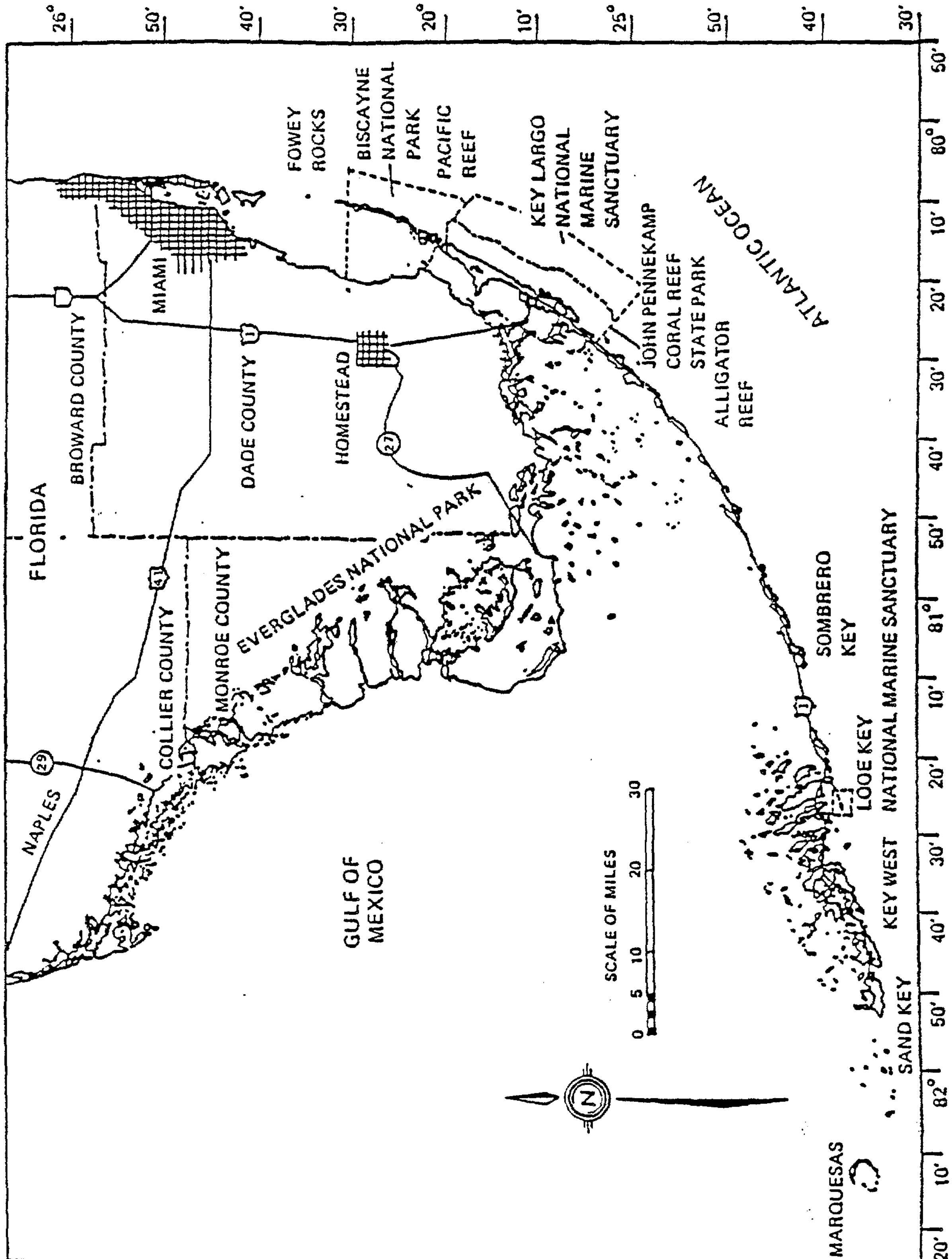

Figure 3. Location of Looe Key Marine Sanctuary among the tropical reef communities of the south Florida Coral Reef Tract.

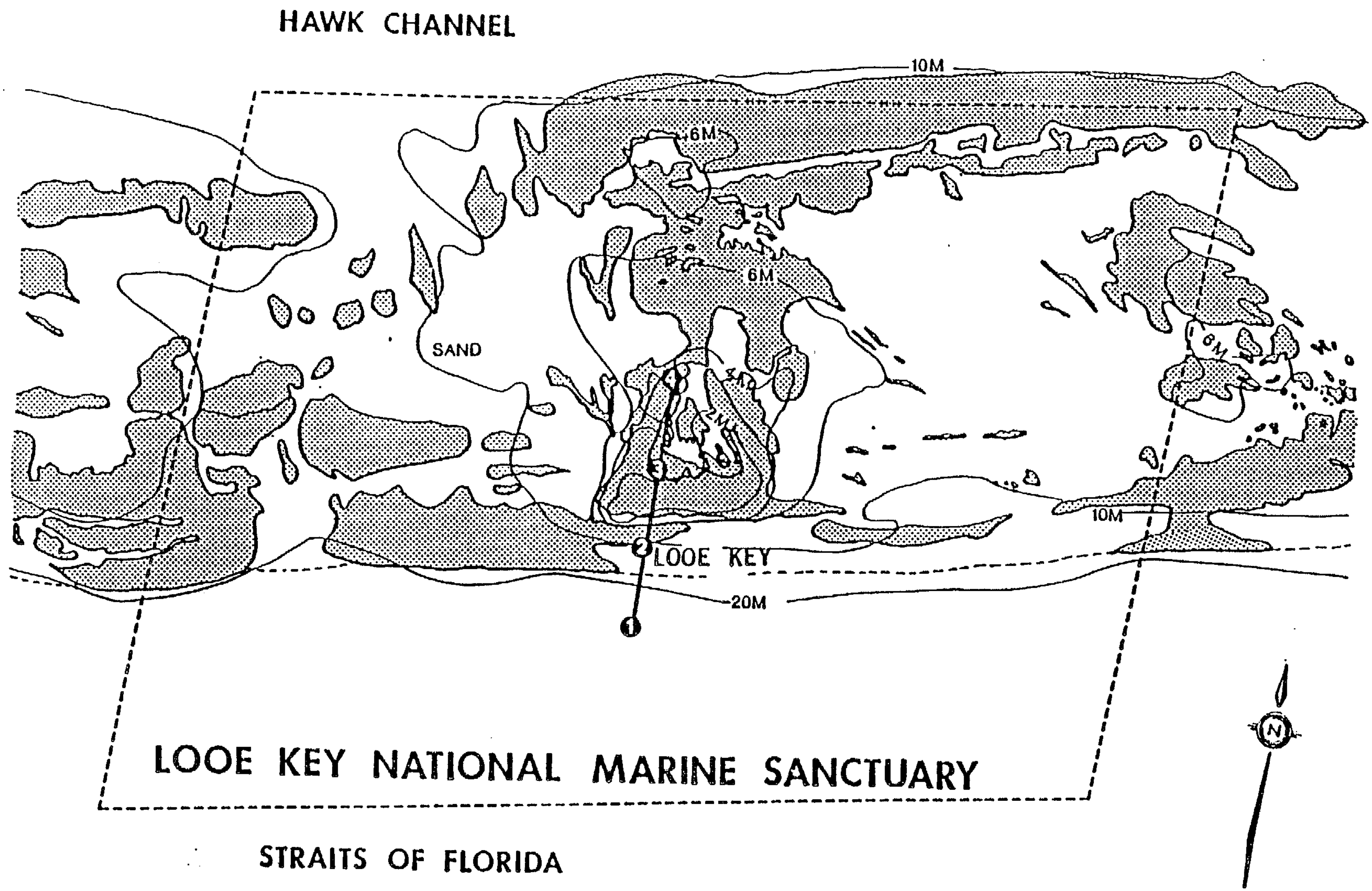

Figure 4. Location of sampling stations along a transect through the core area of Looe Key Marine Sanctuary.

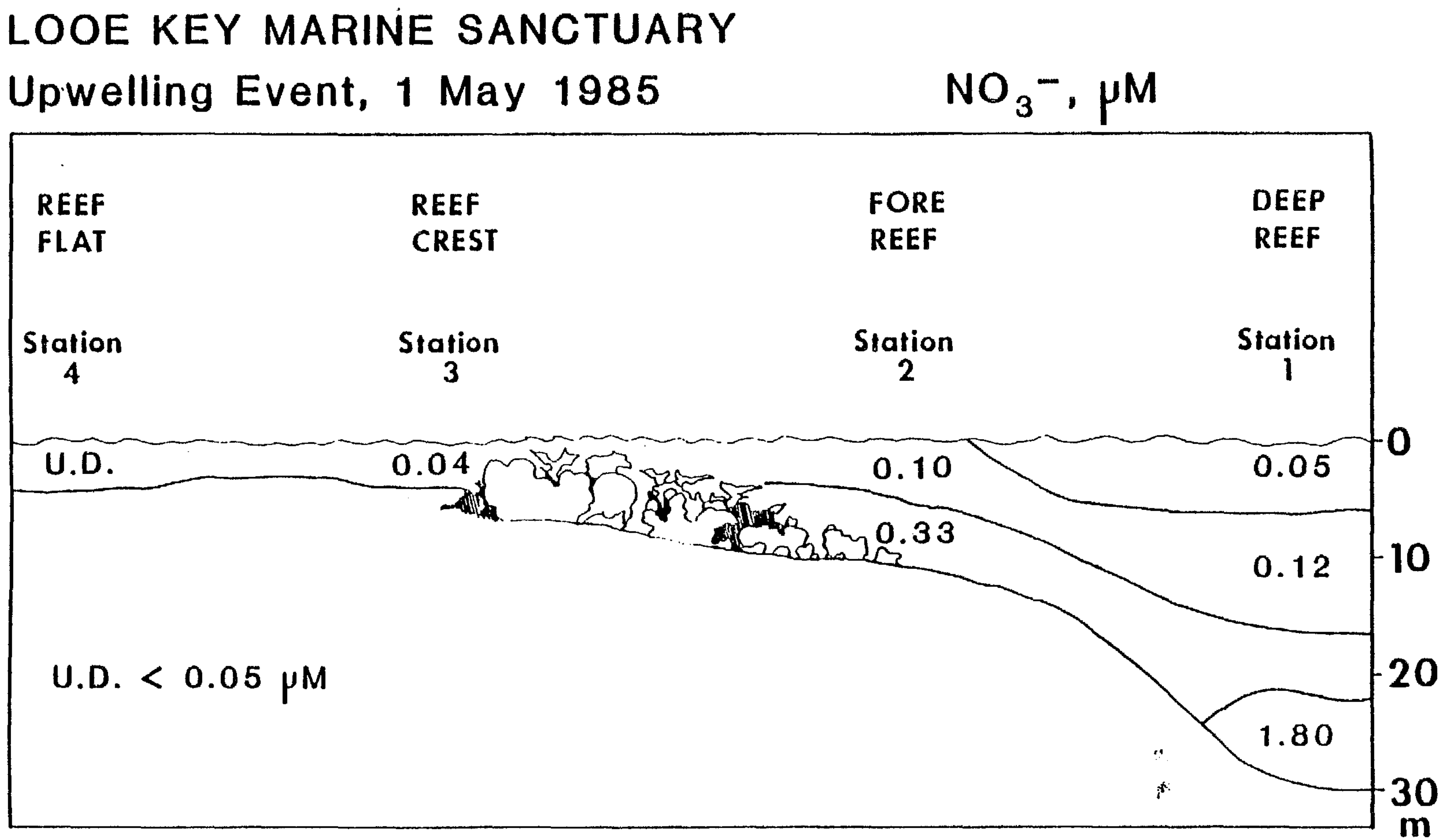

Figure 5. NO_3^- profile in the core area of Looe Key Marine Sanctuary on 1 May 1985. Values represent means (N=2).

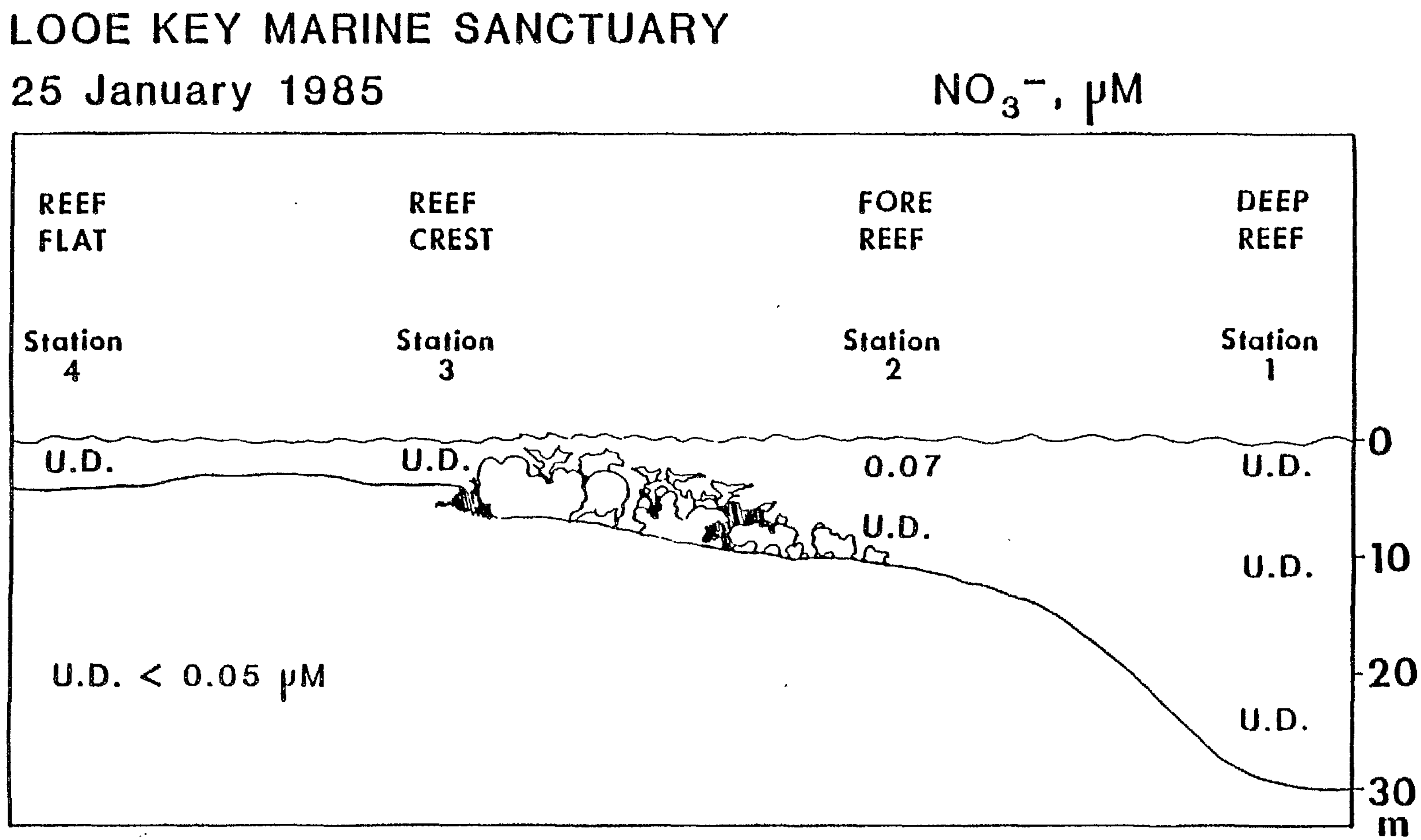

Figure 6. NO_3^- profile in the core area of Looe Key Marine Sanctuary on 25 January 1985. Values represent means (N=2).

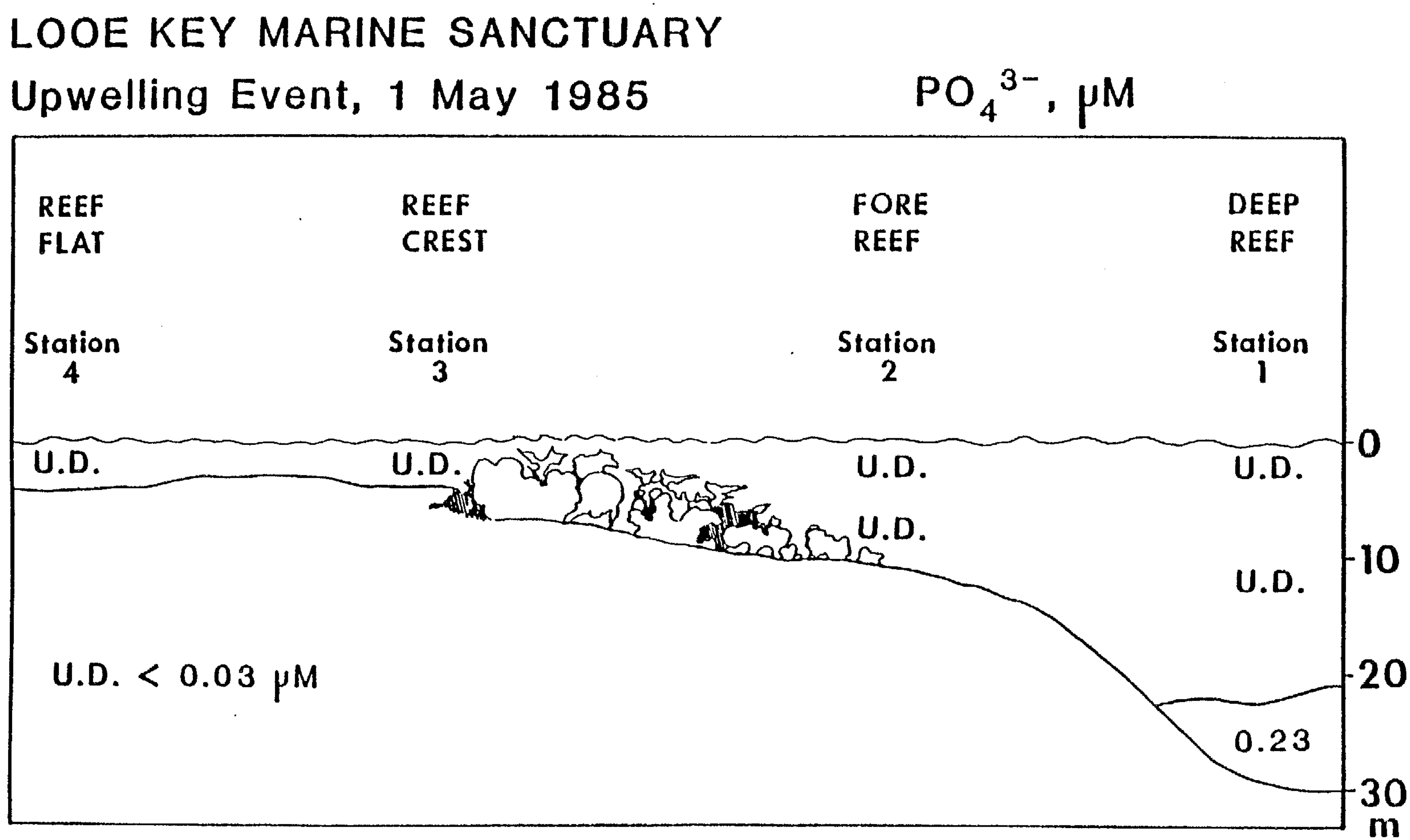

Figure 7. PO_4^{3-} profile in the core area of Looe Key Marine Sanctuary on 1 May 1985. Values represent means (N=2).

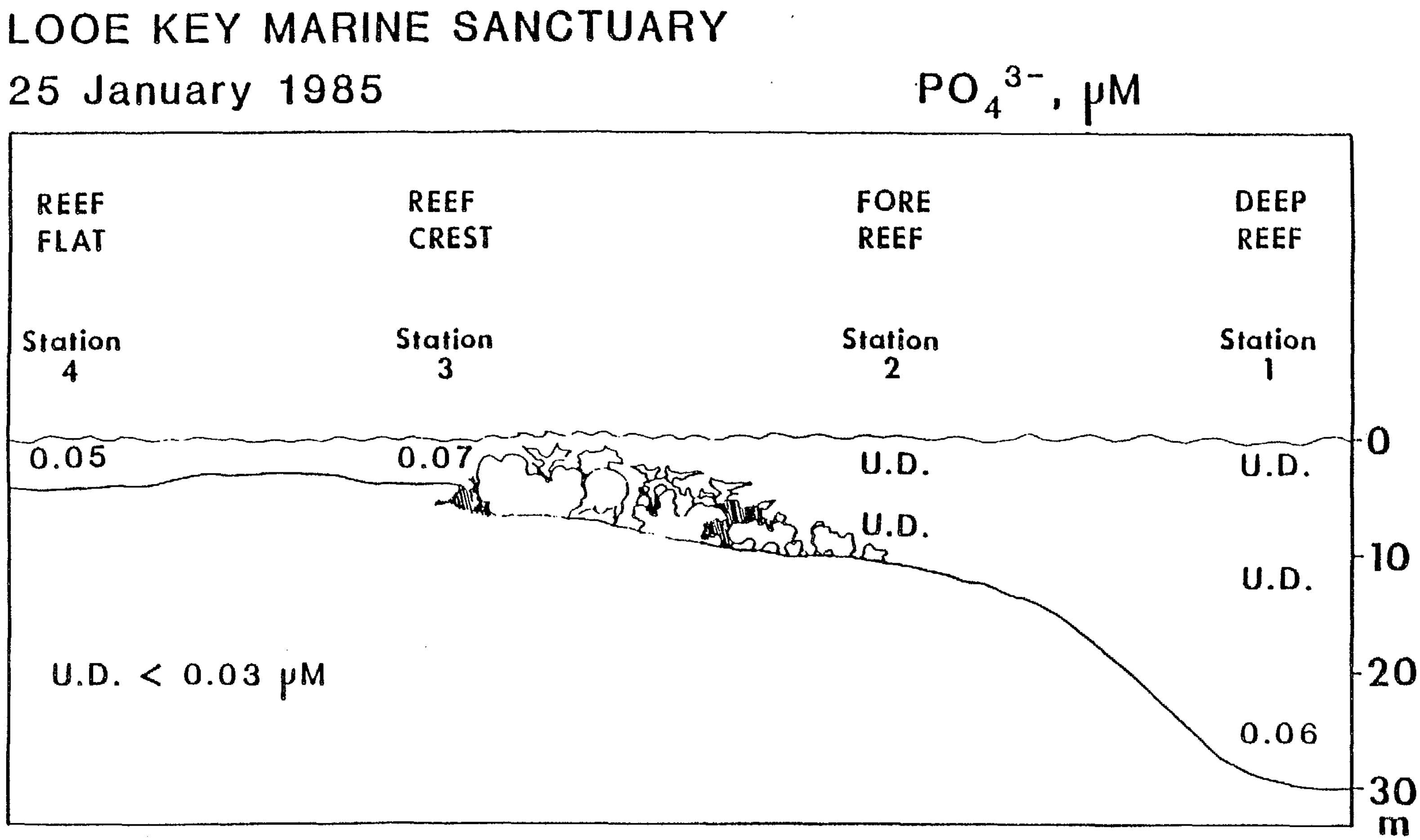

Figure 8. PO_4^{3-} profile in the core area of Looe Key Marine Sanctuary on 25 January 1985. Values represent means (N=2).

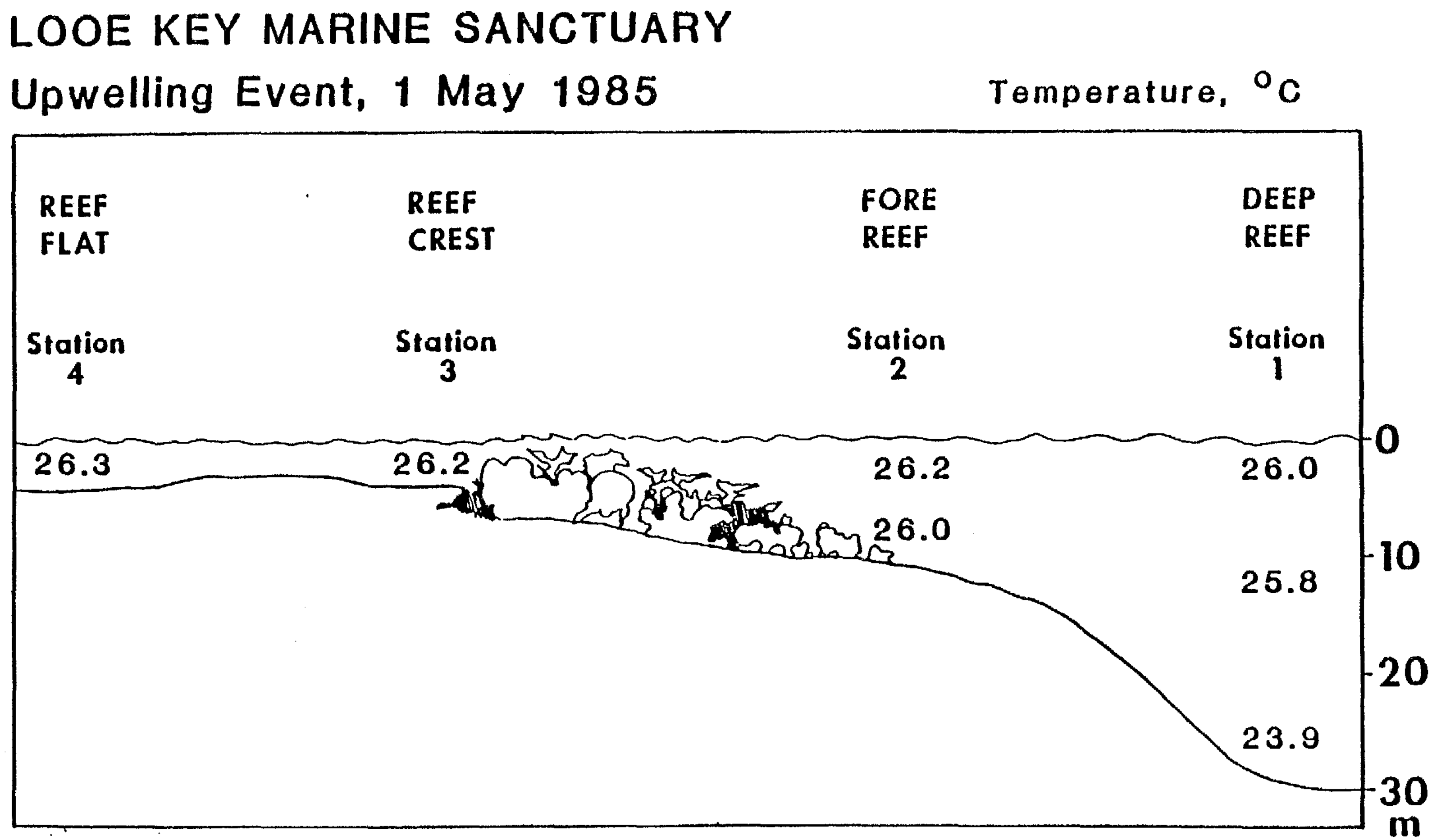

Figure 9. Temperature profile in the core area of Looe Key Marine Sanctuary on 1 May 1985.

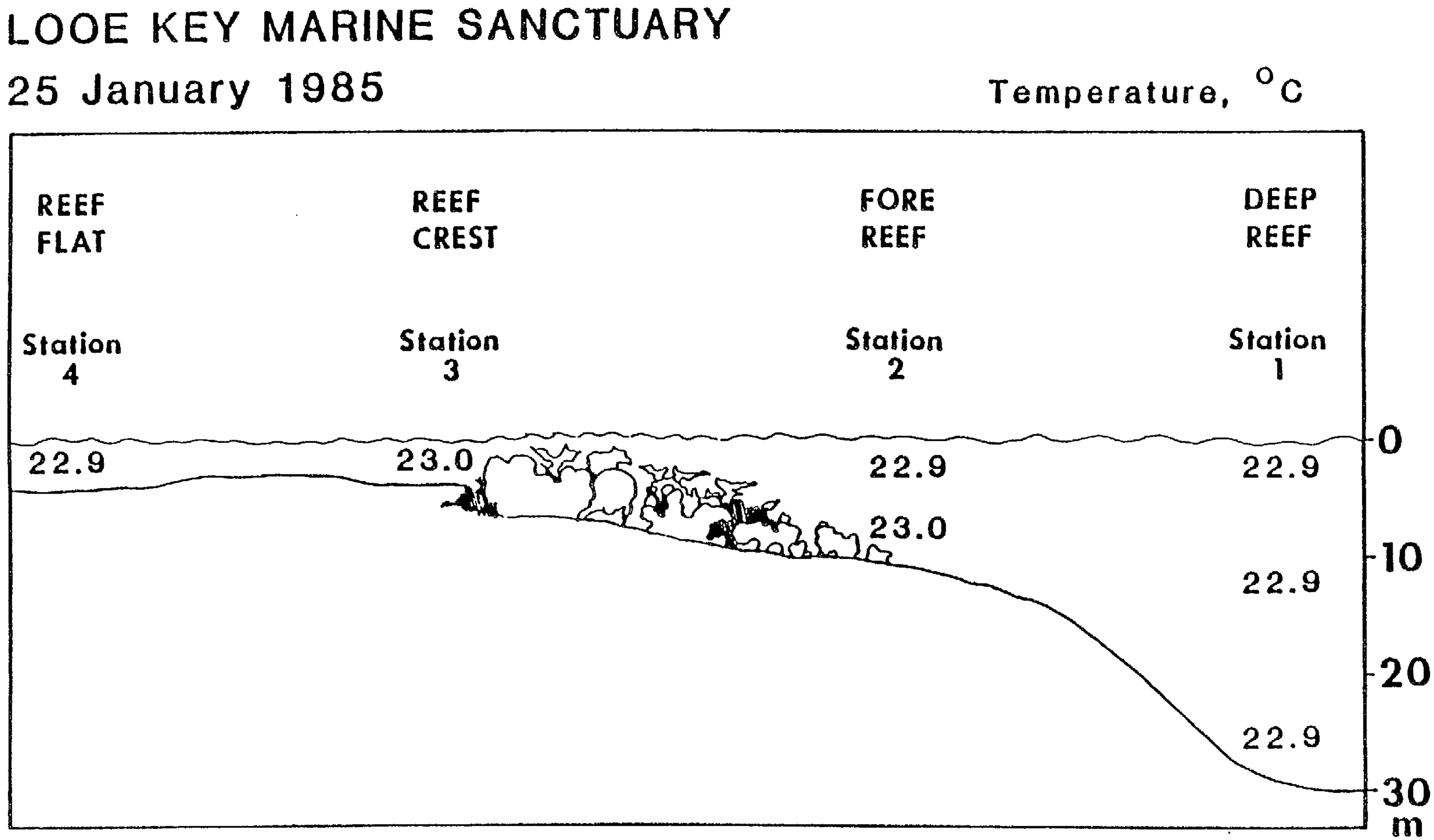

Figure 10. Temperature profile in the core area of Looe Key Marine Sanctuary on 25 January 1985.

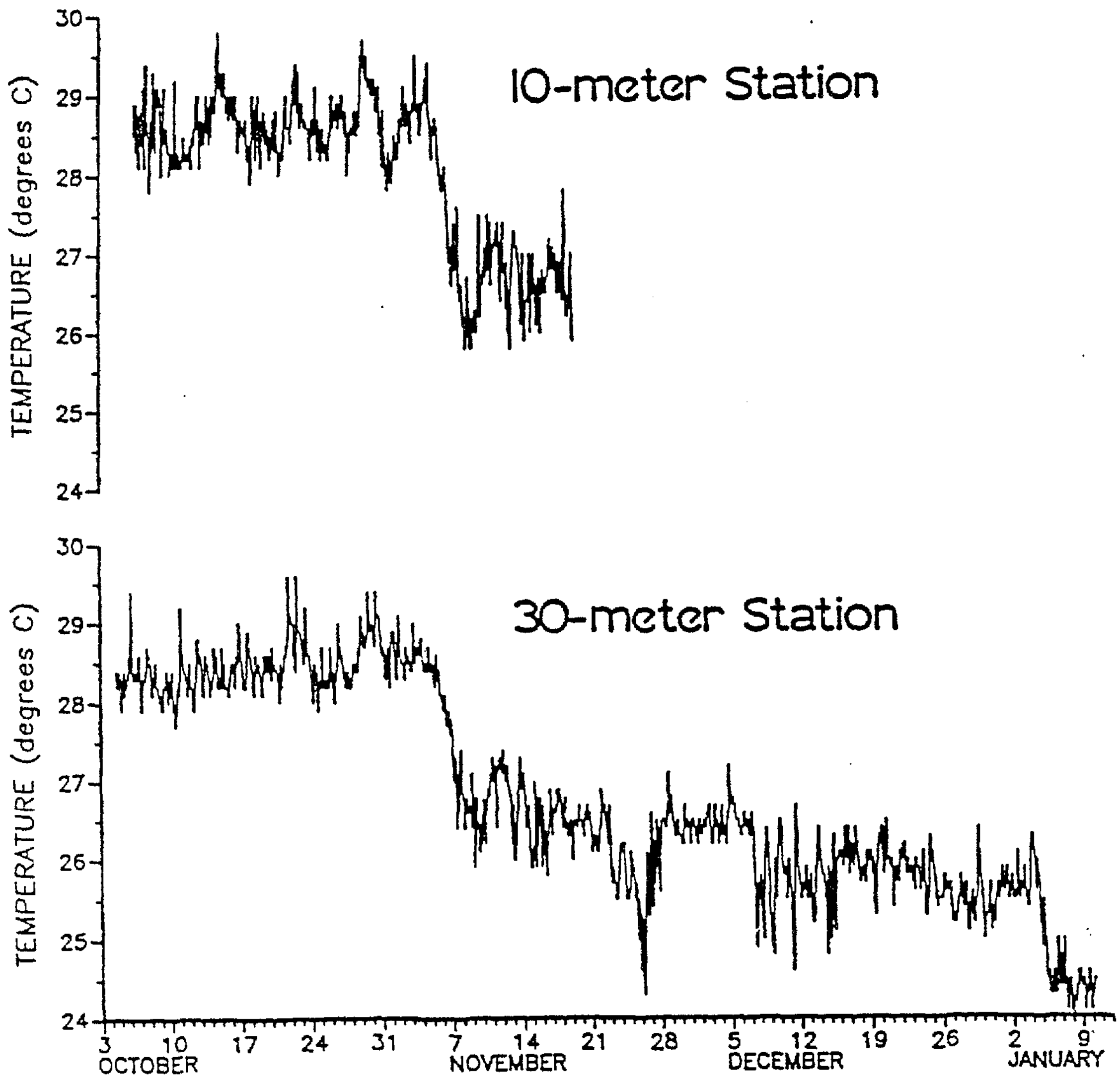

Figure 11. Temporal variation in temperature during the first deployment period at Stations 1 and 2 at Looe Key. Temperatures were recorded just above the bottom.

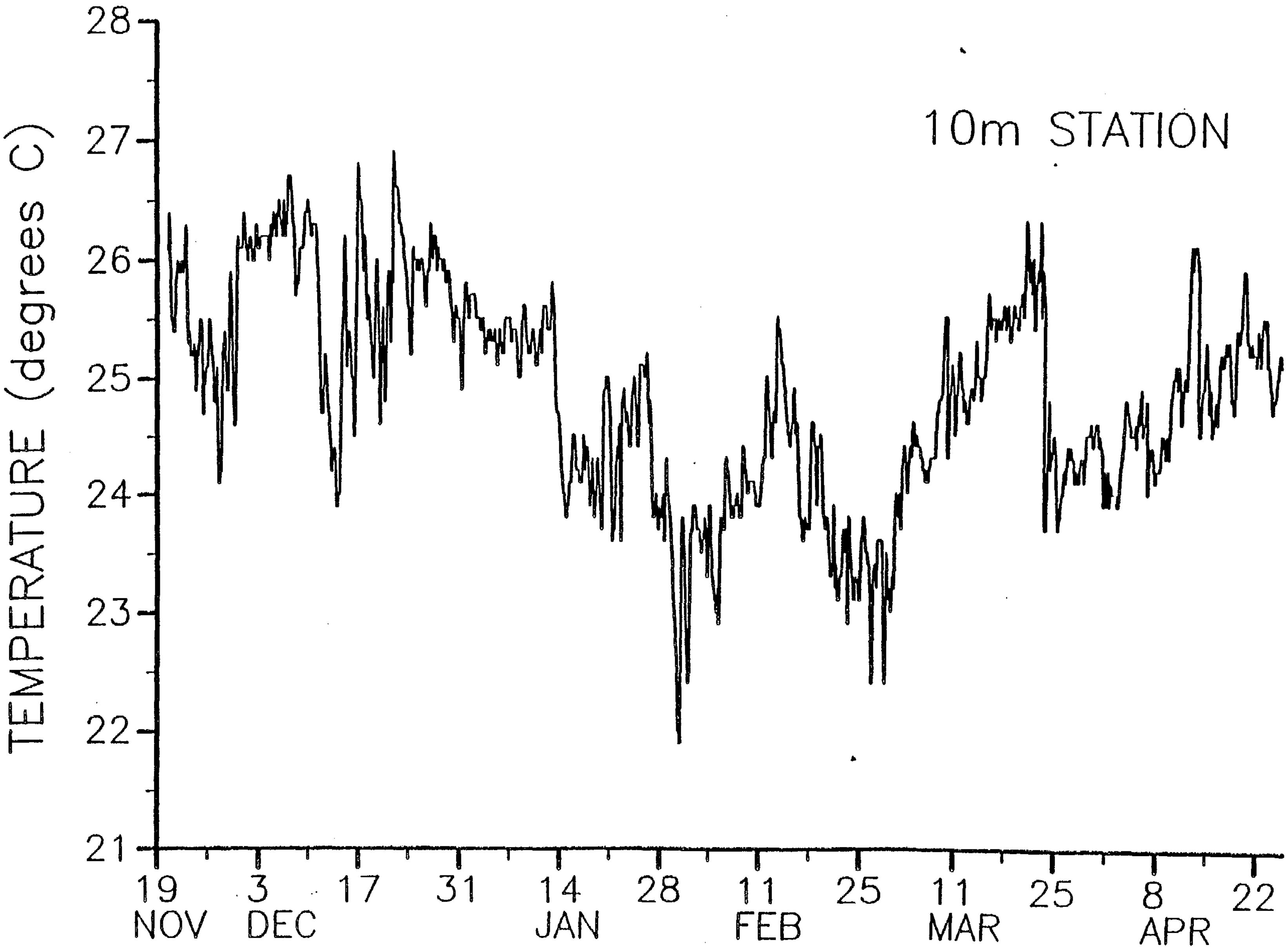

Figure 12. Temporal variation in temperature during the second deployment period at Stations 1 and 2 at Looe Key. Temperatures were recorded just above the bottom.

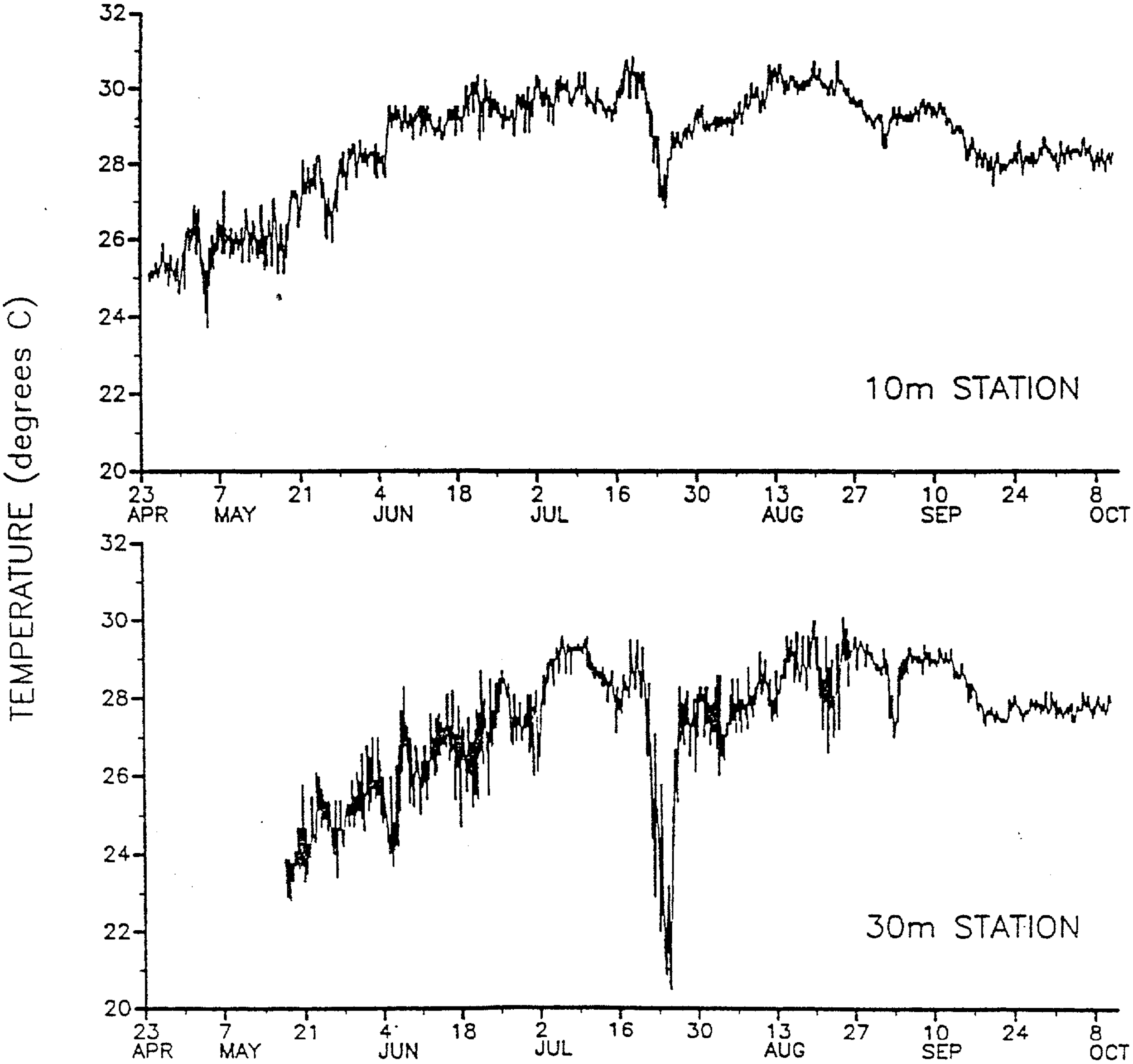

Figure 13. Temporal variation in temperature during the third deployment period at Stations 1 and 2 at Looe Key. Temperatures were recorded just above the bottom.

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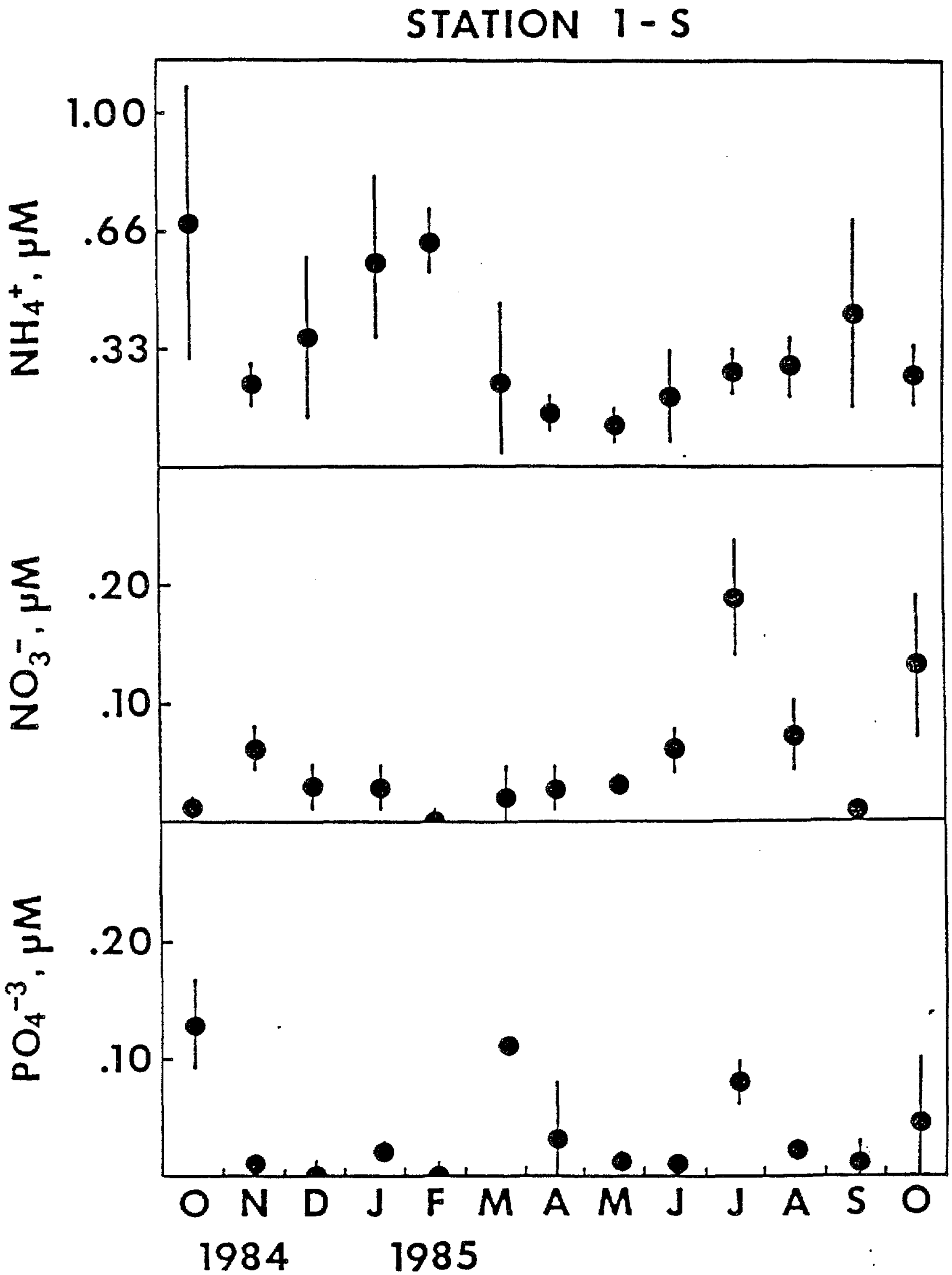
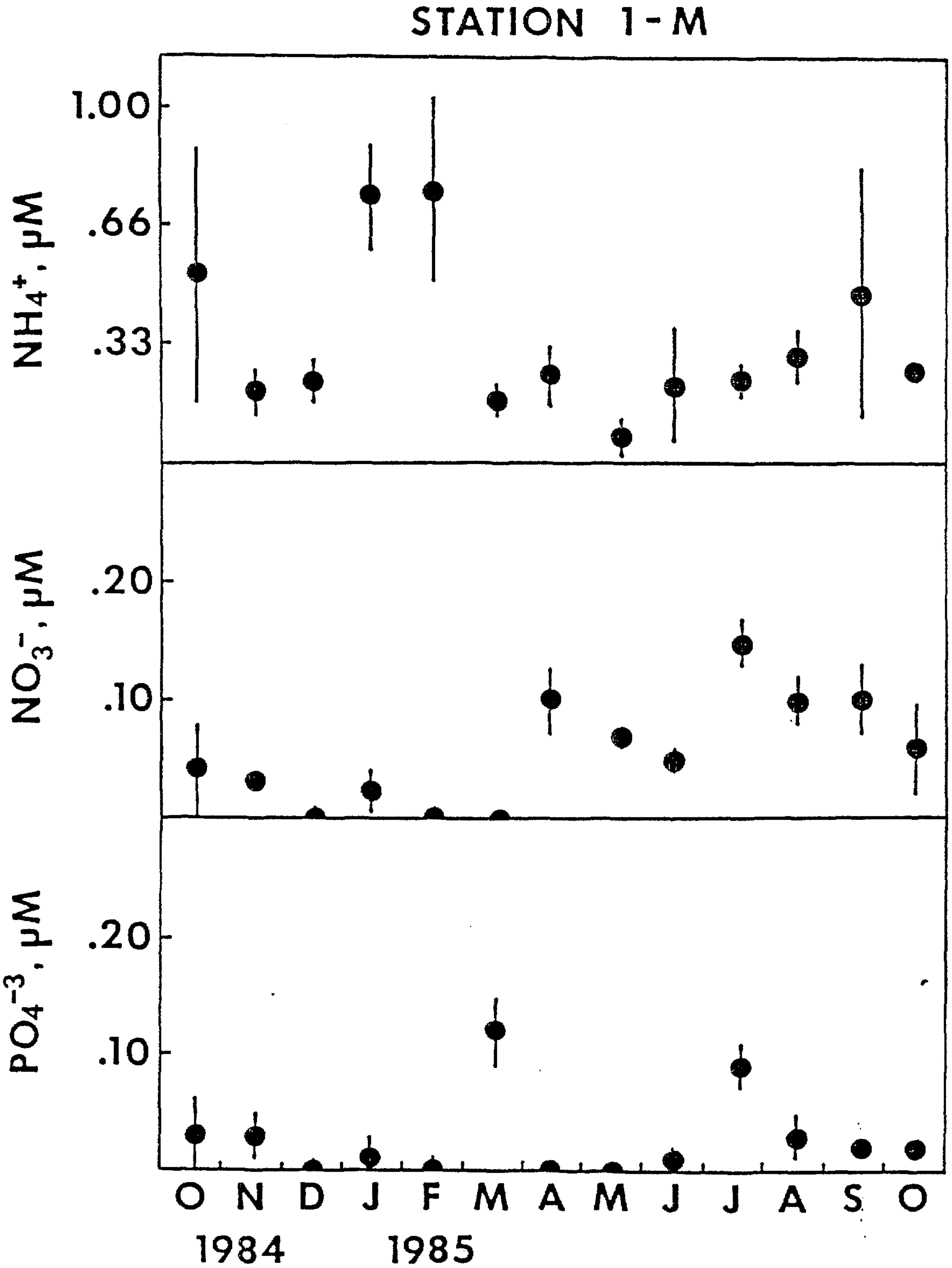
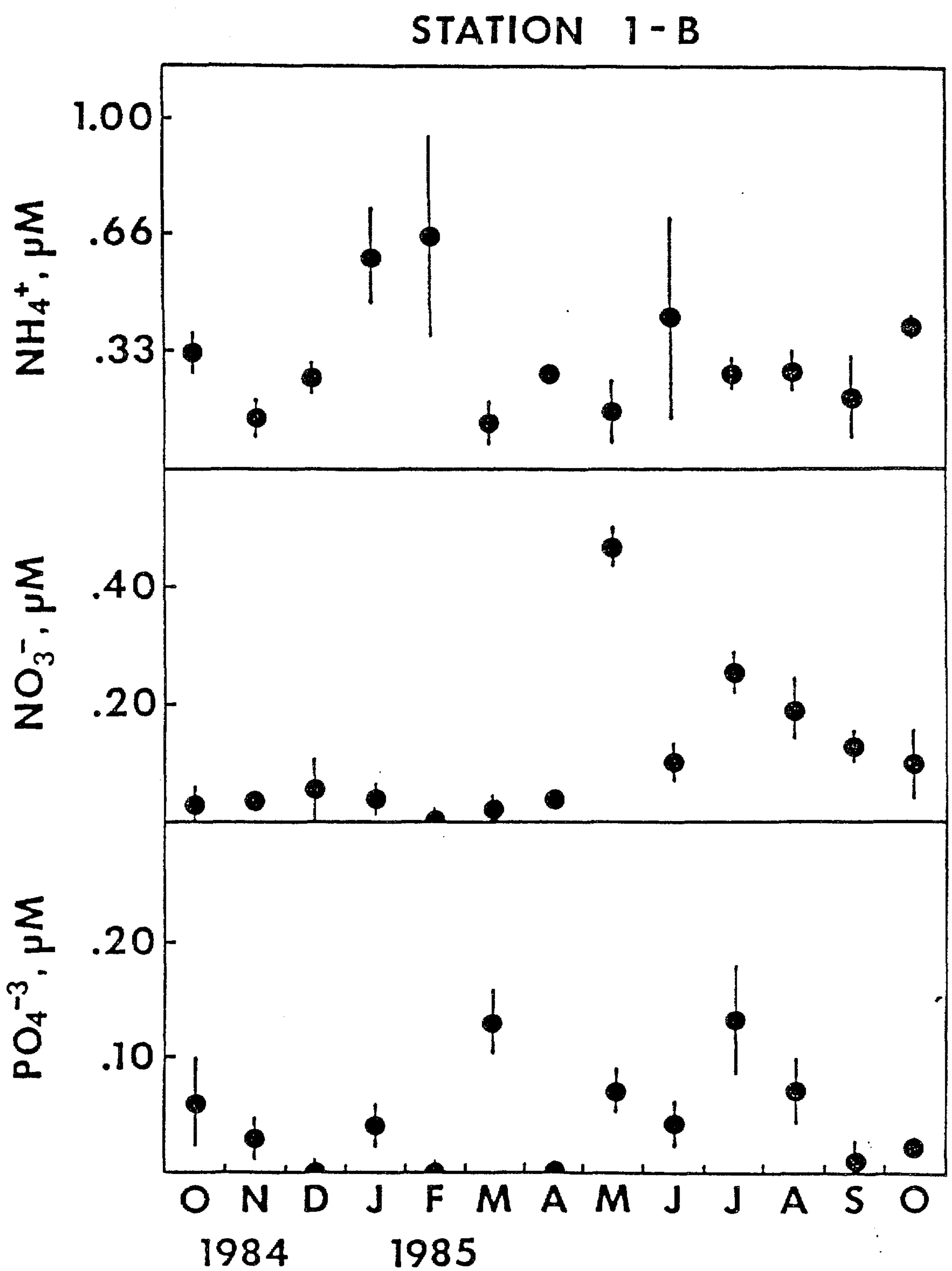
APPENDIX A

Figs. 1-7: Monthly averages of nutrient concentrations (NH_4^+, NO_3^-, PO_4^{3-}) measured at various depths (S = surface; M = midwater; B = bottom) at the four stations during the one year study.

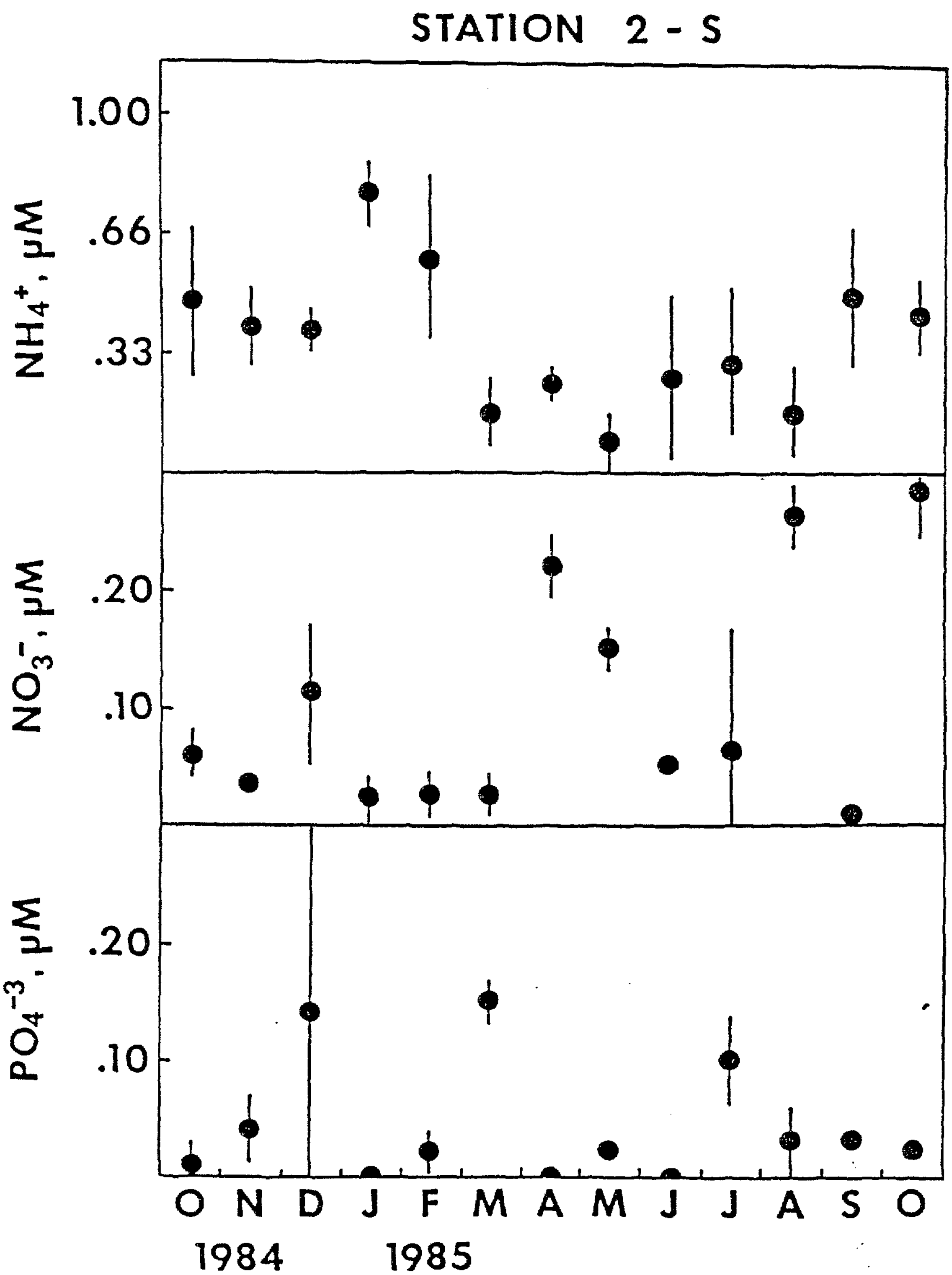

STATION 1-S
NH_4^+, μM
1.00
.66
.33
NO_3^-, μM
.20
.10
PO_4^{-3}, μM
.20
.10
O N D J F M A M J J A S O
1984
1985

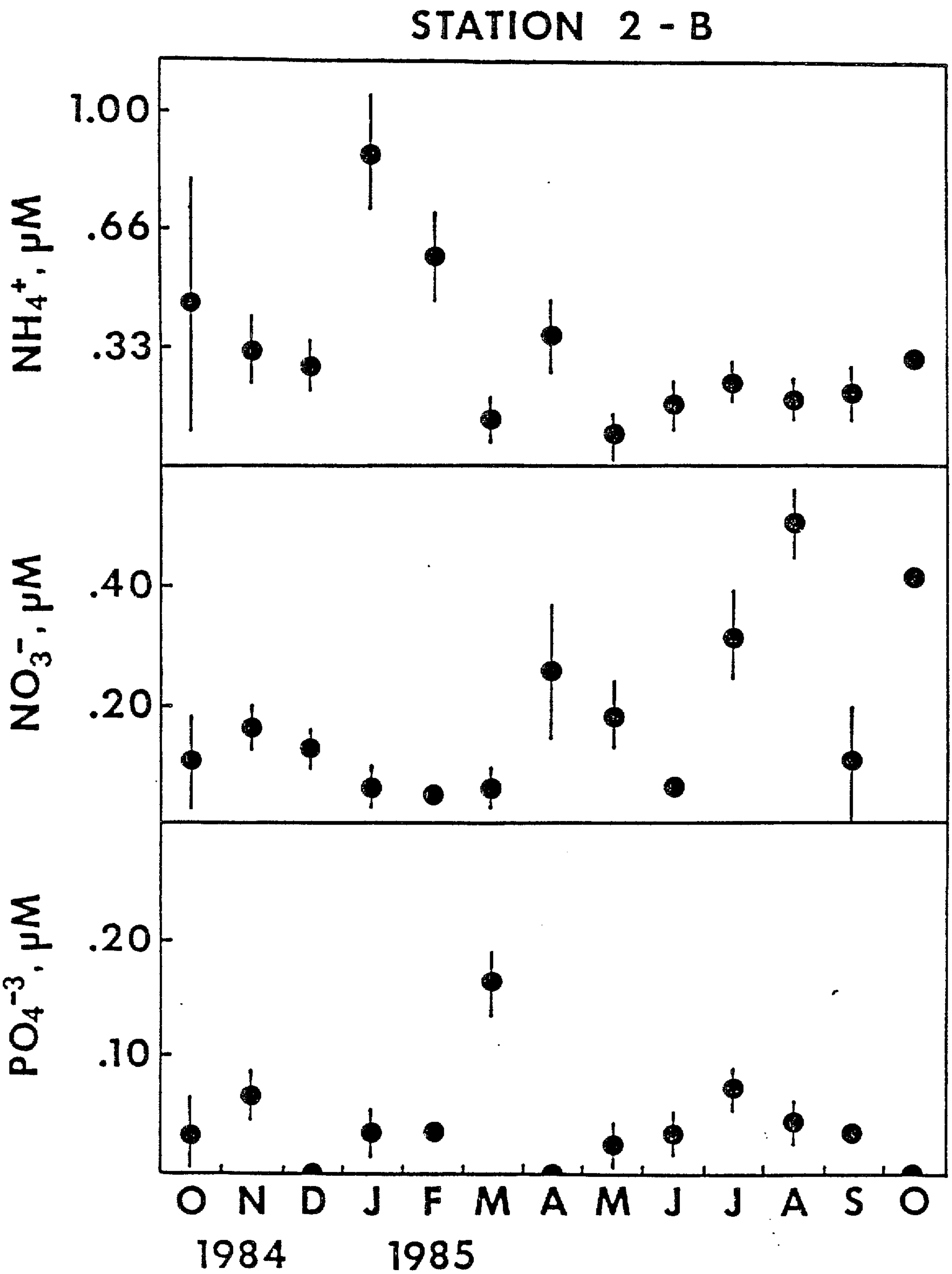


STATION 1-M
1.00
.66
.33
NH4+, μM
.20
.10
NO3-, μM
.20
.10
PO4-3, μM
O N D J F M A M J J A S O
1984
1985

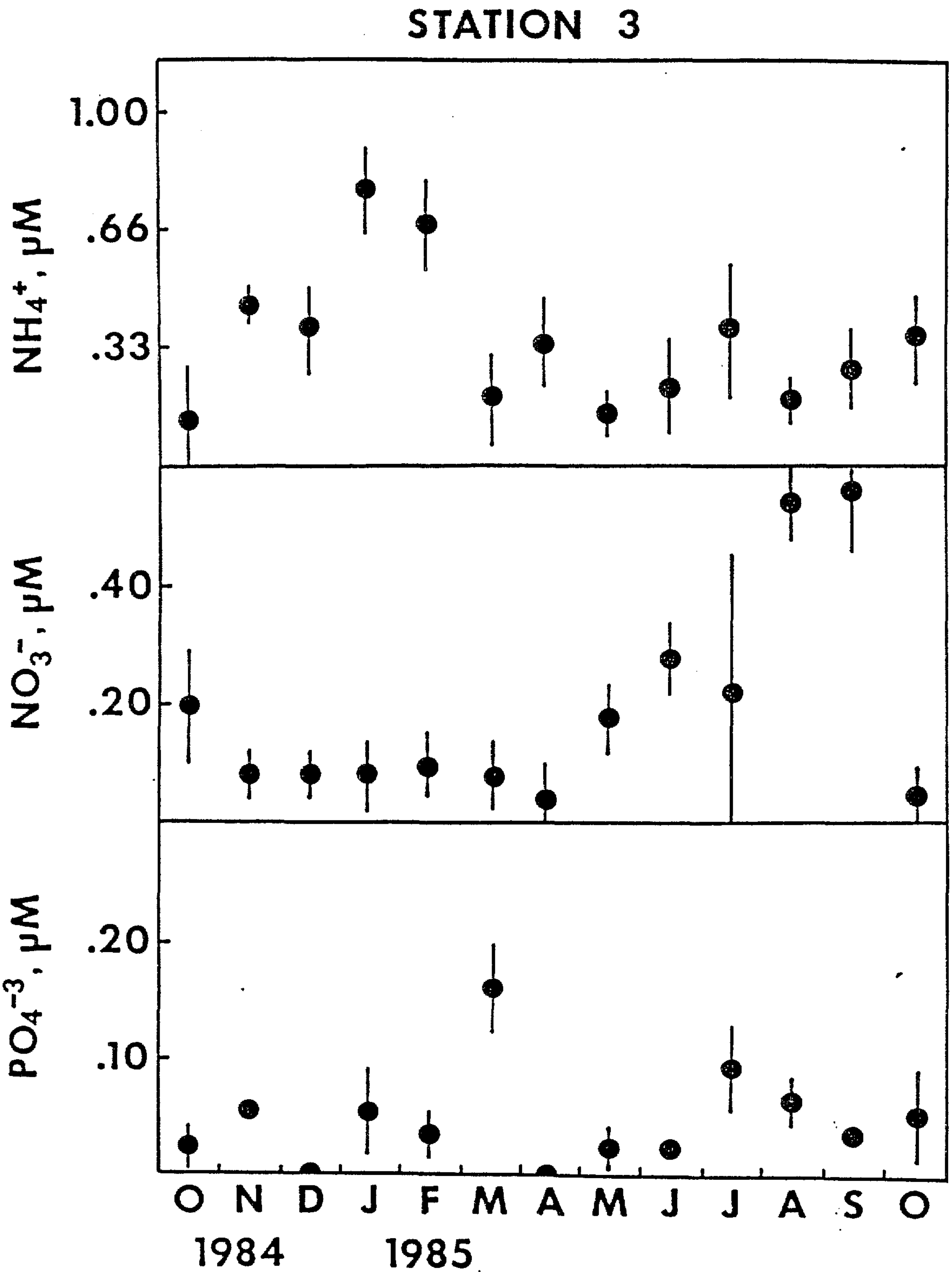


STATION 1-B
1.00
.66
.33
NH_4^+, µM
.40
.20
NO_3^-, µM
.20
.10
PO_4^{-3}, µM
O N D J F M A M J J A S O
1984
1985

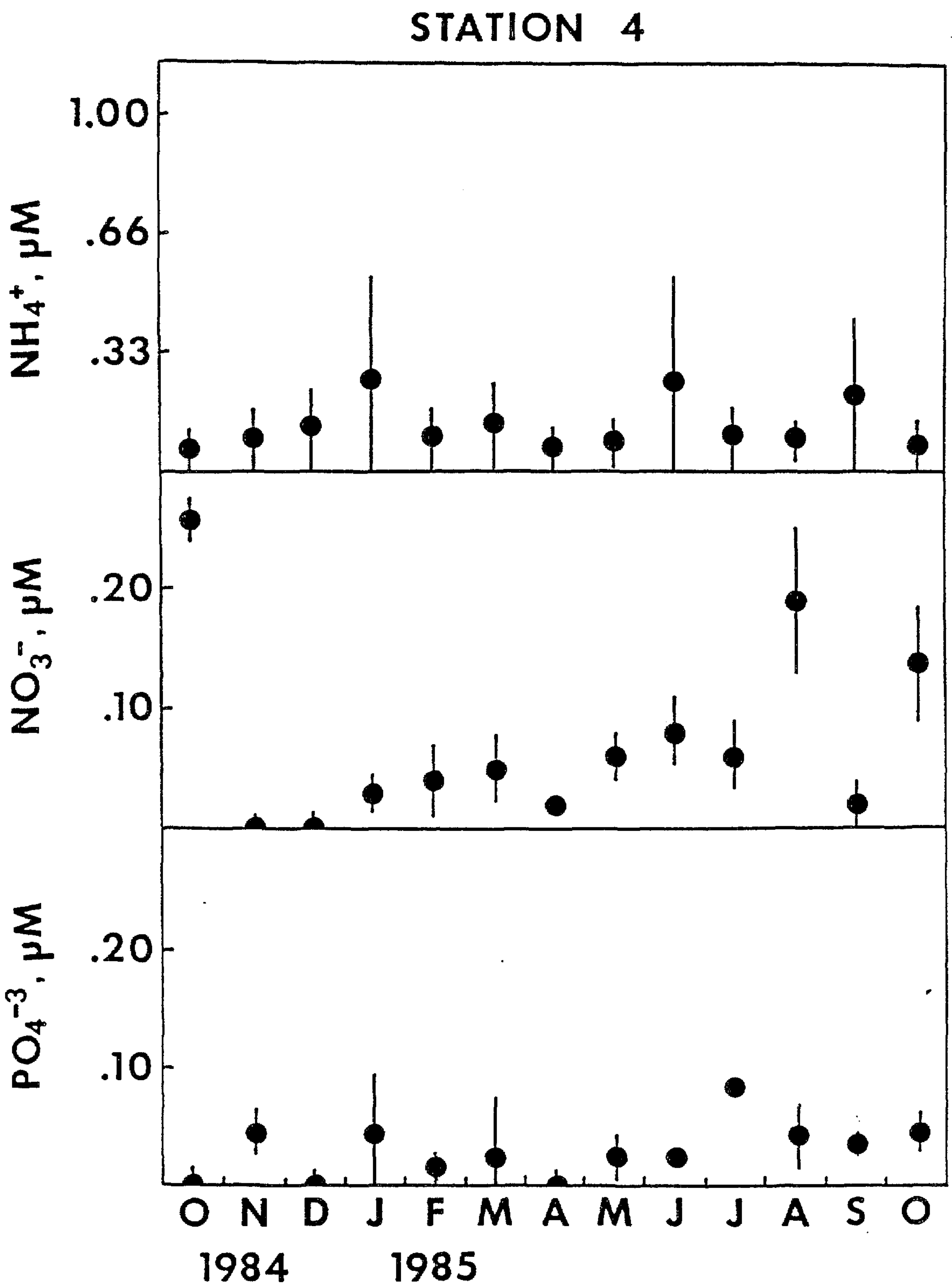

STATION 2 - S
1.00
.66
.33
NH_4^+, μM
.20
.10
NO_3^-, μM
.20
.10
PO_4^{-3}, μM
O N D J F M A M J J A S O
1984
1985



STATION 2 - B
NH4+, µM
1.00
.66
.33
NO3−, µM
.40
.20
PO4−3, µM
.20
.10
O N D J F M A M J J A S O
1984
1985



STATION 3
1.00
.66
.33
NH_4^+, μM
.40
.20
NO_3^-, μM
.20
.10
PO_4^{-3}, μM
O N D J F M A M J J A S O
1984
1985



STATION 4
1.00
.66
.33
NH4+, μM
.20
.10
NO3-, μM
.20
.10
PO4-3, μM
O
N
D
J
F
M
A
M
J
J
A
S
O
1984
1985

Table 1. Concentrations of dissolved inorganic nutrients and temperature of seawater sampled at four stations in Looe Key Marine Sanctuary over a one year period. Nutrient values are given as uM and represent means + 1 S.D. (N=2). UD = Undetectable, NA = Not available.

Nutrient	Station		Date 10-9-84	10-16-84	10-24-84
	#1	Surface	UD	0.53 + 0.03	0.55 + 0.15
		Midwater	0.12 + 0.18	UD	0.21 + 0.17
NH4		Bottom	UD	UD	0.30 + 0.04
	#2	Surface	UD	0	0.10 + 0.10
UD < 0.10		Bottom	UD	UD	0.17 + 0.00
	#3	Surface	UD	0.10 + 0.01	0.12 + 0.04
	#4	Surface	UD	UD	0.10 + 0.12
	#1	Surface	UD	0.05 + 0.00	UD
		Midwater	UD	0.06 + 0.08	0.05 + 0.06
NO3		Bottom	0.07 + 0.00	UD	0.05 + 0.03
	#2	Surface	0.07 + 0.01	0.10 + 0.03	0.07 + 0.00
UD < 0.05		Bottom	0.22 + 0.03	0.05 + 0.02	0.05 + 0.02
	#3	Surface	UD	0.66 + 0.08	0.08 + 0.01
	#4	Surface	UD	UD	UD
	#1	Surface	0.06 + 0.02	0.02 + 0.01	0.05 + 0.04
		Midwater	0.02 + 0.00	0.04 + 0.01	0.04 + 0.01
NO2		Bottom	0.06 + 0.01	0.03 + 0.02	0.09 + 0.01
	#2	Surface	0.04 + 0.00	0.04 + 0.01	0.03 + 0.02
UD < 0.01		Bottom	0.06 + 0.04	0.05 + 0.00	0.03 + 0.02
	#3	Surface	0.05 + 0.01	0.08 + 0.02	0.08 + 0.02
	#4	Surface	0.05 + 0.02	0.03 + 0.02	0.09 + 0.00
	#1	Surface	UD	0.50 + 0.12	UD
		Midwater	UD	0.04 + 0.06	UD
PO4		Bottom	0.03 + 0.01	0.08 + 0.06	0.05 + 0.04
	#2	Surface	UD	0.05 + 0.03	UD
UD < 0.03		Bottom	UD	0.07 + 0.06	UD
	#3	Surface	UD	0.08 + 0.02	UD
	#4	Surface	UD	UD	UD
	#1	Surface	26.8	27.8	27.0
		Midwater	27.0	27.9	27.1
Temperature		Bottom	26.2	27.9	26.9
	#2	Surface	26.8	27.5	26.9
C		Bottom	26.4	27.7	27.1
	#3	Surface	26.9	28.0	27.0
	#4	Surface	26.8	27.8	26.9

Table 1., Continued

Nutrient	Station		10-30-84	11-6-84	11-15-84	11-26-84
	#1	S	1.60 + 1.30	0.16 + 0.00	0.15 + 0.02	0.29 + 0.04
		M	2.00 + 0.96	0.18 + 0.08	0.18 + 0.01	0.24 + 0.00
NH4		B	0.97 + 0.13	0.14 + 0.50	0.15 + 0.02	0.29 + 0.00
	#2	S	1.10 + 0.18	0.33 + 0.24	0.24 + 0.03	0.39 + 0.00
UD < 0.10		B	1.50 + 0.20	0.26 + 0.12	0.30 + 0.04	0.43 + 0.03
	#3	S	0.49 + 0.43	0.31 + 0.03	0.42 + 0.02	0.46 + 0.00
	#4	S	UD	0.47 + 0.09	0.23 + 0.00	0.49 + 0.05
	#1	S	UD	0.14 + 0.01	0.05 + 0.02	UD
		M	UD	0.06 + 0.02	UD	UD
NO3		B	UD	0.05 + 0.00	0.06 + 0.00	UD
	#2	S	UD	0.09 + 0.03	UD	UD
UD < 0.05		B	0.06 + 0.03	0.36 + 0.02	0.05 + 0.01	0.15 + 0.01
	#3	S	0.07 + 0.04	UD	0.11 + 0.02	0.20 + 0.02
	#4	S	0.06 + 0.01	UD	UD	UD
	#1	S	0.03 + 0.02	0.01 + 0.00	UD	0.04 + 0.00
		M	UD	0.02 + 0.01	UD	0.04 + 0.00
NO2		B	0.01 + 0.01	0.02 + 0.01	UD	0.03 + 0.02
	#2	S	0.06 + 0.02	0.02 + 0.00	UD	0.06 + 0.00
UD < 0.01		B	0.02 + 0.03	0.03 + 0.02	UD	0.05 + 0.01
	#3	S	0.02 + 0.02	0.02 + 0.00	0.04 + 0.02	0.06 + 0.00
	#4	S	UD	0.06 + 0.03	0.03 + 0.01	0.04 + 0.02
	#1	S	UD	0.03 + 0.01	UD	UD
		M	0.09 + 0.01	0.04 + 0.02	UD	0.04 + 0.02
PO4		B	0.09 + 0.01	UD	UD	0.08 + 0.02
	#2	S	UD	0.05 + 0.03	UD	0.07 + 0.04
UD < 0.03		B	0.05 + 0.04	0.03 + 0.01	0.06 + 0.02	0.09 + 0.00
	#3	S	UD	0.05 + 0.00	UD	0.10 + 0.00
	#4	S	UD	0.07 + 0.02	UD	0.04 + 0.00
	#1	S	27.4	26.0	25.6	35.8
		M	27.3	25.9	25.2	35.8
Temperature		B	27.1	26.0	24.8	36.2
	#2	S	27.8	26.0	25.6	35.4
C		B	27.7	25.1	24.9	35.8
	#3	S	27.8	26.2	24.8	35.8
	#4	S	27.8	262.1	23.7	35.6

Table 1., Continued

Nutrient	Station		12-5-84	12-20-84	1-4-85	1-10-85
	#1	S	0.51 + 0.29	0.20 + 0.05	0.63 + 0.11	1.00 + 0.34
		M	0.21 + 0.02	0.20 + 0.04	0.59 + 0.05	0.88 + 0.14
NH4		B	0.32 + 0.01	0.24 + 0.00	0.69 + 0.18	0.87 + 0.21
	#2	S	0.43 + 0.05	0.28 + 0.02	0.78 + 0.02	0.92 + 0.07
UD < 0.10		B	0.27 + 0.05	0.35 + 0.06	0.72 + 0.02	1.10 + 0.22
	#3	S	0.28 + 0.05	0.43 + 0.13	0.75 + 0.06	1.10 + 0.23
	#4	S	0.27 + 0.04	0.50 + 0.13	0.91 + 0.22	1.60 + 0.34
	#1	S	UD	0.06 + 0.02	0.06 + 0.01	UD
		M	UD	UD	0.08 + 0.02	UD
NO3		B	0.12 + 0.17	UD	0.09 + 0.01	UD
	#2	S	0.14 + 0.03	0.07 + 0.00	0.12 + 0.01	UD
UD < 0.05		B	0.12 + 0.02	UD	0.16 + 0.00	UD
	#3	S	0.21 + 0.02	UD	0.06 + 0.01	0.07 + 0.02
	#4	S	UD	UD	0.13 + 0.01	UD
	#1	S	0.06 + 0.06	UD	0.02 + 0.01	0.06 + 0.00
		M	0.04 + 0.00	UD	0.02 + 0.00	0.08 + 0.01
NO2		B	0.01 + 0.04	0.03 + 0.02	0.03 + 0.00	0.07 + 0.01
	#2	S	0.05 + 0.00	0.03 + 0.00	0.02 + 0.00	0.04 + 0.02
UD < 0.01		B	0.03 + 0.01	0.11 + 0.02	0.03 + 0.01	0.07 + 0.02
	#3	S	0.07 + 0.01	0.05 + 0.03	0.03 + 0.00	0.09 + 0.00
	#4	S	0.02 + 0.00	0.05 + 0.03	UD	0.08 + 0.00
	#1	S	UD	UD	UD	0.07 + 0.01
		M	UD	UD	UD	UD
PO4		B	UD	UD	0.04 + 0.00	UD
	#2	S	UD	0.27 + 0.33	UD	UD
UD < 0.03		B	UD	UD	UD	0.04 + 0.01
	#3	S	UD	UD	0.03 + 0.01	0.05 + 0.07
	#4	S	UD	UD	UD	0.04 + 0.06
	#1	S	26.0	25.4	24.9	23.6
		M	25.9		24.6	23.7
Temperature		B	25.8	25.0	24.5	23.6
	#2	S	26.1	25.2	24.2	23.8
C		B	25.9	25.3	24.4	23.6
	#3	S	26.1	25.6	24.4	24.0
	#4	S	26.0	24.9	24.2	23.0

Table 1., Continued

Nutrient	Station		1-17-85	1-25-85	2-4-85	2-14-85
	#1	S	0.58 + 0.18	0.15 + 0.10	0.31 + 0.12	0.59 + 0.02
		M	0.75 + 0.17	0.57 + 0.14	0.59 + 0.28	0.74 + 0.31
NH4		B	0.71 + 0.12	0.23 + 0.02	0.44 + 0.17	0.68 + 0.08
	#2	S	0.98 + 0.06	0.59 + 0.09	0.82 + 0.50	0.62 + 0.05
UD < 0.10		B	1.20 + 0.07	0.37 + 0.17	0.67 + 0.06	0.67 + 0.02
	#3	S	0.96 + 0.00	0.32 + 0.09	0.62 + 0.24	0.82 + 0.02
	#4	S	0.98 + 0.18	0.35 + 0.16	0.36 + 0.06	0.75 + 0.05
	#1	S	UD	UD	UD	UD
		M	UD	UD	UD	UD
NO3		B	UD	UD	UD	UD
	#2	S	UD	0.07 + 0.01	UD	UD
UD < 0.05		B	UD	UD	UD	UD
	#3	S	0.12 + 0.02	UD	0.22 + 0.02	UD
	#4	S	UD	UD	UD	UD
	#1	S	0.03 + 0.00	0.03 + 0.02	0.05 + 0.03	0.06 + 0.04
		M	0.04 + 0.01	0.06 + 0.02	0.02 + 0.00	0.03 + 0.01
NO2		B	0.04 + 0.02	0.05 + 0.00	0.03 + 0.00	0.04 + 0.01
	#2	S	0.10 + 0.02	0.01 + 0.00	0.06 + 0.05	0.05 + 0.02
UD < 0.01		B	0.05 + 0.02	0.08 + 0.00	0.10 + 0.01	0.06 + 0.01
	#3	S	0.10 + 0.00	0.06 + 0.05	0.02 + 0.03	0.06 + 0.02
	#4	S	0.08 + 0.00	0.04 + 0.03	0.03 + 0.04	0.05 + 0.01
	#1	S	UD	UD	UD	UD
		M	0.05 + 0.04	UD	UD	UD
PO4		B	0.06 + 0.03	0.08 + 0.00	UD	UD
	#2	S	UD	UD	0.07 + 0.02	UD
UD < 0.03		B	0.06 + 0.01	UD	0.10 + 0.00	UD
	#3	S	0.06 + 0.02	0.07 + 0.03	0.08 + 0.02	UD
	#4	S	0.07 + 0.04	0.05 + 0.07	0.04 + 0.04	UD
	#1	S	24.0	22.9	23.9	
		M	24.0	22.9	23.8	
Temperature		B	24.0	22.9	23.1	
	#2	S	24.0	22.9	24.0	
C		B	24.0	23.0	23.5	
	#3	S	24.0	23.0	24.3	
	#4	S	24.1	22.9	23.9	

Table 1., Continued

Nutrient	Station		2-26-85	3-11-85	3-22-85	3-29-85
	#1	S	1.00 + 0.00	0.20 + 0.28	0.10 + 0.10	0.38 + 0.13
		M	0.82 + 0.03	UD	0.14 + 0.01	0.36 + 0.01
NH4		B	0.85 + 0.49	UD	0.10 + 0.10	0.26 + 0.04
	#2	S	0.39 + 0.01	UD	0.16 + 0.06	0.38 + 0.16
UD < 0.10		B	0.50 + 0.15	UD	0.10 + 0.09	0.38 + 0.01
	#3	S	0.56 + 0.01	0.15 + 0.01	0.10 + 0.06	0.46 + 0.20
	#4	S	0.66 + 0.08	0.19 + 0.04	0.00 + 0.00	0.46 + 0.20
	#1	S	UD	UD	0.05 + 0.07	UD
		M	UD	UD	UD	UD
NO3		B	UD	UD	0.05 + 0.02	UD
	#2	S	0.07 + 0.03	UD	0.06 + 0.04	UD
UD < 0.05		B	0.07 + 0.01	UD	0.06 + 0.00	0.05 + 0.03
	#3	S	0.12 + 0.02	0.11 + 0.00	0.05 + 0.02	0.09 + 0.03
	#4	S	0.12 + 0.08	0.10 + 0.03	0.05 + 0.04	UD
	#1	S	0.04 + 0.03	0.01 + 0.02	0.02 + 0.03	0.03 + 0.01
		M	0.05 + 0.00	0.04 + 0.00	0.06 + 0.01	0.05 + 0.04
NO2		B	0.04 + 0.00	0.06 + 0.01	UD	0.02 + 0.01
	#2	S	0.03 + 0.02	0.02 + 0.03	0.06 + 0.03	0.03 + 0.00
UD < 0.01		B	0.04 + 0.01	0.05 + 0.00	0.02 + 0.03	0.04 + 0.00
	#3	S	0.02 + 0.04	0.05 + 0.00	0.05 + 0.03	0.04 + 0.02
	#4	S	0.04 + 0.05	0.07 + 0.01	0.04 + 0.00	0.04 + 0.02
	#1	S	UD	0.34 + 0.01	UD	UD
		M	UD	0.36 + 0.07	UD	UD
PO4		B	UD	0.36 + 0.05	0.04 + 0.02	UD
	#2	S	UD	0.38 + 0.04	0.08 + 0.00	UD
UD < 0.03		B	UD	0.42 + 0.04	0.07 + 0.03	UD
	#3	S	UD	0.44 + 0.04	0.05 + 0.06	UD
	#4	S	UD	0.49 + 0.11	0.11 + 0.01	UD
	#1	S	23.7	24.9	23.9	24.4
		M	23.7	24.9	23.9	23.7
Temperature		B	23.5	24.9	23.7	23.8
	#2	S	23.8	24.9	24.0	23.9
C		B	23.8	24.9	23.9	23.7
	#3	S	24.0	24.9	24.0	23.9
	#4	S	23.9	24.0	24.0	24.0

Table 1., Continued

Nutrient	Station		4-15-85	4-24-85	5-1-85	5-7-85
	#1	S	0.22 + 0.00	0.11 + 0.04	0.18 + 0.06	0.10 + 0.0
		M	0.27 + 0.06	0.14 + 0.04	0.11 + 0.03	0.19 + 0.0
NH4		B	0.32 + 0.01	0.17 + 0.00	0.18 + 0.05	0.38 + 0.1
	#2	S	0.25 + 0.00	0.24 + 0.04	0.20 + 0.08	0.36 + 0.1
UD < 0.10		B	0.39 + 0.14	0.32 + 0.05	0.11 + 0.03	0.25 + 0.0
	#3	S	0.27 + 0.04	0.40 + 0.13	0.16 + 0.05	0.24 + 0.0
	#4	S	0.27 + 0.03	0.18 + 0.03	0.14 + 0.01	0.14 + 0.0
	#1	S	UD	0.06 + 0.03	0.05 + 0.00	UD
		M	UD	0.19 + 0.05	0.12 + 0.00	0.06 + 0.0
NO3		B	UD	0.05 + 0.00	1.80 + 0.02	0.27 + 0.0
	#2	S	0.09 + 0.02	0.33 + 0.01	0.10 + 0.00	0.38 + 0.0
UD < 0.05		B	0.33 + 0.04	0.19 + 0.07	0.33 + 0.00	0.27 + 0.0
	#3	S	UD	0.07 + 0.03	0.04 + 0.00	0.13 + 0.0
	#4	S	UD	0.05 + 0.01	UD	0.09 + 0.0
	#1	S	0.01 + 0.02	0.01 + 0.02	UD	0.04 + 0.0
		M	0.03 + 0.00	0.04 + 0.00	UD	0.03 + 0.0
NO2		B	0.03 + 0.00	0.02 + 0.03	0.09 + 0.00	0.05 + 0.0
	#2	S	0.02 + 0.03	0.06 + 0.03	UD	0.04 + 0.0
UD < 0.01		B	0.05 + 0.00	0.03 + 0.10	0.02 + 0.00	0.03 + 0.0
	#3	S	0.03 + 0.01	UD	UD	0.04 + 0.0
	#4	S	0.02 + 0.03	0.02 + 0.02	UD	0.03 + 0.0
	#1	S	UD	0.05 + 0.07	UD	0.03 + 0.0
		M	UD	UD	UD	UD
PO4		B	UD	UD	0.23 + 0.02	0.06 + 0.0
	#2	S	UD	UD	UD	0.05 + 0.0
UD < 0.03		B	UD	UD	UD	0.04 + 0.0
	#3	S	UD	UD	UD	0.05 + 0.0
	#4	S	UD	UD	UD	0.02 + 0.0
	#1	S	24.8	25.0	25.2	26.0
		M	24.9	24.9	25.2	25.8
Temperature		B	24.7	24.5	23.9	23.9
	#2	S	24.9	25.0	25.6	26.2
C		B	24.9	25.0	25.6	26.0
	#3	S	25.3	25.0	25.9	26.2
	#4	S	25.3	24.9	26.0	26.3

Table 1., Continued

Nutrient	Station		5-13-85	5-21-85	5-29-85	6-7-85
	#1	S	0.10 + 0.00	0.10 + 0.00	0.10 + 0.00	0.13 + 0.00
		M	UD	0.15 + 0.07	UD	0.10 + 0.02
NH4		B	0.10 + 0.02	0.10 + 0.06	UD	0.28 + 0.05
	#2	S	UD	0.10 + 0.01	UD	0.10 + 0.01
UD < 0.10		B	UD	0.14 + 0.10	UD	0.10 + 0.08
	#3	S	0.10 + 0.01	0.26 + 0.07	UD	0.27 + 0.18
	#4	S	0.16 + 0.16	0.10 + 0.01	UD	0.38 + 0.01
	#1	S	0.05 + 0.02	UD	0.05 + 0.00	UD
		M	UD	0.06 + 0.00	0.05 + 0.00	UD
NO3		B	UD	0.05 + 0.00	0.37 + 0.00	0.05 + 0.05
	#2	S	0.05 + 0.02	0.06 + 0.01	0.16 + 0.00	UD
UD < 0.05		B	0.17 + 0.01	0.09 + 0.04	0.08 + 0.00	UD
	#3	S	UD	0.74 + 0.09	0.05 + 0.00	0.45 + 0.00
	#4	S	0.05 + 0.02	0.13 + 0.01	0.05 + 0.00	0.09 + 0.01
	#1	S	0.02 + 0.03	0.02 + 0.00	0.02 + 0.01	UD
		M	0.02 + 0.00	0.02 + 0.01	0.05 + 0.02	UD
NO2		B	0.05 + 0.01	UD	0.03 + 0.03	UD
	#2	S	0.02 + 0.02	0.01 + 0.00	0.03 + 0.01	UD
UD < 0.01		B	0.04 + 0.02	0.01 + 0.00	0.03 + 0.00	UD
	#3	S	0.03 + 0.01	0.06 + 0.14	0.03 + 0.01	0.02 + 0.00
	#4	S	0.02 + 0.00	0.01 + 0.01	0.04 + 0.01	UD
	#1	S	UD	UD	UD	UD
		M	UD	UD	UD	UD
PO4		B	0.03 + 0.01	0.04 + 0.02	UD	UD
	#2	S	UD	0.06 + 0.01	UD	UD
UD < 0.03		B	UD	0.04 + 0.03	UD	UD
	#3	S	UD	0.06 + 0.06	UD	UD
	#4	S	UD	0.06 + 0.07	UD	UD
	#1	S	26.2	27.1	28.0	29.1
		M	25.0	26.9	27.8	29.1
Temperature		B	24.0	24.6	25.8	27.0
	#2	S	28.0	27.4	28.0	29.0
C		B	25.5	27.0	27.9	28.9
	#3	S	28.0	27.7	28.4	29.4
	#4	S	28.2	27.9	28.5	29.1

Table 1., Continued

Nutrient	Station		6-18-85	6-27-85	7-10-85	7-26-85
	#1	S	0.10 + 0.04	0.36 + 0.27	0.44 + 0.05	0.12 + 0.01
		M	0.10 + 0.01	0.40 + 0.32	0.23 + 0.00	0.18 + 0.04
NH4		B	0.28 + 0.04	0.65 + 0.72	0.36 + 0.01	0.22 + 0.01
	#2	S	0.10 + 0.05	0.72 + 0.64	0.35 + 0.25	0.28 + 0.18
UD < 0.10		B	0.12 + 0.11	0.14 + 0.00	0.18 + 0.01	0.22 + 0.09
	#3	S	0.22 + 0.08	0.29 + 0.03	0.56 + 0.21	0.22 + 0.09
	#4	S	0.23 + 0.00	0.94 + 1.06	0.13 + 0.00	0.03 + 0.07
	#1	S	UD	0.17 + 0.02	0.15 + 0.01	0.20 + 0.09
		M	UD	0.05 + 0.00	0.16 + 0.01	0.12 + 0.00
NO3		B	0.06 + 0.03	0.14 + 0.01	0.21 + 0.02	0.31 + 0.03
	#2	S	UD	0.14 + 0.02	0.08 + 0.00	0.44 + 0.21
UD < 0.05		B	0.06 + 0.01	0.12 + 0.03	0.57 + 0.03	0.09 + 0.00
	#3	S	0.25 + 0.05	0.07 + 0.01	0.11 + 0.03	0.30 + 0.20
	#4	S	0.10 + 0.01	0.07 + 0.04	0.06 + 0.02	0.06 + 0.03
	#1	S	0.03 + 0.04	0.05 + 0.02	0.04 + 0.00	0.09 + 0.01
		M	0.02 + 0.01	0.05 + 0.00	0.01 + 0.01	0.09 + 0.02
NO2		B	0.02 + 0.01	0.05 + 0.00	0.06 + 0.01	0.09 + 0.03
	#2	S	0.02 + 0.02	0.05 + 0.01	0.02 + 0.00	0.06 + 0.00
UD < 0.01		B	0.01 + 0.01	0.03 + 0.01	0.04 + 0.00	0.08 + 0.02
	#3	S	0.03 + 0.04	0.05 + 0.01	0.01 + 0.00	0.10 + 0.01
	#4	S	0.01 + 0.00	0.04 + 0.01	0.01 + 0.00	0.08 + 0.00
	#1	S	UD	0.04 + 0.00	0.07 + 0.01	0.09 + 0.01
		M	UD	0.04 + 0.01	0.05 + 0.02	0.12 + 0.00
PO4		B	0.05 + 0.01	0.06 + 0.02	0.12 + 0.07	0.14 + 0.01
	#2	S	UD	UD	0.07 + 0.03	0.13 + 0.02
UD < 0.03		B	0.09 + 0.02	UD	0.02 + 0.00	0.12 + 0.02
	#3	S	UD	0.05 + 0.00	0.07 + 0.03	0.10 + 0.02
	#4	S	UD	0.05 + 0.00	UD	0.15 + 0.00
	#1	S	29.0		30.1	28.8
		M	28.8		30.5	28.8
Temperature		B	26.2		29.4	28.5
	#2	S	29.2		30.0	28.8
C		B	29.2		30.3	28.8
	#3	S	29.8		30.4	28.9
	#4	S	29.5		30.8	29.0

Table 1., Continued

Nutrient	Station		8-3-85	8-8-85	8-18-85	9-1-85
	#1	S	0.23 + 0.10	0.49 + 0.00	0.14 + 0.04	0.17 + 0.01
		M	0.17 + 0.04	0.56 + 0.00	0.20 + 0.03	0.12 + 0.05
NH4		B	0.31 + 0.03	0.49 + 0.00	0.14 + 0.03	0.10 + 0.03
	#2	S	0.22 + 0.05	0.31 + 0.00	0.15 + 0.11	0.20 + 0.06
UD < 0.10		B	0.24 + 0.01	0.31 + 0.00	0.10 + 0.06	UD
	#3	S	0.26 + 0.04	NA	0.20 + 0.02	0.10 + 0.04
	#4	S	0.23 + 0.04	0.42 + 0.00	0.16 + 0.04	UD
	#1	S	0.06 + 0.02	0.05 + 0.00	0.07 + 0.04	UD
		M	0.14 + 0.00	0.10 + 0.01	0.05 + 0.01	0.18 + 0.01
NO3		B	0.11 + 0.01	0.39 + 0.09	0.06 + 0.01	0.34 + 0.02
	#2	S	0.66 + 0.03	0.10 + 0.05	0.07 + 0.01	UD
UD < 0.05		B	1.10 + 0.01	0.25 + 0.00	0.05 + 0.01	0.08 + 0.12
	#3	S	0.27 + 0.00	1.20 + 0.00	0.13 + 0.02	0.51 + 0.01
	#4	S	0.05 + 0.02	0.47 + 0.05	0.05 + 0.00	0.05 + 0.04
	#1	S	UD	0.01 + 0.02	UD	0.07 + 0.00
		M	0.02 + 0.00	0.02 + 0.00	0.04 + 0.00	0.07 + 0.01
NO2		B	0.02 + 0.01	0.02 + 0.02	0.04 + 0.00	0.05 + 0.03
	#2	S	0.04 + 0.00	UD	0.02 + 0.00	0.08 + 0.07
UD < 0.01		B	0.03 + 0.01	0.03 + 0.01	0.03 + 0.01	0.09 + 0.01
	#3	S	UD	0.11 + 0.02	0.01 + 0.01	0.11 + 0.02
	#4	S	UD	0.07 + 0.02	0.03 + 0.02	0.09 + 0.05
	#1	S	UD	UD	0.06 + 0.00	0.04 + 0.02
		M	0.06 + 0.01	UD	0.04 + 0.02	0.06 + 0.01
PO4		B	0.11 + 0.02	0.04 + 0.02	0.06 + 0.01	0.04 + 0.02
	#2	S	0.05 + 0.04	UD	0.03 + 0.01	0.08 + 0.01
UD < 0.03		B	0.07 + 0.00	UD	0.04 + 0.02	0.09 + 0.00
	#3	S	0.06 + 0.01	0.07 + 0.01	0.05 + 0.02	0.09 + 0.01
	#4	S	0.06 + 0.02	0.04 + 0.01	0.03 + 0.03	0.08 + 0.01
	#1	S	29.9	29.7	31.0	30.0
		M	29.0	29.5	31.0	30.0
Temperature		B	27.2	28.9	29.5	30.0
	#2	S	30.0	29.8	31.0	30.0
C		B	29.1	29.5	31.0	30.0
	#3	S	30.0	29.9	31.5	30.2
	#4	S	29.9	29.9	31.0	30.0

Table 1., Continued

Nutrient	Station		9-9-85	9-16-85	10-6-85
	#1	S	0.43 + 0.34	0.60 + 0.35	0.29 + 0.04
		M	0.28 + 0.21	0.77 + 0.61	0.25 + 0.00
NH4		B	0.15 + 0.03	0.42 + 0.18	0.37 + 0.00
	#2	S	0.52 + 0.39	0.64 + 0.02	0.40 + 0.06
UD < 0.10		B	0.26 + 0.00	0.45 + 0.13	0.32 + 0.00
	#3	S	0.30 + 0.08	0.52 + 0.13	0.37 + 0.09
	#4	S	0.28 + 0.02	0.64 + 0.54	0.32 + 0.03
	#1	S	UD	UD	0.15 + 0.05
		M	0.05 + 0.04	UD	0.08 + 0.03
NO3		B	UD	UD	0.10 + 0.04
	#2	S	UD	UD	0.39 + 0.03
UD < 0.05		B	0.19 + 0.01	0.16 + 0.01	0.41 + 0.00
	#3	S	0.87 + 0.05	0.64 + 0.07	0.07 + 0.02
	#4	S	UD	UD	0.14 + 0.04
	#1	S	0.01 + 0.02	0.02 + 0.01	0.02 + 0.01
		M	0.01 + 0.01	UD	UD
NO2		B	UD	0.02 + 0.00	0.03 + 0.01
	#2	S	0.02 + 0.00	0.02 + 0.03	0.03 + 0.03
UD < 0.01		B	0.03 + 0.01	0.03 + 0.00	0.03 + 0.01
	#3	S	0.08 + 0.02	0.08 + 0.02	0.03 + 0.01
	#4	S	0.03 + 0.01	0.04 + 0.02	0.03 + 0.01
	#1	S	UD	UD	0.04 + 0.05
		M	UD	UD	0.02 + 0.00
PO4		B	UD	UD	0.02 + 0.00
	#2	S	UD	UD	0.02 + 0.00
UD < 0.03		B	UD	UD	UD
	#3	S	UD	UD	0.05 + 0.03
	#4	S	UD	UD	0.04 + 0.01
	#1	S	29.5		28.0
		M	29.2		28.1
Temperature		B	29.2		28.0
	#2	S	29.5		28.5
C		B	29.6		28.5
	#3	S	30.0		28.5
	#4	S	29.9		28.2