BNL-27333

CONF-7910131--1

MASTER

The Role of Nutrient Recycling in Upwelling Ecosystems[1]

by

Terry E. Whitledge
Oceanographic Sciences Division
Brookhaven National Laboratory
Upton, New York 11973

[1] Presented at and published in the proceedings of the symposium on "The Bioproductivity of Upwelling Ecosystems" held in Moscow, USSR, 9-13 October 1979.

This research was supported by National Science Foundation Grant OCE78-05737 as a component of the United States IDOE Coastal Upwelling Ecosystems Analysis (CUEA) program. The analysis was also partially supported by the United States Department of Energy under contract No. DE-AC02-76CH00016.

ABSTRACT

The regeneration of nitrogen is an important process that increases the efficiency of the upwelling ecosystem by enlarging their spatial scales. Ammonium regeneration was considered to contribute 42 to 72 percent of phytoplankton nitrogen requirements in the northwest Africa, Peru, and Baja California upwelling systems. Zooplankton are responsible for the largest portion of regenerated nitrogen, however, fish and benthic sediments may be nearly as large. Comparisons of the importance of ammonium regeneration in upwelling areas with coastal and open ocean regions indicate that the percentage contributions are similar. Future nutrient regeneration studies are needed to assess the recycling of benthic sediments, microzooplankton, gelatinous zooplankton, demersal fish, bacterioplankton, and mollusks.

Who hath desired the Sea? - the immense and contemptuous surges?
The shudder, the stumble, the swerve, as the star-stabbing bow-sprit emerges?
The orderly clouds of the Trades, the ridged, roaring sapphire thereunder -
Unheralded cliff-haunting flows and the headsail's low-volleying thunder -
His Sea is no wonder the same - his Sea and the same through each wonder:
His Sea as she rages or stills?
So and no otherwise - so and no otherwise - hillmen desire their Hills.

- Kipling -

INTRODUCTION

The upwelling areas in the world located off the west coasts of the major continents are typified by cold nutrient rich waters which are condusive to the maintenance of large phytoplankton populations especially in the low latitudes where the quantity of light is always sufficient. The nutrients present in upwelling areas represent recycling of organic matter on different time scales. The input of nutrients into the euphotic zone by the upwelling of waters from depth represents a long term renewal of nutrients which previously had been bound into organic matter, transported into the deep ocean, decomposed into simple subunits, and eventually existing as the fully oxidized state of the nutrient, i.e. nitrate in the case of nitrogen. So in effect this is a decomposition process that occurs slowly. The time scale of such recycling on the average would be in terms of years or even as long as centuries. Since the time scales are so long the rates are essentially below limits of detection with current methods.

The short time scale turnover of nutrients occurs in the upper water column mainly through the action of animal metabolism (although there is some speculation that microbiological decomposition is also important) produces reduced forms of nutrients, i.e., ammonium for the element nitrogen. This latter process has been traditionally termed regeneration or recycling of nutrients although the initial steps are the same as the decomposition process--organic matter is broken into its simpler forms which are available for reuse in primary production processes. Since the ammonium is produced in the upper layers of the ocean it is immediately available for use by phytoplankton and it is utilizied before it is nitrified to nitrate.

With vertical advection bringing nutrient-rich water into the euphotic zone of upwelling areas, relatively large concentrations of nutrients are available to stimulate primary productivity, however, recycled nutrients are also important to increase the efficiency of the production of the ecosystem. This topic has only recently been examined in upwelling ecosystems and is the central focus of this paper.

NORTHWEST AFRICA

Two main locations of study in upwelling areas off Northwest Africa, Cape Blanc off Spanish Sahara and Cape Timiris off Mauritania have been investigated by major oceanographic expeditions of several countries. The discussion will be directed toward the research in the area of Cape Blanc where the most information was collected on the JOINT-I cruise (Barber, 1977). For details of zooplankton and nutrient recycling in the upwelling region off Cape Timiris, consult Herbland, Le Borgne and Voituriez (1973), Le Borgne (1973), and Le Borgne (1978).

Zooplankton

The distribution of zooplankton across the shelf off Cape Blanc (Fig. 1) was determined using vertical tows of bongo nets equipped with 102 μm mesh netting (Blackburn, 1975). The samples were corrected for phytoplankton contamination using chlorophyll as an index. The cross shelf transect of all four size fractions (>1000 μm, 505-1000 μm, 223-505 μm, and 102-223 μm) showed maxima inshore and immediately offshore of the shelf break (Fig. 2). The inshore maximum was located in about 45 m water depth while the offshore position was about 200 m. The total biomass was largest (13.19 g dry wt. m^{-2}) offshore (Table 1) which was probably the result of large number of euphausiids. The inshore maximum in zooplankton biomass (3.78 mg dry wt. m^{-2}) was dominated by the 223-505 μm size class and was composed mainly of copepods. Excretion rate measurements ranged from 1.68 to 32.26 μg N mg dry wt.$^{-1}$ d^{-1} for ammonium excretion and 0.67 to 5.38 μg N mg dry wt^{-1} d^{-1} for urea release (Table 2). When the excretion rates were combined with biomass values at each of the locations, the regeneration rates of zooplankton across the shelf (Table 3) were largest at the areas of high zooplankton biomass both inshore and offshore. The inshore was relatively larger than the offshore as a consequence of the smaller organisms located there and the shallow depth. An independent estimate of zooplankton ammonium excretion using respiratory electron transport activity had a mean value equivalent to 4.75 mg-at m^{-2} d^{-1} (Packard, in press), a value that is only slightly smaller than the mean of 5.4 mg-at m^{-2}d^{-1} calculated for the four inshore shelf locations.

Nekton

Nekton biomass was determined in the Cape Blanc area by acoustic mapping surveys and bottom trawls. Results of the acoustic surveys indicated that the mean pelagic biomass over the shelf was 40 to 60 g wet weight m^{-2} (Thorne et al., 1977). Analysis of fish egg and larvae samples further indicated that the relative abundance of sardines and anchovies in the study area was about 4:1 (Blackburn and Nellen, 1976). Demersal fish stocks, sampled by bottom trawls, were estimated to be 2.2 g wet weight m^{-2}, cephalopods were about 1 g wet weight m^{-2} and shrimp were about 1.44 g wet wt m^{-2} to give a total of 4.7 g wet weight m^{-2} for demersal biomass (Haedrich, Blackburn, and Brulhet, 1976 ~~1975~~). This is about an order of magnitude smaller than the pelagic biomass estimates.

Nekton excretion rate measurements were made in experiments using several kinds of demersal and pelagic fish, sharks, and mollusks (Table 4). Samples for nitrogen compounds like ammonium, urea and total nitrogen were collected every 10 minutes. The sample concentrations in the experimental tank showed a nearly linear increase with time (Fig. 3) with ammonium accounting for more than 50% of excreted nitrogen. These rate measurements ranged from 0.42 to 4.62 $\mu g\ NH_4\text{-}N\ mg\ dry\ wt^{-1}\ d^{-1}$. Excretion rates were combined with biomass values to produce nutrient regeneration estimates over the shelf and beyond the shelf break (Table 5). The nekton nitrogen regeneration was largest near the outer part of the shelf by a factor of 2. The ammonium and urea nitrogen regeneration rates by nekton are equal in size in contrast to zooplankton which regenerate mostly ammonium.

Sediments, Benthos, and Bacterioplankton

Nutrient release into the water column from sediments was investigated by placing bell jars on the bottom, collecting box cores, and obtaining pore water nutrient samples (Rowe, Clifford, and Smith, 1975). The bell jar experiments indicated that 5.64 $mg\cdot at\ NH_4\text{-}N\ m^{-2}\ d^{-1}$ is released into the water column (Table 6). This quantity is nearly equivalent to the zooplankton regeneration rate at the nearest inshore station. There are only two stations so the variability may be quite large. However, station 171 which had a larger ammonium flux rate than station 162 also had a larger ammonium gradient between the water column and the sediments (Fig. 4). The sediment subsurface ammonium concentrations (pore water) were about 150 $\mu gat\ l^{-1}$ in the top 20 cm (Fig. 5). This indicates the benthic release of ammonium is probably very constant over time with the possible exception of reduced rates when the temperature decreases.

The impact of bacteria in the Northwest Africa upwelling ecosystem was investigated by Watson (1978) using a new bacterial biomass technique. It was found that phytoplankton biomass in the water column was much larger in the shallow shelf stations while bacteria had the greater biomass when water depths were larger than 350 m. Analysis of microbial activity in the sediments indicates that there is a larger percentage of bacterial organic carbon in the sediments on the shallow shelf stations than samples collected on the slope. It was estimated that the mean bacterial biomass of the shelf and slope regions of 6.68 g C m^{-2} was about 10% of the yearly amount of carbon incorporated into bacterial cells. This could result in a yearly consumption of 133 g C m^{-2} which is 44% of the yearly phytoplankton productivity. On a daily basis this would recycle about 0.06 μgat N l^{-1} d^{-1} assuming a C:N ratio of 5 by atoms. This value is included in the sediment release rate estimate since the bell jar technique measures the net change over the sampling duration.

Nutrient Regeneration Budget

The major ecosystem components related to regeneration processes are summarized in Table 7 for two areas of the Northwest African upwelling system. The inshore area represented by station "R" is located in a water depth of about 40m. The zooplankton are dominated in biomass by copepods of 223-505 μm size range so their recycling rate is relatively large compared to the mid shelf region. Nekton biomass is lower than the shelf break area where most of the pelagic biomass was located. The release rate of the sediments was measured directly in bell jars and was similar to the nekton recycling rate. Bacterial recycling estimates were not used because the major fraction of bacterial biomass is located in the sediments rather than the water column so that rate should be already included as part of the sediment release rate. The total recycling rate of 16.9 mg-at N m^{-2} d^{-1} is quite large compared to the measured phytoplankton ammonium uptake rate of 7.5 mg-at m^{-2} d^{-1}. Thus the total recycling rate of all of the trophic levels represents 225% of the phytoplankton ammonium requirement and produces large concentrations of ammonium nearshore (Fig. 6). This oversupply of available ammonium has been noted previously in the nearshore area off Cape Blanc (Coste and Slawyk, 1974; Codispoti and Friederich, 1978). The relatively low phytoplankton uptake rate due to poor in situ light conditions is most likely the causal factor for the large observed ammonium concentrations (Huntsman and Barber, 1977).

The outer shelf region near the position of Station "O" has one of the lowest zooplankton biomasses of the transect and contains a mixture of large and small organisms. The zooplankton regeneration rate is about 70% of the inshore value. The nekton rate, however, is nearly twice as large as the inshore estimate as a result of the large pelagic nekton biomass in this region. The release of nitrogen from the sediments has been decreased to 33% of the inshore value based largely on the lower sediment bacterial biomass estimates offshore (Watson, 1978). Nutrient pore water concentrations decreased offshore also. The total recycling rate in this deep shelf region is 13.68 mg-at m^{-2} d^{-1}. This is 84% of the 16.2 mg-at m^{-2} d^{-1} phytoplankton uptake rate estimates.

PERU

Several sets of data have been collected in the Peru upwelling ecosystem during the years 1966, 1969, 1976, and 1977. Most of the descriptions have been taken from the years 1976 and 1977 when zooplankton rate measurements were collected. Unfortunately in those latter years the anchoveta biomass had been reduced drastically to about 10% of its previous amount. This decrease in biomass has probably been accompanied by other changes in the nekton stocks such as increases in the biomass of sardine and hake. There are also probable increases in the zooplankton biomass after the decline of anchoveta biomass (Walsh et al., in press).

Zooplankton

The zooplankton stocks were determined for the Peru upwelling ecosystem at 10°S and 15°S using vertical bongo net tows (Dagg et al., in press). The zooplankton dry weight biomass at 10°S where the shelf is relatively wide was larger than 8 g m^{-2} inshore. This is certainly an overestimate on the two innermost stations because of phytoplankton contamination (Fig. 7). The numerical counts were dominated by Paracalanus spp., Oncea spp., Oithona spp., and Appendicularia (Judkins, in press; and Geynrikh, 1973). Just offshore of the shelf break which is located at about 100 km the >1050 μm size class shows an increased number of Calanus. Zooplankton dry weight biomass was larger on the 15°S transect where the shelf is only about 25 km wide (Fig. 8). More larger types of zooplankton were found at most stations at 15°S such as Eucalanus inermis, Centropages brachiatus and Calanus chilensis. These three species average 31% of the biomass on the 15°S transect and 9.6% on the 10°S transect. The dry weights of zooplankton over the shelf was similar at 10°S and 15°S. The shelf is nearly 100 km wide at 10°S with a mean ± standard deviation dry weight biomass of 2.30 ± 0.53 g m^{-2} (Table 8). At 15°S the shelf is about 25 km wide and has a biomass of 3.76 ± 2.23 g m^{-2}, an increase of about 60%. In the offshore area beyond the shelf break there is an increased biomass at 10°S to about 3.23 ± 0.81 g m^{-2}, however, at 15°S the mean dry weight is 9.53 ± 5.36 g m^{-2}, an increase of 295%. In general this conforms to the distribution of zooplankton observed in the same area in 1978 (Timonin and Flint, this issue).

An alongshore transect over the shelf at 15°S shows the range of the alongshore variability in zooplankton biomass (Fig. 9). This range from 6.5 to 18 g dry wt m^{-2} is similar in distribution to alongshore variations in chlorophyll concentrations (Walsh et al., in press) which may vary by an order of magnitude alongshore.

Time series stations were occupied for two days at 3 locations along the 15°S across shelf transect to investigate the temporal variability of zooplankton biomass. The inshore time series station was occupied near the shelf break in 118 m of water (Fig. 10). There is a suggestion of vertical migration in the time series for the >1050 μm size category. The maximum total zooplankton biomass measured on this station was about 45 g dry weight m^{-2}. Further offshore the next time series was located in 480 m of water and the >1050 μm size zooplankton very definitely exhibited diel vertical migration on both nights just after midnight with identical maxima of about 20 g dry weight m^{-2} (Fig. 11). At the offshore end of the transect the time series station had a reduced zooplankton biomass of about 8 g dry weight m^{-2} with no vertical migration (Fig. 12).

Zooplankton excretion rate measurements were collected on large sized organisms that were being studied in ingestion experiments (Table 9). The rate of release ranged from 4.4 to 29.9 μg N mg dry wt^{-1} d^{-1} for ammonium and 0.63 to 21.9 μg N mg dry wt^{-1} d^{-1} for urea. Both of these ranges are similar to measurements collected in the Northwest Africa upwelling experiments. The size class excretion rates were also determined in 1976 at the same location (Table 10). The rates are nearly identical to those for Northwest Africa (Table 2) with the exception of the smallest size class of 102-223 μm which is about 50% larger than the same size range in Northwest Africa.

Nekton

The nekton stocks inhabiting the Peru upwelling ecosystem has been the focus of attention since the decline in the anchoveta biomass and with the introduction of acoustic surveys of the total pelagic fish stocks. Speculation exists on the quantity of anchoveta remaining and the possible increase of hake and sardine (Walsh et al., in press). Acoustic methods were used to estimate the total pelagic nekton biomass in the study area at 15°S (Fig. 13). Zig-zag mapping tracks were followed both day and night. In the area within 13 km of the coast (to about the 150 m isobath) there was an estimated mean of 127 g wet weight pelagic nekton biomass m^{-2} which was probably composed of anchovy and sardine (Lee, Mathisen, and Thorne, 1979). Between 13 and 26 km offshore (within the 150-700m isobaths) there was about 83.3 g wet weight m^{-2} of pelagic nekton which were thought to be jack mackerel, mackerel and saury. These estimates are subject to daily variations, but nevertheless represent a composite of several runs.

The excretion rate measurements of some of the pelagic nekton were made on the anchoveta (Engraulis ringens), sardine (Sardinops sagax), and silverside (Austromenidia regia regia) (Table 11) using the methods described by Whitledge (1978). An additional measurement for jack mackerel (Trachurus symmetricus) was collected off California (McCarthy and Whitledge, 1972). The largest ammonium excretion value measured on the silverside (5.2 μg N mg dry wt^{-1} d^{-1}) was comparable to the rate measured for Sardinella spp. off northwest Africa while the sardine and anchoveta excreted 2.2 and 1.7 μg N mg dry wt^{-1} d^{-1}.

Nutrient Regeneration Budget

A nitrogen budget for the shelf and offshore Peruvian upwelling areas at 15°S was constructed using the nekton ammonium excretion rates combined with mean nekton biomass estimates (Table 12). The calculation assumed all the inshore nekton biomass was anchoveta since there is not a good estimate of sardine biomass available. The shelf nitrogen budget, which used the 3 stations nearest inshore, estimated the zooplankton regeneration rates to be 4.11 mg-at m^{-2} d^{-1} (Table 8). The loss of ammonium from the sediments based on ^{35}S

experiments, estimated the quantity of carbon utilized by the bottom community to be ∿180 g C m^{-2} y^{-1} (Rowe, personal communication). Converting to nitrogen using a C:N ratio of 5, about 8.3 mg-at N m^{-2} d^{-1} is released from the sediments. The sediments are relatively rich in carbon, i.e. the C:N ratio in sediments are greater than 5 so this could be an underestimate. The ammonium-N regeneration of 12.1 mg-at m^{-2} d^{-1} compares favorably with the measured ammonium uptake rate of about 15 mg-at m^{-2} d^{-1} as estimated by N^{15} uptake measurements (unpublished results of MacIsaac and Dugdale). The difference between these two estimates (∿2.9 mg-at m^{-2} d^{-1}) is about 19%, a value near the expected experimental variability.

The offshelf nitrogen budget used the offshore pelagic nekton biomass estimate and jack mackerel excretion rates. The demersal nekton regeneration rate used an estimated standing stock for hake (Gullard, 1970) and excretion rates for a starry flounder (Wood, 1958). The resulting regeneration rate for demersal stocks is very low (0.07 mg-at m^{-2} d^{-1}) but the biomass estimate of 60,000 metric tons for the whole Peru upwelling area (∿4.3 g dry wt m^{-2}) may be low. The zooplankton ammonium regeneration rate, calculated using the five offshore stations (Table 8), was 7.33 mg-at m^{-2} d^{-1}. This rate was larger than the shelf value (∿178%) mainly because of the large zooplankton biomass just offshore of the shelf break.

The release of ammonium from the sediments was made the same as the shelf value because there were no strong offshore gradients in the ^{35}S data used to estimate the sediment release rates. The total quantity of 13.28 mg-at ammonium-N m^{-2} d^{-1} regenerated in the offshore region is 74% of the measured phytoplankton ammonia uptake rate of 17.88 mg-at m^{-2} d^{-1} (MacIsaac and Dugdale, unpublished results).

Distribution of Recycled Nutrients

As a result of the relatively large quantity of regenerated ammonium recycled by the resident biological population in the Peruvian upwelling ecosystem the ambient concentrations of ammonium and other substances are often quite large (Fig. 14a-14b). The cross shelf distribution of ammonium and urea at 15°S and 10°S (Figs. 14a-14d) each show a maximum concentration about 50 to 100 km offshore. At 15°S the maximum for ammonium and urea is beyond the shelf break located at 25 km and is located at the surface. The elevated concentrations of ammonium and urea occur over the shelf at 10°S (shelf break at ∿ 90 km) and are located near the bottom of the euphotic zone. Careful examination of the urea distributions at 15°S and 10°S reveal that the maxima are located inshore of their respective ammonium maxima. This could be the result of different utilization pattern for ammonium and urea. Previous measurements have shown that urea may be utilized in primary productivity almost as rapidly as ammonium and nitrate (McCarthy, 1972). An alternate explanation could be related to the relative rates of release of ammonium and urea by nekton and zooplankton populations. The percentage of urea in excreted nitrogen is larger for nekton than for zooplankton (Table 5) and the nekton ammonium excretion over the shelf is nearly the same as for zooplankton (4.11/3.86 = 106%), while offshore the zooplankton regeneration is comparatively much larger (7.33/1.72 = 426%). So the urea maximum inshore is probably regenerated by the anchovy and sardine populations while the more offshore ammonium maximum is created by zooplankton.

The distributions of total nitrogen (the sum of nitrate, nitrite, ammonium, and urea) across the shelf at 15°S and 10°S (Fig. 14e and 14f) show the dominance of the upwelling of nitrate laden water near the coast and decreasing concentrations in the surface layers as the water mass moves offshore.

The surface water nearshore at 15°S displays a relatively wide band of water containing more than 25 μg at l^{-1} total nitrogen with a sharp gradient where the concentration decreases to less than 5 μg at l^{-1} at about 125 km offshore. The nearshore area at 10°S doesn't appear to be upwelling as rapidly as at 15°S. This may be a result of the much wider shelf at 10°S which would affect the residence time of the water over the shelf. Consequently the nitrogen could go through uptake-regeneration pathways more times while over the shelf. This would suggest the upwelling area off 10°S might be more dependent on regenerated nitrogen than the region off 15°S.

The relative amounts of regeneration is demonstrated well in the percent regenerated nitrogen in the water column (ammonium plus urea/total nitrogen). The nitrogen at 15°S is less than 10% regenerated nitrogen in the nearshore area where the nitrate concentrations are high (Fig. 14g), but the percentage increases to greater than 50 beyond the shelf break. In a similar fashion at 10°S the inshore water has a low percentage of regenerated nitrogen but increases to greater than 90% in the surface layer at the shelf break (Fig. 14h).

Dissolved organic nitrogen (DON) as measured by the ultraviolet irradiation technique (Armstrong, Williams, and Strickland, 1966) exhibits a distribution with uniformly high concentrations nearshore as if the source of DON was in deep water and lower concentrations were observed offshore where uptake may have occurred (Fig. 15). The distribution of DON is distinctly different than ammonium or urea distributions so the source of DON must not be pelagic organisms. The bottom sediments of the shelf could be a source, however, no known measurements exist in this area.

BAJA CALIFORNIA

The upwelling off Baja California is seasonal with strong upwelling starting in March or April (Walsh et al., 1974). So the biological populations have adapted to an area where upwelling occurs for only part of the year and is structured to withstand fluctuations in available food. In the upwelling area off Baja California a pelagic red crab, Pleuroncodes planipes, is probably the dominant herbivore during the upwelling season (Walsh et al., 1977). During the nonupwelling time of the year the red crabs can remain on the bottom and switch to detritus as an alternate food source (Boyd, 1962).

Zooplankton

The zooplankton biomass range during the two spring samplings in March 1972 and April 1973 was 0.2 to 1.0 g wet weight m^{-3} and was composed principally of stage V nauplii of Calanus helgolandicus the first year. The second year consisted of 72% copepodites, 22% adult Acartia and 6% Calanus with an estimated biomass of 1.15 g wet wt m^{-3}. So it appears that the zooplankton biomass in the Baja upwelling system increases from about 1.15 to 6.38 g dry wt m^{-2} during the spinup of upwelling. Ammonium excretion rates for this population of zooplankton was estimated to be 14.3 μg N mg dry wt^{-1} d^{-1} (Martin, 1968) and were combined with the biomass to estimate ammonium regeneration.

Micronekton

The red crab, Pleuroncodes planipes, was estimated with acoutic gear (Fig. 16) to have a pelagic wet weight biomass of 100 g m^{-2} (Blackburn and Thorne, 1974) although earlier in the cruise a series of net tows estimated the biomass to be $\sim$ 5 g wet weight m^{-3}. The previous year biomasses as high as 7 g wet weight m^{-3} were observed (Walsh et al., 1977). The March biomass of the red crab is about 7 g wet weight m^{-3} and the April biomass is ∿5 g wet weight m^{-3}. An excretion rate of 2.9 μg N mg dry wt^{-1} d^{-1} was used (Walsh et al., 1977) in ammonium regeneration rate calculations.

The red crabs also gather in large populations on the bottom, especially those 3 years or older (Boyd, 1962; Smith et al., 1974). Bottom photographs were used to estimate a density of about 8.2 red crab m^{-2} of bottom and the mean weight of these benthic crabs were 5.58 g $animal^{-1}$ (Walsh et al., 1977) so there was about 8.06 g dry wt m^{-2}.

Nekton

The net hauls used to calibrate the acoustic assessment surveys of nekton and micronekton in the Baja California upwelling region found that Pleuroncodes planipes and the northern anchovy, Engraulis mordax, inhabited the area in a ratio of 9:1 by weight (Blackburn and Thorne, 1974). This is a biomass of about 2.5 g dry wt m^{-2}.

Nutrient Regeneration Budget

A nitrogen budget for the shelf area of the Baja California upwelling system was constructed for the time periods of March and April (Table 13). The budget for March has a relatively small zooplankton ammonium regeneration rate of 1.2 mg-at m^{-2} d^{-1}. The pelagic red crabs recycled 12.7 and the benthic red crabs recycled 1.68 for a total of 14.38 mg-at m^{-2} d^{-1}. The regeneration from the small biomass of anchovies was about 0.30 mg-at m^{-2} d^{-1}. The carbon utilized by benthic respiration was estimated to be 200 mg m^{-2} d^{-1} so the nitrogen release rates from the sediments was 2.86 mg-at N m^{-2} d^{-1} if a C:N conversion factor of 5 is used (Rowe, personal communication).

The April budget has a larger zooplankton regeneration rate (6.28 mg-at m^2 d^{-1}) than March because the biomass had increased almost five fold. The pelagic red crab regeneration decreased to 9.1 and the benthic estimate remained constant at 1.68 for a total of 10.78 mg-at ammonium released m^{-2} d^{-1} by all of the Pleuroncodes. The drop in red crab regeneration in April was due to the loss of red crab biomass, possibly to foraging tuna. The anchovy biomass and nitrogen release from the sediments remained the same as March. A total of 20.22 mg-at ammonium-N m^{-2} d^{-1} was regenerated each day. The phytoplankton uptake of ammonium at this time was estimated to be 17.5 mg-at m^{-2} d^{-1} (Whitledge and Conway, 1977), an excess of 16% of ammonium produced.

IMPORTANCE OF REGENERATION IN UPWELLING AREAS

Nutrient regeneration in a stable environment like the euphotic zone in the middle of an oceanic gyre has been considered vital to maintain low levels of productivity. The regenerated nutrients are thought to cycle through the nutrient-phytoplankton-zooplankton chain several times before they are lost from the upper mixed layer in the form of sinking or swimming particles. This regeneration lengthens the time and possibly the spatial scales of the original nutrient input. The same process occurs in upwelling areas even though very strong upwelling brings enormous quantities of new nutrients into the euphotic zone. At what space and time scale would all of the upwelled nutrients be stripped from the water column? Our experience shows that it would not be many kilometers (perhaps 20-50 km) before the nutrients would be converted to plant material. So regeneration of nutrients in an upwelling area is an important process that extends the upwelling effect to longer spatial and temporal scales. One of the best examples of this effect was observed on the Anton Bruun cruise 15 to Peru in 1966. A drogue was placed near an upwelling center and it was followed from the high nitrate-low chlorophyll water to low nitrate-high chlorophyll water (Fig. 17). The ammonium increased during the latter part of the drogue observation where it could be measured in large quantities. This increase in ammonium was observed because dissolved silicon was depleted, therefore the diatom population was placed under silica limitation. On most occasions when dissolved silicon is not limiting, high concentrations of ammonium are not observed because it is used as rapidly as it is recycled.

As the newly upwelled water enters the euphotic zone the principal form of nitrogen in the water is nitrate (Fig. 18a). With some delay the phytoplankton start active uptake of the nitrate to increase the phytoplankton biomass. As this occurs there is usually a strong advective flow alongshore (often equatorward)and a smaller advective flow offshore. This Ekman flow of nutrients and phytoplankton gives the appearance of a plume of chlorophyll if the origin is a point source. (Fig. 18b). This plume is in effect the isolines of nutrient concentrations as they decrease or phytoplankton as they increase while they are being advected and diffused along. A large zooplankton biomass appears at the fringes of the plume although some zooplankton are in the freshly upwelled water and they increase in numbers along with the chlorophyll content until the nutrients are reduced to low levels. This is when regeneration is important in maintaining phytoplankton growth. Eventually the ecosystem loses all of the inorganic nitrogen because a fraction is lost at each step in the food chain as a result of biological inefficiencies or loss of sinking and swimming particles.

Simulation models constructed to mimic nutrient-phytoplankton-zooplankton relationship in various ecosystem (Dugdale and Whitledge, 1970; Dugdale and Walsh, 1971; and Walsh, 1975) have incorporated ammonium uptake as an intergral part of the nutrient-phytoplankton relationship. If ammonium is omitted and phytoplankton growth is simulated using only nitrate the resulting standing crop of phytoplankton never reaches observed concentrations. So even in areas with small concentrations of ammonium, phytoplankton growth is enhanced by ammonium uptake.

An additional aspect of zooplankton excretion in the ocean should be considered with regard to "water conditioning". The loss of substances from zooplankton may be a potential factor that "conditions" water and makes it suitable for phytoplankton growth (Barber and Ryther, 1969). Although it is debatable whether the substances chelate potentially toxic elements and render them harmless or enhance the ability to gather needed trace constituents, it appears that regeneration may have some secondary effects in promoting primary productivity.

In terms of the percentage of phytoplankton production that utilizes regenerated nitrogen upwelling areas have rates very comparable to most other coastal and estuarine systems that do not have appreciable upwelling. The upwelling areas discussed previously have 42 to 72 percent of total nitrogen productivity being supplied by regeneration (Table 14). This rather narrow range of values implies that regeneration must be a rather stable and constant feature of upwelling ecosystems. The upwelling areas investigated are very productive and rank among the highest in terms of fish production.

The zooplankton ranks as the group of organisms which recycle the major fraction of nitrogen in upwelling ecosystems, although zooplankton were not as important in the Peru upwelling ecosystem when the anchoveta stocks were large (Beers et al., 1971; Whitledge and Packard, 1971; and Dugdale, 1972). The importance of zooplankton varies somewhat between the different regions which is probably a clue to pathways of material flow through the different upwelling ecosystems. The largest percentage of zooplankton nitrogen recycling occurred in the Cape Blanc N.W. African ecosystem and was slightly smaller in Peru, Cape Timiris off N.W. Africa and Baja California, with a range for the three systems from 3 to 33 per cent. The larger values occurred after the spin-up of upwelling had been completed for each of the areas while the low value in March for Baja California was collected as the seasonal upwelling was starting. This lag in time may be likened somewhat to the spatial lag that produces a plume downstream from an active upwelling center. So after upwelling conditions have stabilized it appears that 20-30% of primary productivity is driven by ammonium recycled by zooplankton.

A contrary idea of the importance of ammonium regeneration by zooplankton was presented by Jawed (1973) for the nearshore summer upwelling areas off Washington and Oregon. He concluded that ammonium regeneration was not a crucial nitrogen source in the upwelled waters. However no nitrogen uptake rate studies were undertaken so the actual use of ammonium could have been substantial since large quantities of ambient ammonium were observed in the water column. Evidently he presumed that large concentrations of nitrate reduces the importance of ammonium in the ocean.

The regeneration of ammonium by nekton is most important in the two upwelling systems where commercial quantities of small pelagic nekton exist. Since the decline in the anchoveta biomass, Peru has slightly smaller regeneration rates than N.W. Africa while the clupeid population is very small off Baja California. Micronekton are important in the Baja California ecosystem because the red crab has taken the herbivore-omnivore role of the clupeid in the other two upwelling areas. Demersal fish play an insignificant role in the recycling of nutrients according to the best data, however a thorough examination has not been reported for any areas with large benthic fish populations.

The regeneration of nitrogen from the sediments appear to be most important in N.W. Africa and Peru although the rates are only slightly smaller for Baja California. Large amounts of organic material are thought to sink to the bottom in Peru where the sediments have a high organic carbon content. A substantial quantity of organic material may also sink in Baja California, however, the older benthic red crabs are possibly using that as a principal means of support. More details of sediment-water column interactions can be found in the chapter by Rowe in this volume.

The zooplankton studied were mesoplankton so all protozoa, ciliates and nauplii were excluded from the measurements. There are indications that microplankton may be very important in upwelling ecosystems although there is some difference of opinion of various investigators. Energy budgets for equatorial upwelling regions show heterotrophic respiration constituted 90% of the total (Sorokin, 1979) and in the coastal upwelling region constituted 30 to 90% of the total (Sorokin et al., this issue). So the focus of zooplankton sampling may have missed a significant component in the upwelling ecosystem.

Regeneration studies in non-upwelling area have mainly focused their attention on zooplankton (Corner and Davies, 1971). However, Harris (1959) in his study on Long Island Sound found that zooplankton recycling was responsible for 43-66% of nitrogen utilized in primary production and the benthic input accounted for 9-12%. Similarly Martin (1968) estimated zooplankton in Naragansett Bay regenerated 64% of nitrogen utilized by phytoplankton. Both of these areas are often depleted of nitrate in the upper euphotic zone after the spring bloom, the sediments are in close proximity to the euphotic zone and circulation is relatively sluggish. In effect the zooplankton cannot migrate to deep layers and particulate material which sinks in the shallow water reaches the bottom quickly and can be rapidly returned to the euphotic zone. Any recycled nutrients are in the immediate vicinity of nitrogen limited phytoplankton cells so the effect is a closely coupled nutrient uptake-regeneration cycle.

The importance of nutrient recycling in coastal shelf waters found that recycling supported 36% of the productivity off the N.W. Coast of the United States (Jawed, 1973). This value is comparable to the upwelling region estimates but only zooplankton were included. The overall amount for the continental shelf off Washington and Oregon may be somewhat smaller because fish biomass is small and nutrient release from the sediments have not been reported.

The importance of regeneration in the open ocean was studied in the north Pacific gyre where zooplankton was found to produce 44-83 per cent of phytoplankton nitrogen requirements (Eppley et al., 1973). This study used comparable methods to those employed in the upwelling regions. The investigators measured all the dissolved forms of inorganic nitrogen plus urea, phytoplankton biomass, uptake of ammonium, nitrate and urea using ^{15}N techniques, zooplankton biomass and excretion rates. The turnover time for ammonium was found to be 3-5 days and the phytoplankton crop was very small so it was concluded that grazing was important in keeping the phytoplankton below maximum possible levels. The remaining 17-56 per cent of nitrogen needed to fulfill phytoplankton requirements was explained as possibly coming from micro-zooplankton smaller than 183 m or from vertical turbulent diffusion. Urea was also considered to be an important nitrogen source.

The importance of ammonium regeneration has not been measured directly in the Sargasso Sea but an investigation in the temporal variation of ammonium concentrations suggested that zooplankton were responsible for the variations observed (Beers and Kelly, 1965). Preliminary computer simulations in the Sargasso Sea also indicated the importance of ammonium to productivity processes (Walsh, 1977).

Future Directions

Our knowledge of nutrient recycling in the sea is very fragmentary. The initial work on the excretion of organisms was associated with physiological studies investigating the type and amount of excreted nitrogenous substances and their importance to the biochemistry of the organism. The first ecosystem approach to the importance of nutrient recycling by organisms was the now classic work of Harris (1959) in Long Island Sound. Since that time the number of studies in various marine ecosystem examing zooplankton regeneration has increased markedly. Other organisms such as fish were ignored until Dugdale and Goering (1970) proposed that the anchoveta in Peru recycle large quantities of nitrogen. Subsequently Whitledge and Packard (1971) presented an estimate of relatively large nitrogen recycling rates by the anchoveta. Similarly the sediments as a source of recycled nutrients has only recently been examined (Rowe et al., 1977) and shown to be significant. Now that these various elements in a few scattered upwelling areas have been examined their potential importance has been shown but not proven. The comprehensive examination of the pathways of nutrient recycling in marine ecosystems has not been attained. The lack of data is apparent in the partially filled Table 14, which can be a starting place for assessing needs in terms of future research in nutrient recycling. A short comment will be made about each of the deficiencies in Table 14 listed in their approximate order of importance.

1. Benthic sediments, bacteria and meiofauna.

These items are listed together because it is difficult experimentally to separate them. Using standard bell jar techniques a net composite rate is measured. The problems that arise are not necessarily associated with present methods, but while present equipment is readily available it is cumbersome and costly. A large number of in situ measurements is probably the best approach rather than removal-incubation techniques which are subject to difficult systematic errors like temperature and pressure changes.

2. Microzooplankton.

Recycling, ingestion rate, and biomass measurements of microzooplankton are missing from most oceanic areas because of the difficulties of sampling and subsequent handling although their importance has been suggested (Beers and Stewart, 1969). Highly productive upwelling areas with large concentrations of phytoplankton make the problems impossibly difficult using today's techniques exept for hand-picking using a microscope. The small number of biomass and rate estimates that exist are often contradictory. Included in this group are marine protozoa (Johannes, 1965) and the early stages of larger zooplankton.

3. Jellies, ctenophores and chaetognaths.

Recent work on the distribution, respiration and ammonium excretion of oceanic jellies (Biggs, 1977) and earlier work on Sagitta hispida (Beers, 1964) indicates that the importance of these predators can be significant in the recycling of nutrients. Unusually large concentrations of those carnivores are often encountered in both coastal and open ocean environments but we are seldom equipped to adequately study them.

4. Demersal Fish.

The importance of recycling demersal fish stocks has not been addressed in the open literature. Biomass assessment has been exhaustively taken but there has been an omission of their effect on the ecosystem. Admittedly, most large demersal fish stocks are being exploited to some degree so their biomass is probably reduced from earlier times. However, fishing could increase the recycling rate as it does the growth rate because like growth, excretion is exponentially related to body size. Macrobenthos such as crabs, starfish, sea urchins, and lobsters should be included in this group.

5. Bacterioplankton.

Bacterioplankton in the marine environment has been examined for a number of years but an easy trouble-free technique for measuring bacterial biomass and metabolism has not been developed. In areas with large amounts of particulate matter and high temperatures bacterioplankton may contribute significantly to the nutrient budgets.

6. Mollusks.

The population estimates of swimming mollusks like cephlalopods are often large yet little is known about their feeding and excretion rates. In areas where the largest populations exist, specimens should be collected, excretion measurements made and budget constructed to assess their potential impact.

ACKNOWLEDGMENTS

The research was sponsored by both the International Decade of Ocean Exploration (IDOE) of the National Science Foundation under grants OCE78-05737, OCE75-23721, and GX33502 as part of the Coastal Upwelling Ecosystems Analysis (CUEA) program, and by the Department of Energy (DOE) under contract No. EY-76-C-02-0016 as a part of the Atlantic Coastal Ecosystem (ACE) program. The author is indebted to G. Friederich and C. J. Patton for nutrient analyses, to Dr. H. L. Conway for dissolved organic nitrogen analyses, and to Dr. R. C. Dugdale and J. J. MacIsaac for unpublished nitrogen uptake rates.

REFERENCES

Armstrong, F. A. J. P. M. Williams and J. D. H. Strickland, 1966: Photo-oxidation of organic matter in seawater by ultraviolet radiation. Nature, 211, 481-483.

Barber, R. T., 1977: The JOINT-I expedition of the coastal upwelling ecosystems analysis program. Deep-Sea Res., 24, 1-6.

Barber, R. T. and J. H. Ryther, 1969: Organic chelators: Factors affecting primary production in the Cromwell current upwelling. J. exp. mar. Biol. Ecol., 3, 191-199.

Beers, J. R., 1964: Ammonia and inorganic phosphorus excretion by the planktonic chaetognath, *Sagitta hispida* Conant. J. Cons. Int. Explor. Mer, 29, 123-129.

Beers, J. R. and A. C. Kelly, 1965: Short-term variation of ammonia in the Sargasso Sea off Bermuda. Deep-Sea Res., 12, 21-25.

Beers, J. R. and G. L. Stewart, 1969: Micro-zooplankton and its abundance relative to the larger zooplankton and other seston components. Mar. Biol., 4, 182-189.

Beers, J. R., M. R. Stevenson, R. W. Eppley and E. R. Brooks, 1971: Plankton populations and upwelling off the coast of Peru, June 1969. Fish. Bull., 69, 859-876.

Biggs, D. C., 1977: Respiration and ammonium excretion by open ocean gelatinuous zooplankton. Limnol. Oceanogr., 22, 108-117.

Blackburn, M. and W. Nellen, 1976: Distribution and ecology of pelagic fishes studied from eggs and larvae in an upwelling area off Spanish Sahara Fish. Bull., 74, 885-895.

Blackburn, M. and R. Thorne, 1974: Composition, biomass and distribution of pelagic nekton in a coastal upwelling area off Baja California, Mexico. Téthys, 6, 281-290.

Boyd, C. M., 1962: The biology of a marine decopod crustacean, *Pleuroncodes planipes* Stimpson, 1860. Ph.D. thesis, Univ. Calif., San Diego. 123 pp.

Codispoti, L. A. and G. E. Friederich, 1978: Local and mesoscale influences on nutrient variability in the northwest Africa upwelling region near Cabo Corbeiro. Deep-Sea Res., 25, 751-770.

Corner, E. D. S. and A. G. Davies, 1971: Plankton as a factor in the nitrogen and phosphorus cycles in the sea. Adv. mar. Biol., 9, 101-204.

Coste, B. and G. Slawyk, 1974: Structures de répartitions superficielles des sels nutritifs dans une zone d'upwelling (Cap Corveiro, Sahara espagnol). Téthys, 6, 123-132.

Dagg, M., T. Cowles, T. Whitledge, S. Smith, S. Howe and D. Judkins, 1979: Grazing and excretion by zooplankton in the Peru upwelling system during April 1977. Deep-Sea Res. (in press).

Dugdale, R. C., 1972: Chemical oceanography and primary productivity in upwelling regions. Geoforum, 11, 47-61.

Dugdale, R. C. and J. J. Goering, 1970: Nutrient limitation and the path of nitrogen in Peru current production. Anton Brunn: Rep. No. 4, Texas A and M Press, P. 5.3-5.8.

Dugdale, R. C. and T. Whitledge, 1970: Computer simulation of phytoplankton growth near a marine sewage outfall. Rev. Intern. Oceanogr. Med., 17, 201-210.

Eppley, R. W., E. H. Renger, E. L. Venrick, and M. M. Mullin, 1973: A study of plankton dynamics and nutrient cycling in the central gyre of the north Pacific ocean. Limnol. Oceanogr., 18, 534-551.

Geynrikh, A. K., 1973: Horizontal distribution of copepods in the Peru current regions. Oceanology, 13, 94-103.

Gulland, J. A., 1970: The fish resources of the ocean. FAO Fish. Tech. paper No. 97, Rome, 425 pp.

Haedrich, R. L., M. Blackburn, and J. Brulhet, 1976: Distribution and biomass of trawl-caught animals off Spanish Sahara, West Africa. Matsya, 2, 38-46.

Harris, E., 1959: The nitrogen cycle in Long Island Sound. Bull. Bingham oceanogr. Coll., 17, 31-65.

Herbland, A., R. Le Borgne, and B. Voituriez, 1973: Production primaire et secondaire et regeneration des sels nutritifs dans l'upwelling de Mauritanie. Doc. Scient. Centre Rech. Oceanogr. Abidjan, T.4, 75 pp.

Huntsman, S. A. and R. T. Barber, 1977: Primary production off northwest Africa: the relationship to wind and nutrient conditions. Deep-Sea Res., 24, 25-33.

Jawed, M., 1973: Ammonia excretion by zooplankton and its significance to primary productivity during summer. Mar. Biol., 23, 115-120.

Johannes, R. E., 1965: Influence of marine protozoa on nutrient regeneration. Limnol. Oceanogr., 10, 434-442.

Judkins, D. C., 1979: Vertical distribution of zooplankton in relation to the oxygen minimum off Peru. Deep-Sea Res. (in press).

Le Borgne, R. P., 1973: Etude de la respiration et de l'excretion d'azote et de phosphore des populations zooplanctoniques de l'upwelling Mauritanien (March-April, 1972). Mar. Biol., 19, 249-257.

Le Borgne, R. P., 1978: Ammonium formation in Cape Timiris (Mauritania) upwelling. J. exp. mar. Biol. Ecol., 31, 253-265.

Lee, K. C., O. A. Mathisen, and R. E. Thorne, 1979: Acoustic observations on the distribution on nekton off the coast of Peru. Coastal Upwelling Ecosystems Analysis, Data report 59, Fisheries Research Institute, Univer. of Washington, Seattle, 84 pp.

Martin, J. H., 1968: Phytoplankton-zooplankton relationships in Narragansett Bay. III. Seasonal changes in zooplankton excretion rates in relation to phytoplankton abundance. Limnol. Oceanogr., *13*, 63-71.

McCarthy, J. J., 1972: The uptake of urea by natural populations of marine phytoplankton. Limnol. Oceanogr., *17*, 738-748.

McCarthy, J. J. and T. E. Whitledge, 1972: Nitrogen excretion by anchovy (*Engraulis mordax* and *E. ringens*) and jack mackerel (*Trachurus symmetricus*). Fish. Bull., *70*, 395-401.

Packard, T. T., 1979: Respiration and respiratory electron transport activity in plankton from the northwest African upwelling area. J. Mar. Res. (in press).

Rowe, G. T., C. H. Clifford and K. L. Smith, Jr., 1977: Nutrient regeneration in sediments off Cap Blanc, Spanish Sahara. Deep-Sea Res., *24*, 57-63.

Smith, K. L., Jr., G. R. Harbison, G. T. Rowe and C. H. Clifford, 1975: Respiration and chemical composition of *Pleuroncodes planipes* (Decapoda: Galatheidae): Energetic significance in an upwelling system. J. Fish. Res. Bd. Can., *32*, 1607-1612.

Smith, S. L., 1978: Nutrient regeneration by zooplankton during a red tide off Peru, with notes on biomass and species composition of zooplankton. Mar. Biol., *49*, 125-132.

Smith, S.L. and T. E. Whitledge, 1977: The role of zooplankton in the regeneration of nitrogen in a coastal upwelling system off northwest Africa. Deep-Sea Res., *24*, 49-56.

Smith, S. L. and T. E. Whitledge, 1979: Regeneration of nutrients by zooplankton and fish off northwest Africa. Rapp. Proces-Verb. Cons. int. Explor. Mer. (in press).

Sorokin, Y.I., 1979: Decomposition of organic matter and nutrient regeneration. In: Marine Ecology, Vol. 4., O. Kinne [ed.], John Wiley, New York, p. 501-616.

Thorne, R. E., O. A. Mathisen, R. J. Trumble and M. Blackburn, 1977: Distribution and abundance of pelagic fish off Spanish Sahara during CUEA expedition JOINT-I. Deep-Sea Res., *24*, 75-82.

Walsh, J. J., 1975: A spatial simulation model of the Peru upwelling ecosystem. Deep-Sea Res., *22*, 201-236.

Walsh, J. J., 1977: A biological sketchbook for an eastern boundary current. In: The Sea: Ideas and observations on progress in the study of the seas, E.D. Goldberg [ed.], John Wiley, p 923-968.

Walsh, J. J. and R. C. Dugdale, 1971: A simulation model of the nitrogen flow in the Peruvian upwelling system, Invest. Pesq., 35, 309-330.

Walsh, J. J., J. C., Kelley, R. C. Dugdale and B. W. Frost, 1971: Gross features of the Peruvian upwelling system with special reference to possible diel variation. Invest. Pesq., 35, 25-42.

Walsh, J. J., J. C. Kelley, T. E. Whitledge, J. J. MacIsaac, and S. A. Huntsman, 1974: Spin-up of the Baja California upwelling ecosystem. Limonol., 19, 553-572.

Walsh, J. J., T. E. Whitledge, J. C. Kelley, S. A. Huntsman, and R. D. Pillsbury, 1977: Further transition states of the Baja California upwelling ecosystem. Limnol. Oceanogr., 22, 264-280.

Walsh, J. J., T. E. Whitledge, W. E. Esaias, R. L. Smith, S. A. Huntsman, H. Santander and B. R. DeMendiola, 1979: The spawning habitat of the Peruvian anchovy, Engraulis ringens. Deep-Sea Res. (in press).

Watson, S. W., 1978: Role of bacteria in an upwelling ecosystem. In: Upwelling Ecosystems, R. Boje and M. Tomczak [eds.], Springer-Verlag, Berlin, p. 139-54.

Whitledge, T. E., 1978: Regeneration of nitrogen by zooplankton and fish in the northwest Africa and Peru upwelling ecosystems. In: Upwelling Ecosystems, R. Boje and M. Tomczak [eds.], Springer-Verlag, Berlin, p. 90-100.

Whitledge, T. E. and H. L. Conway, 1977: R/V T.G. Thompson crusie 78 (Mescal II-Outfall II) Part II: Productivity, micronekton biomass, current meters and drogue velocities. Coastal Upwelling Ecosystems Analysis Data Report 37, 143 pp.

Whitledge, T. E. and R. C. Dugdale, 1972: Creative in seawater. Limnol. Oceanogr., 17, 309-314.

Whitledge, T. E. and T. T. Packard, 1971: Nutrient excretion by anchovies and zooplankton in Pacific upwelling regions. Invest. Pesq., 35, 243-250.

Wood, J.D., 1958: Nitrogen excretion in some marine teleosts. Can. J. Biochem. Physiol, 36, 1237-1242.

Table 1. Mean zooplankton biomass±one standard deviation at buoy locations (g dry wt m^{-2}).

Location	Size Fraction μm 102-223	223-505	505-1000	>1000	Total
Offshore	0.71±0.47	0.88±0.48	1.06±0.62	10.54±9.05	13.19±10.62
G	0.56±0.26	1.66±1.04	1.21±0.65	4.10±2.90	7.53±4.85
O	1.06±0.50	0.86±0.40	0.24±0.14	0.62±0.14	2.78±1.18
U	0.58±0.58	0.98±0.18	0.50±0.16	0.45±0.25	2.51±1.17
R	1.28±0.39	1.64±0.80	0.42±0.17	0.44±0.33	3.78±1.69
D	0.75±0.31	0.69±0.61	0.08±0.03	0.13±0.04	1.65±0.99

Table 2. Ammonia and urea nitrogen release rates and oxygen consumption rate measured on four size fractions of zooplankton collected off Spanish Sahara.

Description	Mean size (mg dry wt ind-1)	Ammonia Nitrogen Released		Urea Nitrogen Released		Oxygen consumed	
		(µg N mg dry wt^{-1} d)				(µg O_2 mg dry wt^{-1} d^{-}	
102-223 µm	0.002	19.82±20.16[a]	(4)	5.38±3.02	(6)	180.9±79.9	(5)
223-505 µm	0.003	32.26±26.88	(6)	4.03±4.03	(7)	286.8±93.7	(6)
Pleuromamma sp.	0.304	8.74±7.06	(36)	2.35±2.35	(30)	9.98±71.4	(27
Euphausiids	5.040	1.68±1.34	(6)	0.67±0.34	(6)	49.9±31.9	(3)

---

[a] Mean ± one standard deviation; number of observations in parentheses.

Table 3. Ammonia regenerated by size fractions of zooplankton at buoy locations (mg-atoms N m^{-2} d^{-1}) (Smith and Whitledge, 1977).

	Size Fraction μm				
Location	102-223	223-505	505-1000	>1000	Total
Offshore	1.82	2.26	0.14	6.58	10.80
G	1.44	4.26	0.15	2.56	8.41
O	2.72	2.21	0.03	0.39	5.35
U	1.49	2.52	0.06	0.28	4.35
R	3.29	4.21	0.05	0.27	7.82
D	1.93	1.93	0.01	0.08	3.95

Table 4. Nitrogen and phosphorus release by selected species of fish collected over the shelf off northwest Africa. The number of organisms in each experiment is shown in parentheses (Smith and Whitledge, in press).

Species	Condition	Ammonia-N	Urea-N	Phosphate-P
		(μg mg dry wt^{-1} d^{-1})		
Diplodus senegalensis (12)	Fresh	1.44	0.76	0.23
Diplodus senegalensis (9)	Starved-1 day	0.90	0.26	0.15
Diplodus senegalensis (6)	Starved-2 days	0.64	0.35	0.22
Glyphis glaucus (2)	Fresh	0.44	0.55	0.08
Octopus vulgaris (4)	Fresh	0.78	0.11	0.42
Sardinella sp. (5)	Fresh	4.61	4.78	1.68
Pomadasys incisus (1) & Diplodus senegalensis (9)	Fresh	1.22	0.33	0.18
Pagellus couperi (2) & Cantharus cantharus (1)	Fresh	0.91	-	0.12
Pagellus couperi (2) & Cantharus cantharus (1)	Starved-1 day	0.64	0.08	0.05

Table 5. Nutrient regeneration by zooplankton and nekton and nutrient uptake by phytoplankton in the upwelling system off northwest Africa. Units are mg-at m^{-2} d^{-1}. (after Smith and Whitledge, in press)

Location	Ammonia-N			Urea-N		Phosphate-P		Sicicate-Si	
	Uptake	Zooplankton	Nekton	Zooplankton	Nekton	Zooplankton	Nekton	Uptake	Zooplankton
P	–	7.46	–	0.41	–	–	–	–	–
T	–	7.17	–	0.56	–	–	–	–	–
OFF	15.5[a]	10.80	–	2.20	–	0.86	–	–	3.01
G	5.6	8.41	7.11	2.95	7.22	0.89	1.14	17.48[b]	1.78
O	16.2	5.35	6.45	1.35	6.54	0.53	1.04	15.36	1.13
U	11.9	4.35	6.78	1.53	6.88	0.51	1.09	–	0.99
S	–	1.30	–	0.95	–	–	–	–	–
R	7.5	7.82	3.48	2.79	3.48	0.79	0.55	6.77	1.31
D	8.3	3.95	3.15	0.97	3.14	0.37	0.50	2.08	0.55

---

[a] unpublished data from J.J. MacIsaac and R.C. Dugdale.

[b] Converted from Nelson and Goering (1977) assuming a 12-hour day.

Table 6. Nutrient fluxes out of bottom surface sediment. Calculations based on bell jar volume, area of bottom covered and duration in hours over which the observed changes in concentrations occurred. (Rowe, Clifford, and Smith, 1977)

Sta. 162 21°20'N x 17°05'W, 25m depth

	PO_4	SiO_3	NO_3	NO_2	NH_4	
Initial bottom water concentrations	0.26	1.92	2.51	0.16	0.76	
12-h incubation concentrations	4.48	35.6	40.9	2.7	13.6	
Fluxes (μg-atoms m^{-2} h^{-1})	36	290	330	22	110	$\Sigma N = 460$
Sta. 171 21°00'N x 17°05'W, 25 m depth						
Initial bottom water concentrations	3.11	24.1	4.47	0.33	6.64	
3.5-h incubation	3.86	34.4	3.15	0.44	19.8	
5-h incubation	8.20	87.2	5.54	0.70	23.2	
Fluxes (μg-atoms m^{-2} h^{-1})	22	300	-39	3.2	390	
	105	1300	22	7.6	340	
Sta. 171 averages	64	800	-8	5.4	360	$\Sigma N = 360$
Fluxes at Stas. 162 and 171 averaged	50	550	160	14	235	$\Sigma N = 410$

Table 7. Ammonium budget for northwest Africa upwelling ecosystem. Units are mg-at m^{-2} d^{-1}.

	Ammonium Regeneration	Phytoplankton Uptake
Shelf (40m water depth)		
Zooplankton	7.82	
Nekton	3.48	
Sediments	5.64	
Total	16.94	7.5*
Outer Shelf (150m water depth)		
Zooplankton	5.35	
Nekton	6.45	
Sediments	1.88	
Total	13.68	16.2*

---

* Unpublished nitrogen uptake data of MacIsaac and Dugdale.

Table 8. Zooplankton dry weight and regeneration rates by size fraction in the Peru upwelling system at 10°S and 15°S.

		Size fractionated Zooplankton Dry Weights ($g\ m^{-2}$)					Zooplankton nitrogen regeneration rates ($mg\text{-}at\ m^{-2}\ d^{-1}$)				
Station	Depth m	102–223 µm	223–505 µm	505–1050 µm	>1050 µm	Total	102–223 µm	223–505 µm	505–1050 µm	>1050 µm	Tota
10°S											
182	60	.408	3.047	.752	5.008*	9.215*	.91	7.01	.53	–	8.4
183	90	.383	1.308	1.058	2.594*	5.343*	.85	3.01	.74	–	4.6
184	100	.171	.558	.419	1.770	2.918	.38	1.28	.29	.67	2.6
185	100	.123	.586	.660	1.114	2.483	.27	1.35	.46	.42	2.5
186	100	.092	.676	.431	.895	2.094	.21	1.55	.30	.34	2.4
188	100	.120	.545	.376	.645	1.686	.27	1.25	.26	.25	2.0
189	100	.103	.655	.598	2.619	3.975	.23	1.51	.42	1.00	3.1
190	100	.105	.458	.432	1.363	2.358	.23	1.05	.30	.52	2.1
191	100	.072	.405	.174	2.692	3.343	.16	.93	.12	1.02	2.7
15°S											
192	35	.175	.443	1.020	.719	2.357	.39	1.02	.71	.27	2.39
193	60	.780	1.750	1.517	2.291	6.338	1.74	4.03	1.06	.87	7.70
194	100	.175	.465	.135	1.814	2.589	.39	1.07	.09	.69	2.24
195	100	.227	1.726	.506	15.793	18.252	.51	3.97	.35	6.00	10.83
196	100	.448	1.256	.280	7.845	9.829	1.00	2.89	.20	2.98	7.07
197	100	.611	1.748	.338	1.174	3.871	1.36	4.02	.24	.45	6.07
198	100	.104	.875	1.357	6.189	8.525	.23	2.01	.95	2.35	5.54
236	85	.241	1.838	1.326	3.765	7.170	.54	4.23	.93	1.43	7.13

---

* phytoplankton contamination in sample.

Table 9. Nitrogen excretion rates of zooplankton measured in the Peru upwelling system at 15°S in April 1977. after Dagg et al. (in press).

		Excretion (µg N mg dry wt^{-1} d^{-1})				
Species	Location	Ammonium	Urea	Primary Amines	Total	Body N(µg)
Eucalanus inermis	14°52'S 75°52'W	29.88 (5)*	7.31 (7)	2.09 (9)	39.28	6.7
Eucalanus inermis	15°06'S 75°28'W	7.31 (2)	0.63 (3)	0.42 (3)	8.36	6.7
Eucalanus inermis	15°10'S 75°36'W	18.77 (5)	9.07 (3)	5.09 (4)	32.93	8.8
Calanus chilensis	15°06'S 75°28'W	4.39 (4)	1.03 (3)	0.65 (4)	6.07	15.0
Calanus chilensis	15°36'S 76°07'W	19.52 (1)	1.04 (1)	2.59 (1)	18.15	5.4
Centropages brachiatus	15°36'S 76°07'W	19.69 (4)	21.88 (3)	0 (4)	41.56	3.2

---

* Number of observations

Table 10. Nitrogen release (μg N mg dry wt^{-1} d^{-1}) by zooplankton off Peru. Values are means $\pm$1 standard deviation, with number of observations in parenthesis. –: no data (after Smith, 1978)

Size Fraction (μm)	Mean size (mg dry wt ind-1)	Ammonium Nitrogen Released		Urea Nitrogen Released	
102 - 223	0.002	31.25±23.86	(27)	38.98±19.15	(5)
223 - 505	0.006	32.26±17.14	(29)	22.18±19.15	(5)
505 - 1050	0.042	9.47±9.41	(25)	–	
>1050 (*Eucalanus inermis*)	0.128	5.38±6.38	(3)	–	
>1050 (*Euphausia* sp.)	4.955	0.07	(1)	–	
<505	–	31.92±1.34	(56)	27.22±16.13	(10)
>505	–	8.40±7.39	(27)	–	

Table 11. Ammonium excretion rates for nekton inhabiting Peru upwelling ecosystem.

	Mean dry wt (g)	NH_4 exretion rate ± std dev (μg N mg dry wt^{-1} d^{-1})	
Engraulis ringens (7)	1.70	1.74±1.48	ref 1
Sardinops sagax (4)	1.52	2.19±0.24	
Trachurus symmetricus (1)	47.5*	1.26	ref 2
Austromenidia regia regia (14)	3.26	5.17±1.78	

---

* Calculated from 190 g wet wt.
ref 1. Whitledge and Dugdale, 1972.
ref 2. McCarthy and Whitledge, 1972.

Table 12. Ammonium budget for Peru upwelling ecosystem. Units are mg-at m^{-2} d^{-1}.

	Ammonium Regeneration	Phytoplankton Uptake
Shelf		
Zooplankton	4.11	
Pelagic Nekton	3.86	
Sediments	4.16*	
Total	12.13	15.0**
Offshore		
Zooplankton	7.33	
Pelagic Nekton	1.72	
Demersal Nekton	0.07†	
Sediments	4.16*	
Total	13.28	17.88**

---

* From S^{35} estimate (Rowe, personal communication).

**Unpublished N^{15} data of MacIsaac and Dugdale.

† Based on 1970 stock estimate (Gulland, 1970) and flounder excretion rates (Wood, 1958).

Table 13. Ammonium budget for Baja California upwelling ecosystem. Units are mg-at m^{-2} d^{-1}.

	Ammonium Regeneration	Phytoplankton Uptake
March		
Zooplankton	1.17	
Nekton	0.30	
Pleuroncodes-Pelagic	12.70	
Pleuroncodes-Benthic	1.68	
Sediments	2.86	
Total	18.71	22.3
April		
Zooplankton	6.28	
Nekton	0.30	
Pleuroncodes-Pelagic	9.10	
Pleuroncodes-Benthic	1.68	
Sediments	2.86	
Total	20.22	17.5*

---

* From Whitledge and Conway (1977).

Table 14. Percent regenerated productivity in marine ecosystems and percentage of total nitrogen uptake originating from different animal groups.

	Regenerated Prod (% of total Prod)	Zoo-plankton	Nekton	Micro-Nekton	Demersal Fish	Benthos & Sediments	Reference
<u>Upwelling Areas</u>							
NW Africa							
Cape Blanc Shelf	72	33	15	–	–	24	Herbland et al 1973
Cape Blanc Outer Shelf	61	24	29	–	–	8	
Cape Timiris Shelf	15	15	–	–	–	–	
Peru							
Shelf	56	19	18	–	–	19	
Off Shelf	42	23	5	–	1	13	
Baja California							
Shelf-March	47	3	1	32	–	11	
Shelf-April	52	16	1	23	–	12	
Oregon							
Shelf	?	?	–	–	–	–	Jawed, 1973
<u>Coastal Areas</u>							
NE United States							
Narragansett Bay	64	64	–	–	–	–	Martin, 1968
Long Island Sound	55–75	43–66	–	–	–	9–12	Harris, 1959
NW United States							
Shelf	36	36	–	–	–	–	Jawed, 1973
Columbia River Plume	90	90	–	–	–	–	Jawed, 1973
<u>Open Ocean</u>							
N. Pacific Gyre	44–83	44–83	–	–	–	–	Eppley et al., 1973

FIGURE LEGENDS

Figure 1.	Station locations on JOINT-I cruise off NW Africa. G,O,U,R and D are locations where experiments were run and biomass samples were collected.
Figure 2.	Biomass of zooplankton (g dry wt m^{-2}) collected on a transect near 21° 40'N off northwest Africa (after Smith and Whitledge, in press).
Figure 3.	Tank concentrations of ammonium, urea and total excreted nitrogen measured during an excretion experiment with <u>Diplodus senegalensis</u> off northwest Africa.
Figure 4.	Station locations where sediment pore water nutrient concentrations were measured. Contours are of ammonium gradients between water and sediments. Units are µg-at l^{-1} cm^{-1}. (Rowe, Clifford and Smith, 1977)
Figure 5.	Ammonium and nitrate concentrations (µg at l^{-1}) in pore waters. Open circles are nearshore ammonium and open triangles are offshore ammonium. Solid circles are nearshore nitrate and solid triangles are offshore nitrate (Rowe, Clifford and Smith, 1977).
Figure 6.	Concentration of ammonium (µg-at l^{-1}) on a cross shelf transect near 21° 40'N off northwest Africa.
Figure 7.	Biomass of zooplankton (g dry wt m^{-2}) for size classes 102-223 µm, 223-505 µm, 505-1050 µm and >1050 µm collected on a cross shelf transect near 10°S off Peru.
Figure 8.	Biomass of zooplankton (g dry wt m^{-2}) for size classes 102-223 µm, 223-505 µm, 505-1050 µm and >1050 µm collected on a cross shelf transect near 15°S off Peru.

Figure 9. Biomass of zooplankton (g dry wt m^{-2}) for size classes 102-223 μm, 223-505 μm, 505-1050 μm and >1050 μm collected on an alongshore transect near 15°S off Peru.

Figure 10. Biomass of zooplankton (g dry wt m^{-2}) for size classes 102-223 μm, 223-505 μm, 505-1050 μm and >1050 μm collected on an inshore times series station near 15°S off Peru.

Figure 11. Biomass of zooplankton (g dry wt m^{-2}) for size classes 102-223 μm, 223-505 μm, 505-1050 μm and >1050 μm collected on a shelf break time series station near 15°S off Peru.

Figure 12. Biomass of zooplankton (g dry wt m^{-2}) for size classes 102-223 μm, 223-505 μm, 505-1050 μm and >1050 μm collected on an offshore time series station near 15°S off Peru.

Figure 13. Distribution of nekton biomass (g wet wt m^{-2}) from acoustic integrations for 2 June 1976 near 15°S off Peru (Lee, Mathisen and Thorne, 1979).

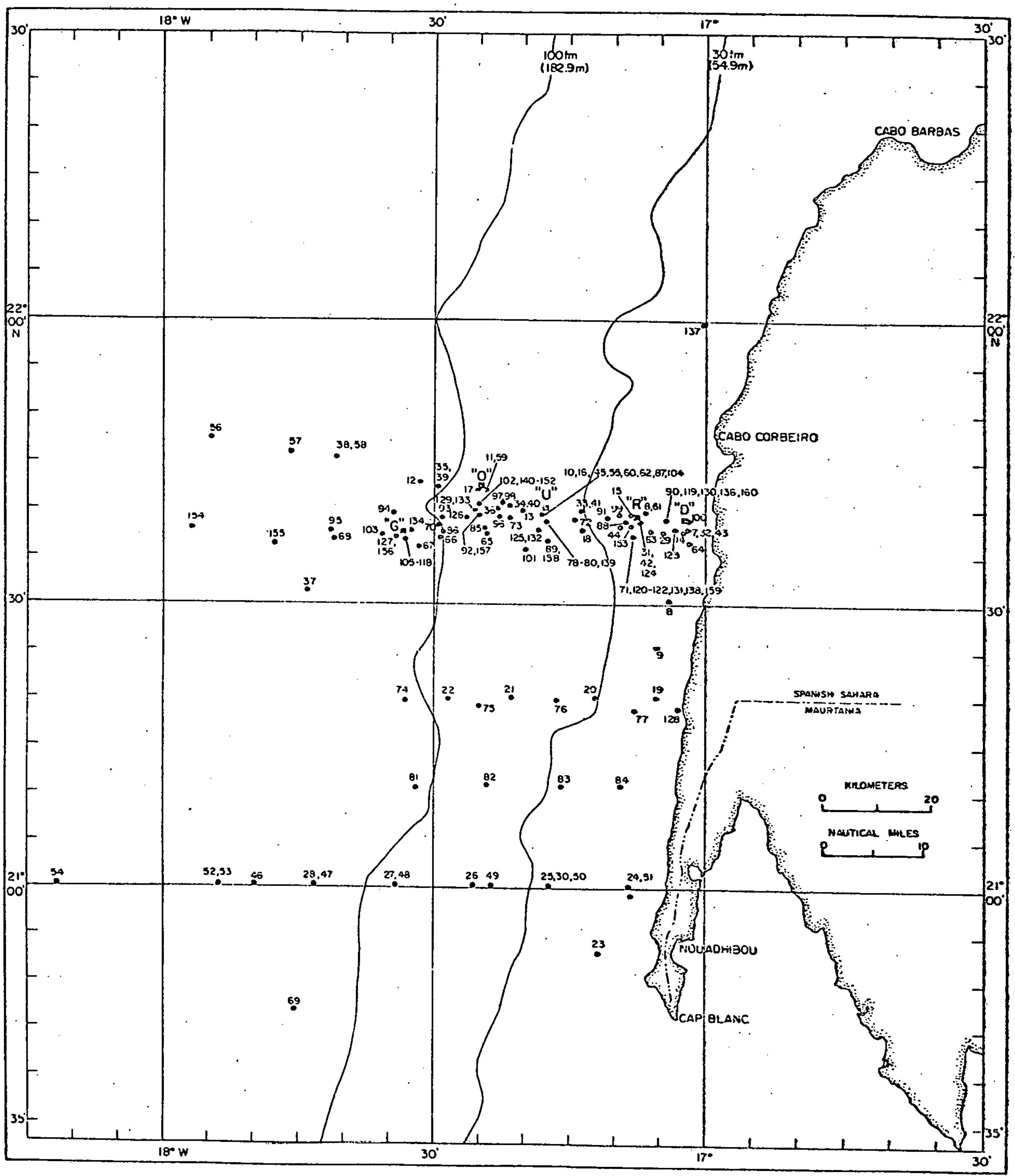
Figure 14. Concentrations of dissolved nitrogen nutrients (μg-at l^{-1}) in cross shelf transects. a) ammonium at 15°S; b) ammonium at 10°S; c) urea at 15°S; d) urea at 10°S; e) Total nitrogen (NO_3+NO_2+NH_4+UREA) at 15°S; f) Total nitrogen (NO_3+NO_2+NH_4+UREA) at 10°S; g) Per cent regenerated nitrogen (NH_4+UREA/Total nitrogen) x 100 at 15°S; h) Percent regenerated nitrogen (NH_4+UREA/Total nitrogen) x 100 at 10°S.

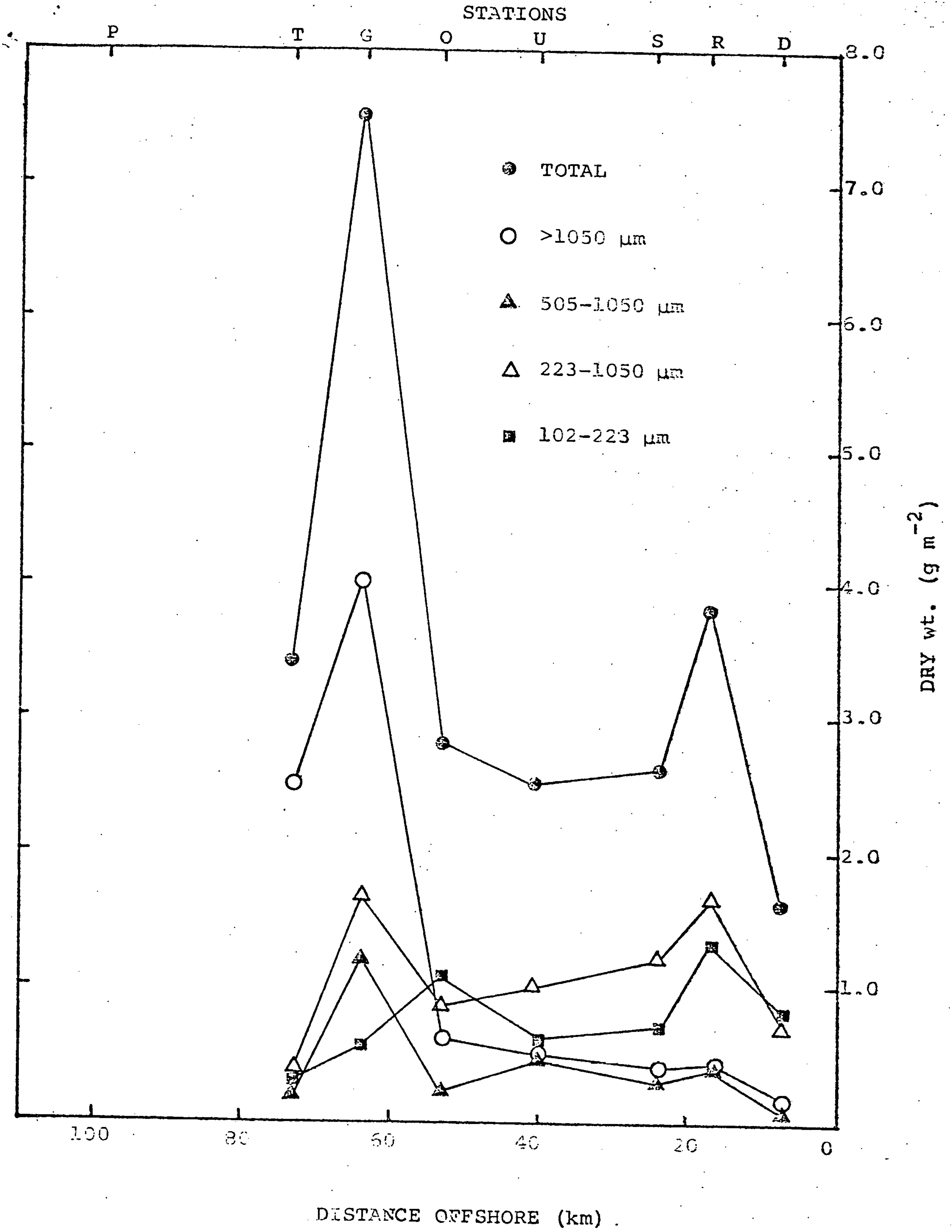
Figure 15. Concentration of dissolved organic nitrogen (μg-at l^{-1}) on a cross shelf transect near 15°S off Peru.

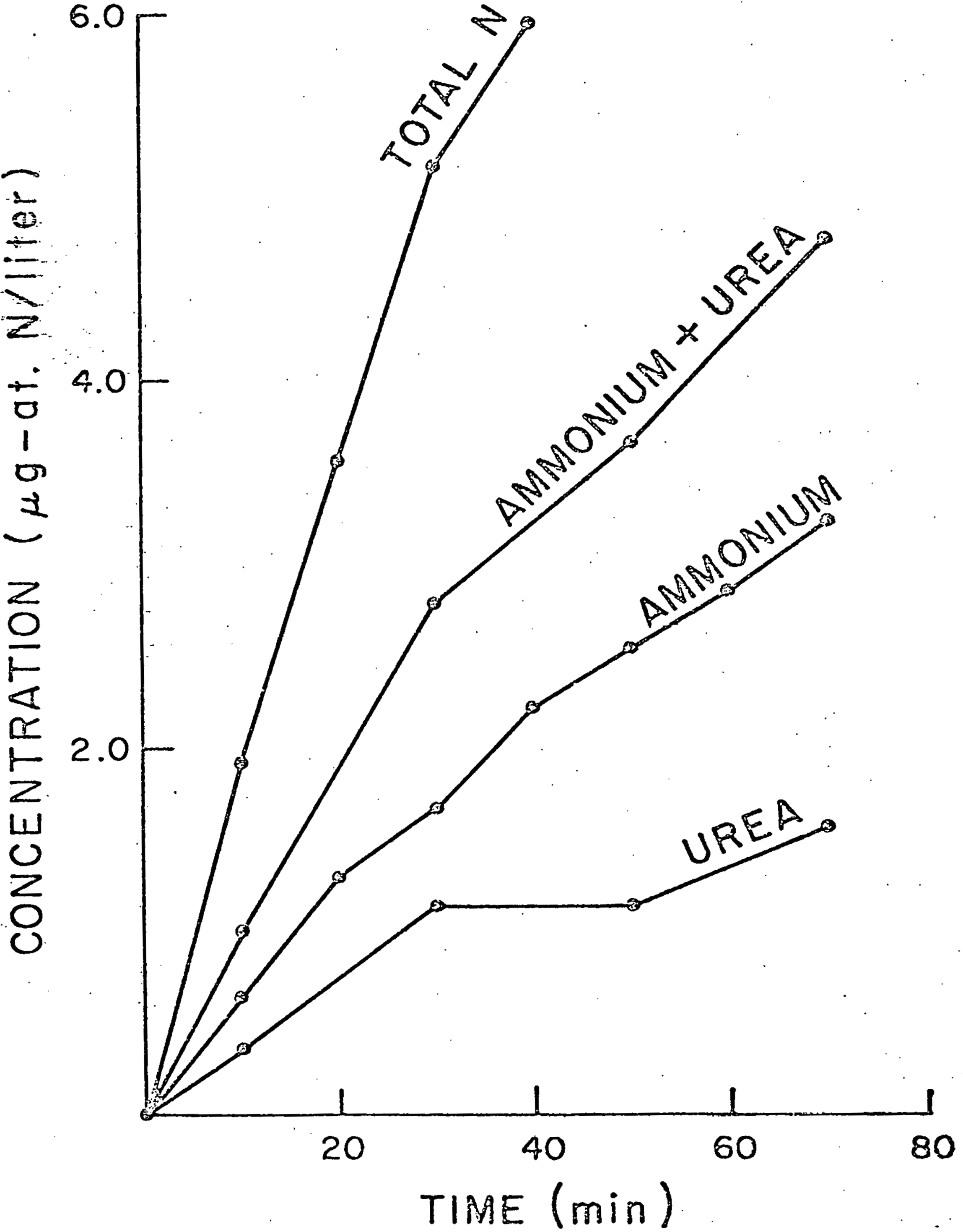
Figure 16. Mean nekton biomass (g wet wt m^{-2}) estimated from acoustic integrations for the depths 17-47m near 27°N off Baja California (Blackburn and Thorne, 1974).

Figure 17. Integrated concentrations (mg-at m^{-2}) of nitrate, silicate and ammonium in the euphotic zone along drogue track of Anton Bruun 15 near 15°S off Peru.

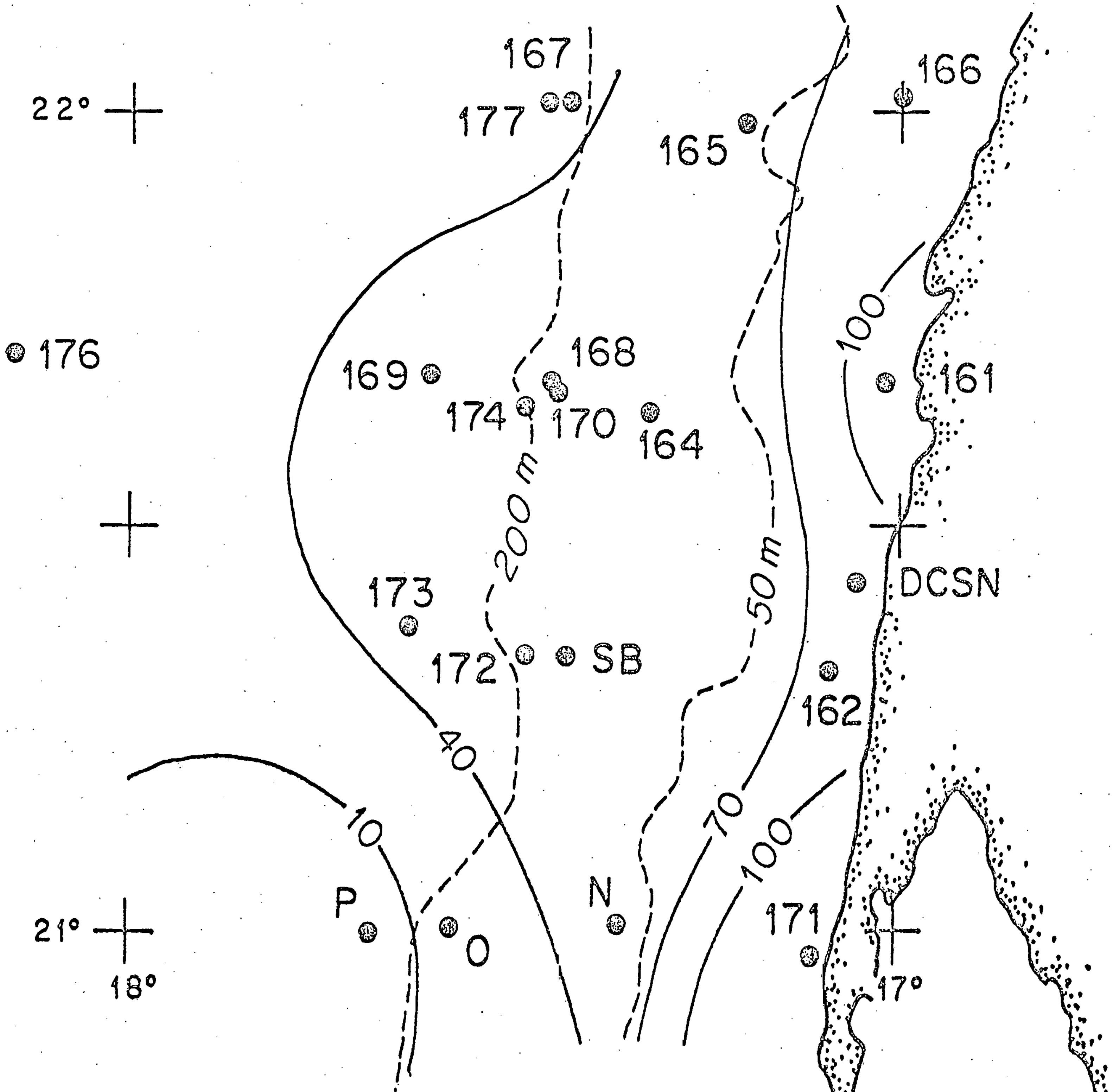
Figure 18. a) Nitrate concentrations (μg-at l^{-1}) at 3m and b) chlorophyll concentration (μg l^{-1}) integrated from 100% to 10% light depths on stations near 15°S off Peru (Walsh et al., 1971).

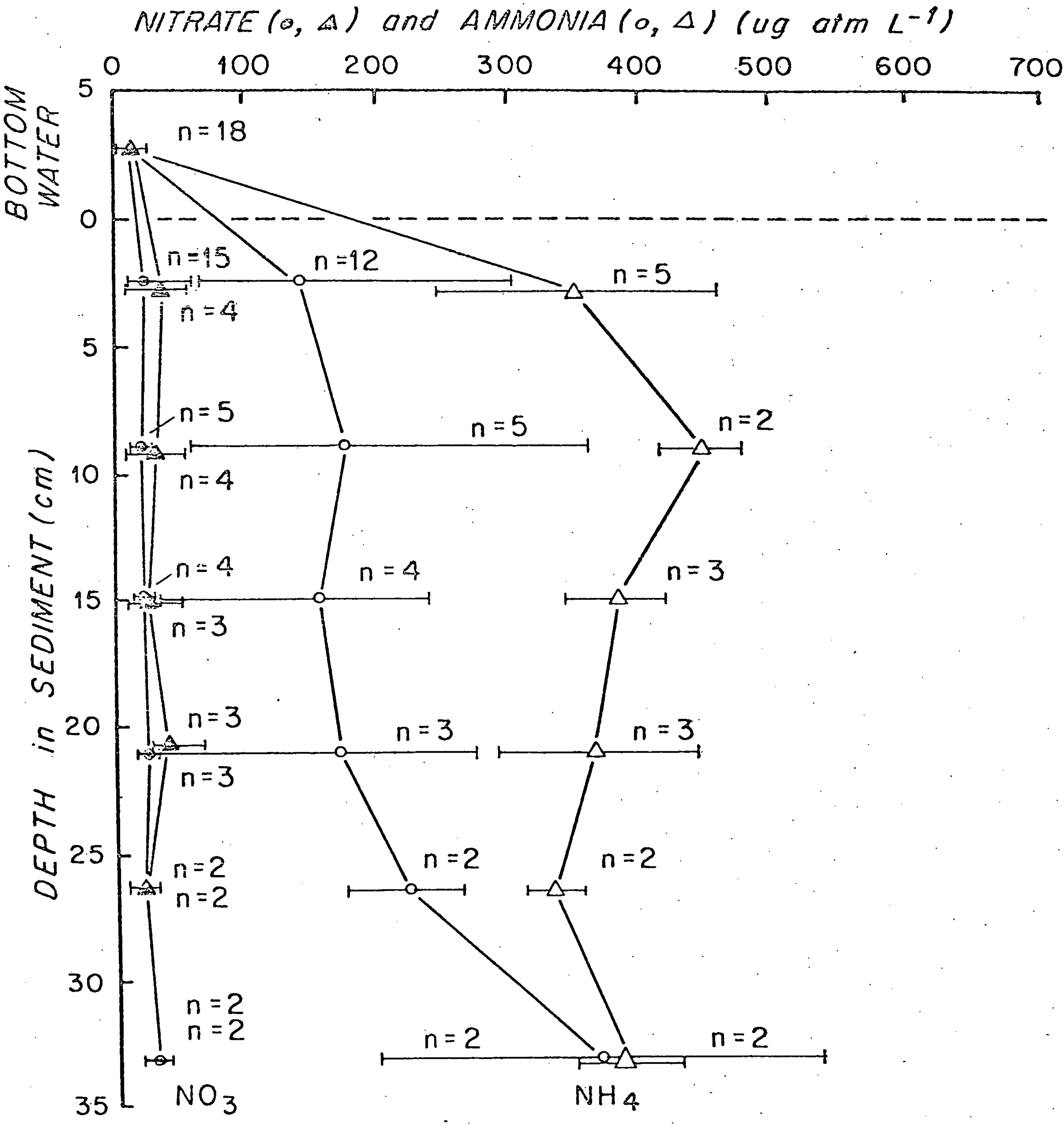

18° W
30'
17°
30'
22° 00' N
21° 00'
35'
100 fm (182.9 m)
30 fm (54.9 m)
CABO BARBAS
CABO CORBEIRO
SPANISH SAHARA
MAURTANIA
NOUADHIBOU
CAP BLANC
KILOMETERS
0
20
NAUTICAL MILES
0
10
"G"
"O"
"U"
"R"
"D"
137
56
57
38,58
12
35, 39
11,59
17
102,140-152
10,16,45,55,60,62,87,104
90,119,130,136,160
15
129,133
97,98
34,40
33,41
91
8,61
100
154
155
95
69
94
103
134
70
93
126
36
13
72
88
44
153
53
29
14
7,32,43
64
123
127, 156
67
105-118
86
66
85
65
92,157
99
73
125,132
101
89, 158
78-80,139
18
31, 42, 124
71,120-122,131,138,159
37
8
9
74
22
21
20
19
75
76
77
128
81
82
83
84
54
52,53
46
28,47
27,48
26
49
25,30,50
24,51
23
69

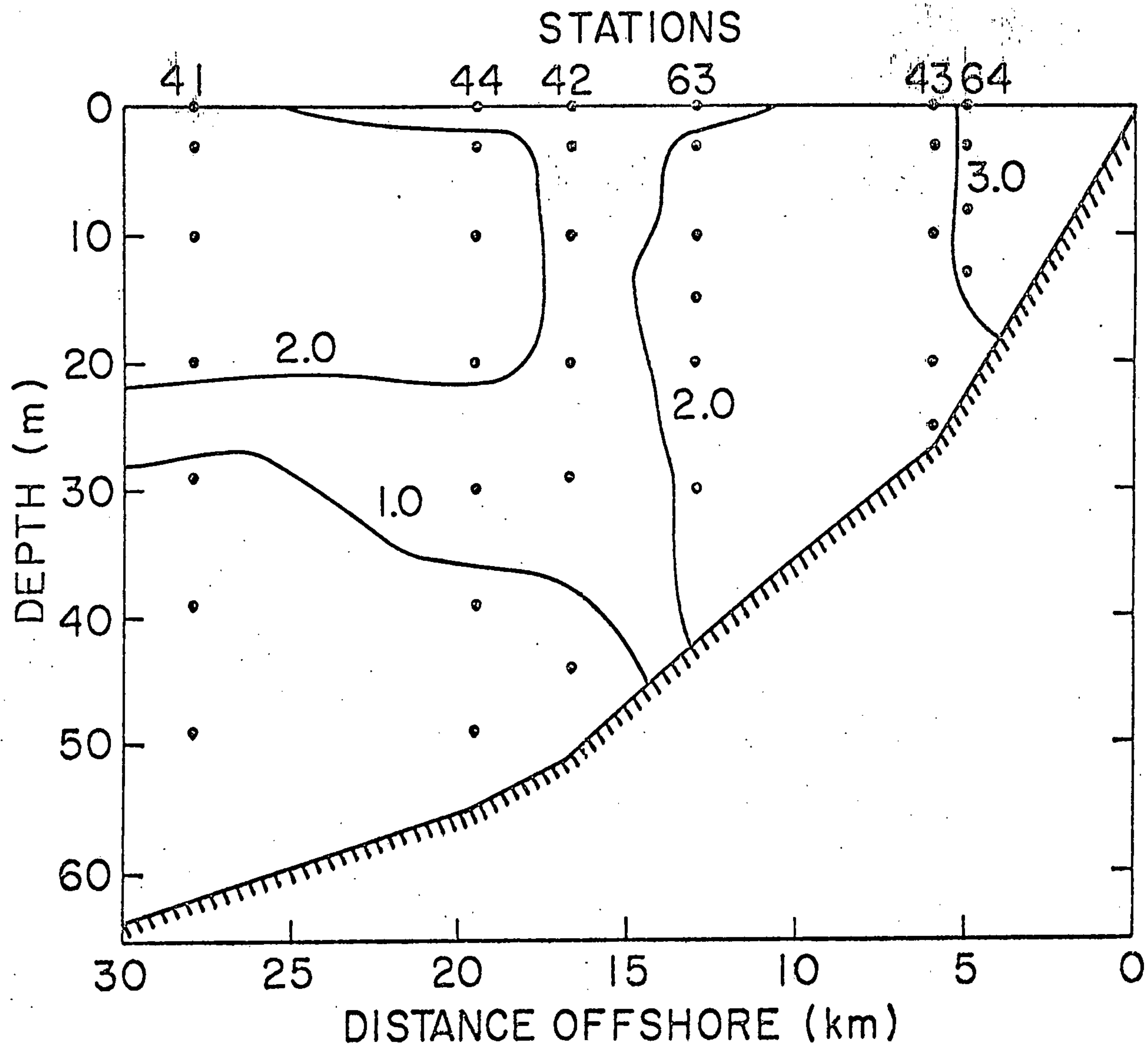

STATIONS
P
T
G
O
U
S
R
D
● TOTAL
○ >1050 μm
▲ 505-1050 μm
△ 223-1050 μm
■ 102-223 μm
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
DRY wt. (g m^{-2})
100
80
60
40
20
0
DISTANCE OFFSHORE (km)

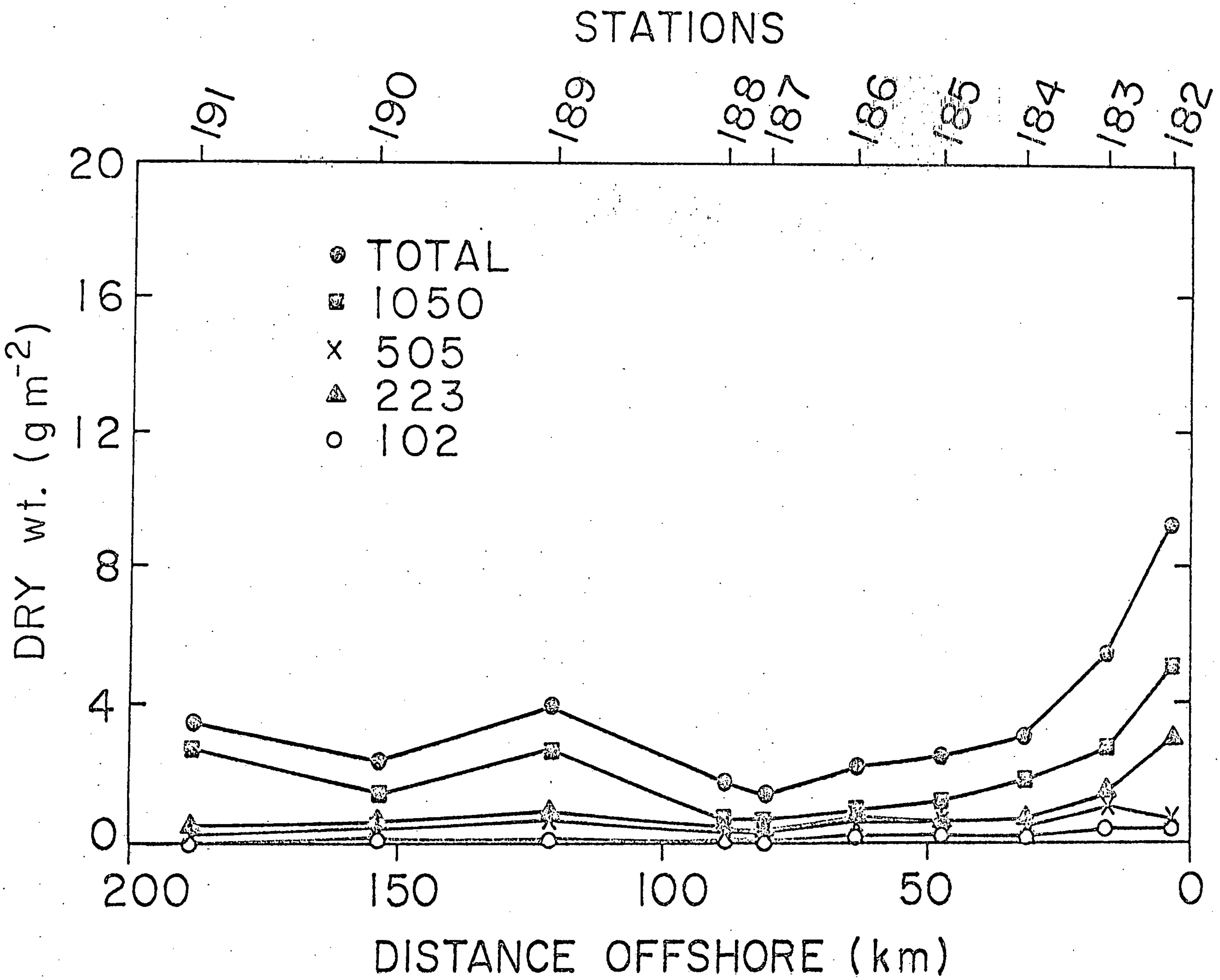


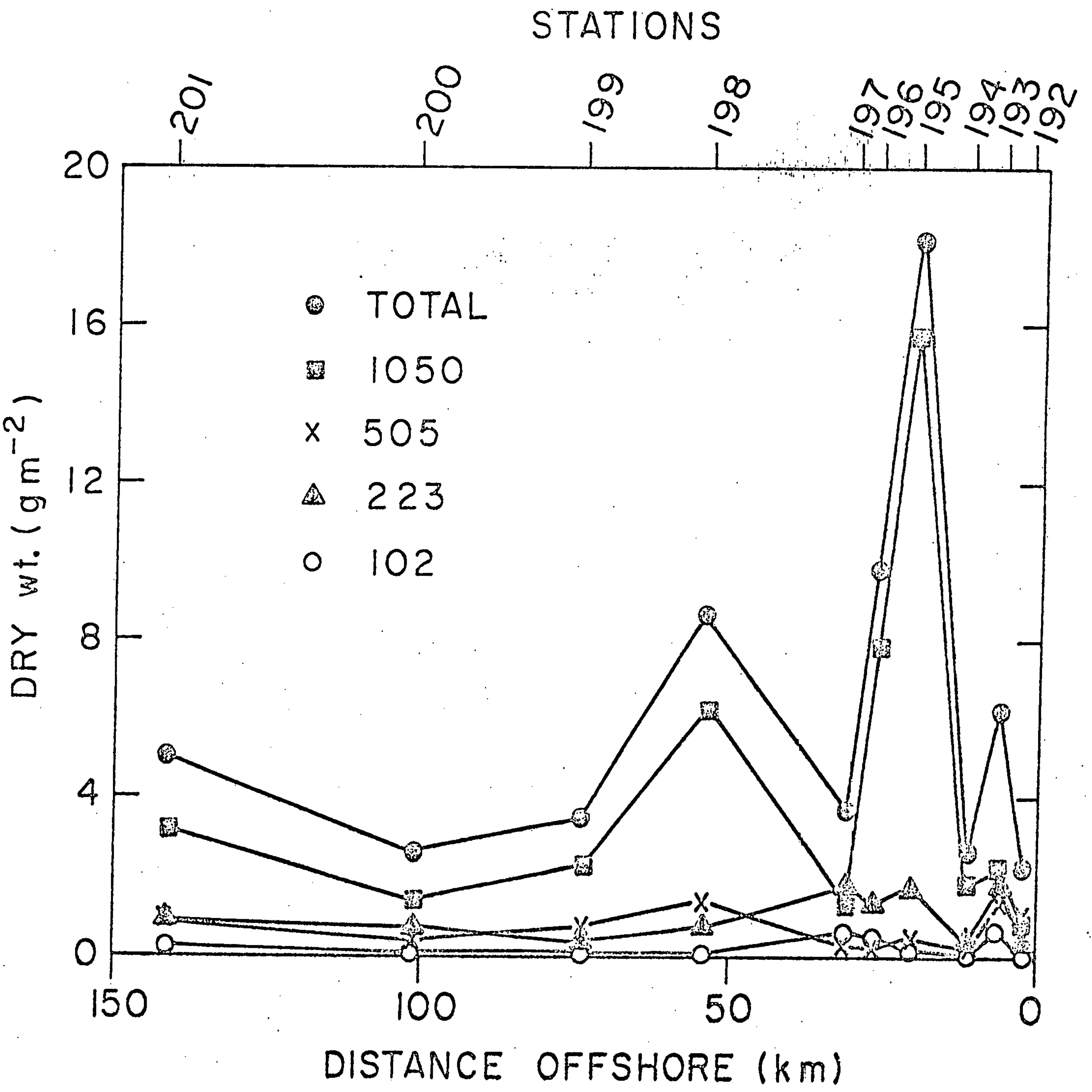
6.0
4.0
2.0
CONCENTRATION (μg-at. N/liter)
20
40
60
80
TIME (min)
TOTAL N
AMMONIUM + UREA
AMMONIUM
UREA

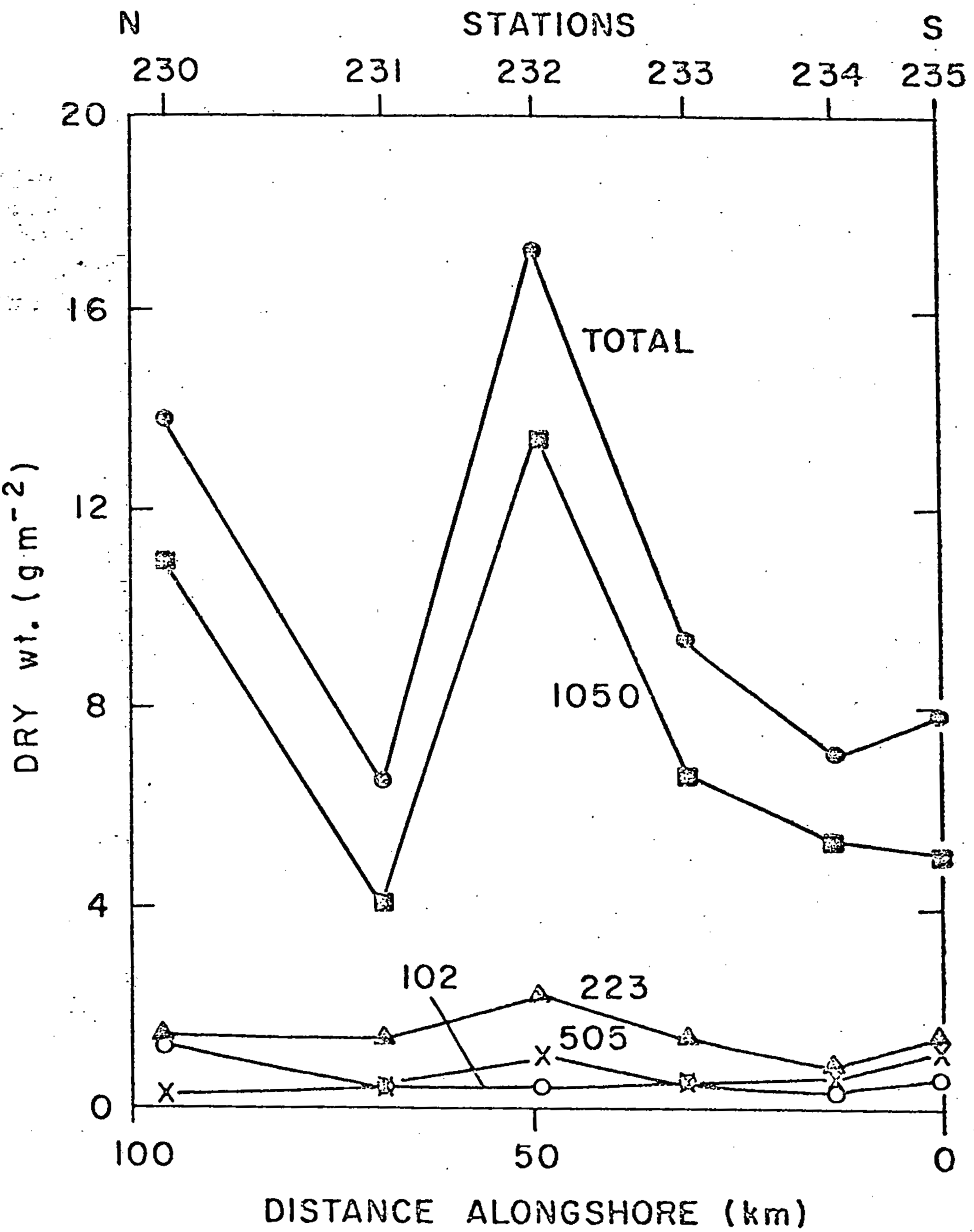

167
177
165
166
22°
176
169
168
174
170
164
161
100
200 m
50 m
DCSN
173
SB
172
162
40
10
70
100
P
O
N
171
21°
18°
17°

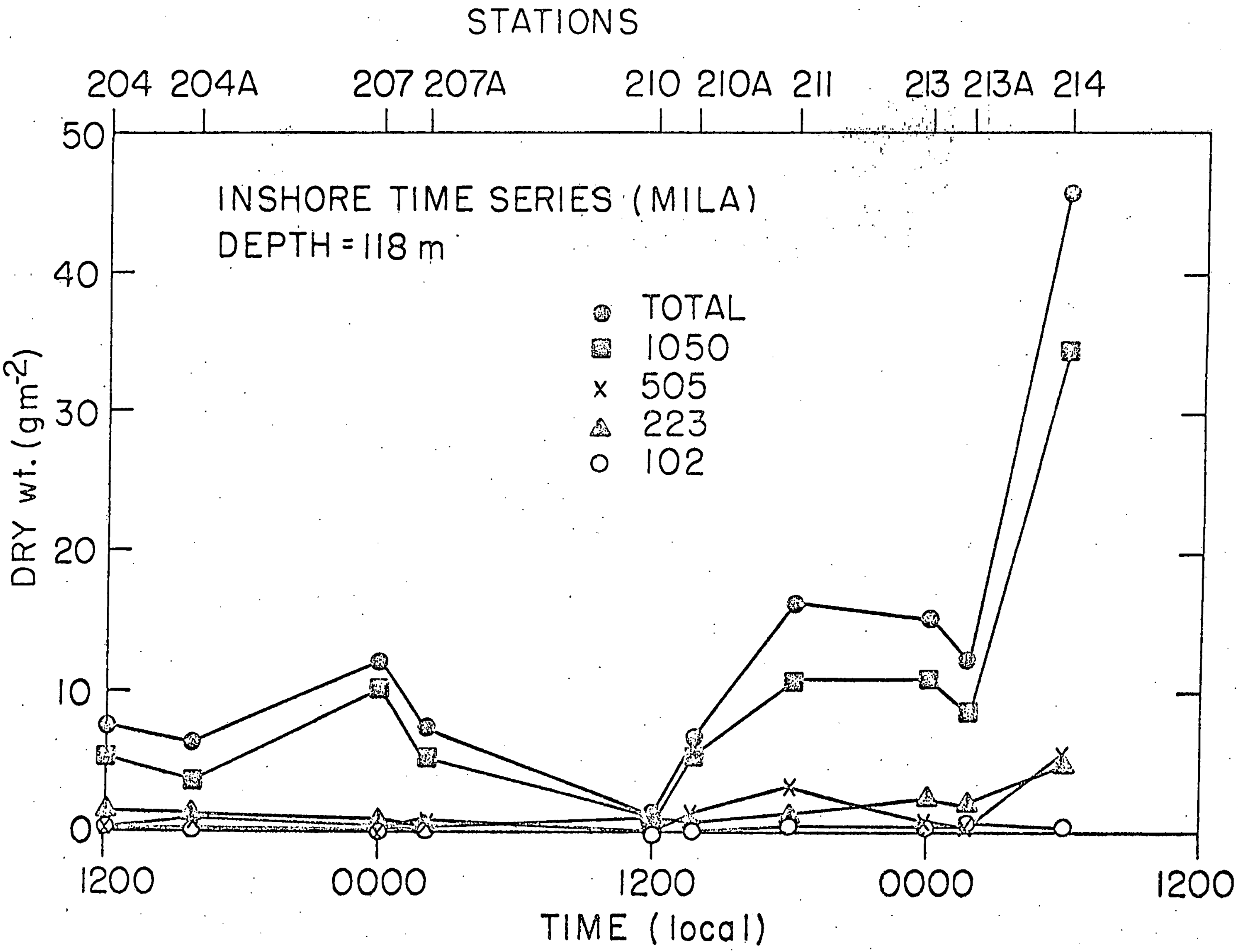

NITRATE (o, ▲) and AMMONIA (o, Δ) (ug atm L^{-1})
0
100
200
300
400
500
600
700
BOTTOM WATER
DEPTH in SEDIMENT (cm)
5
0
5
10
15
20
25
30
35
n = 18
n = 15
n = 12
n = 5
n = 4
n = 5
n = 5
n = 2
n = 4
n = 4
n = 4
n = 3
n = 3
n = 3
n = 3
n = 3
n = 3
n = 2
n = 2
n = 2
n = 2
n = 2
n = 2
n = 2
n = 2
NO3
NH4


STATIONS
41
44
42
63
43
64
0
10
20
30
40
50
60
DEPTH (m)
2.0
1.0
2.0
3.0
30
25
20
15
10
5
0
DISTANCE OFFSHORE (km)

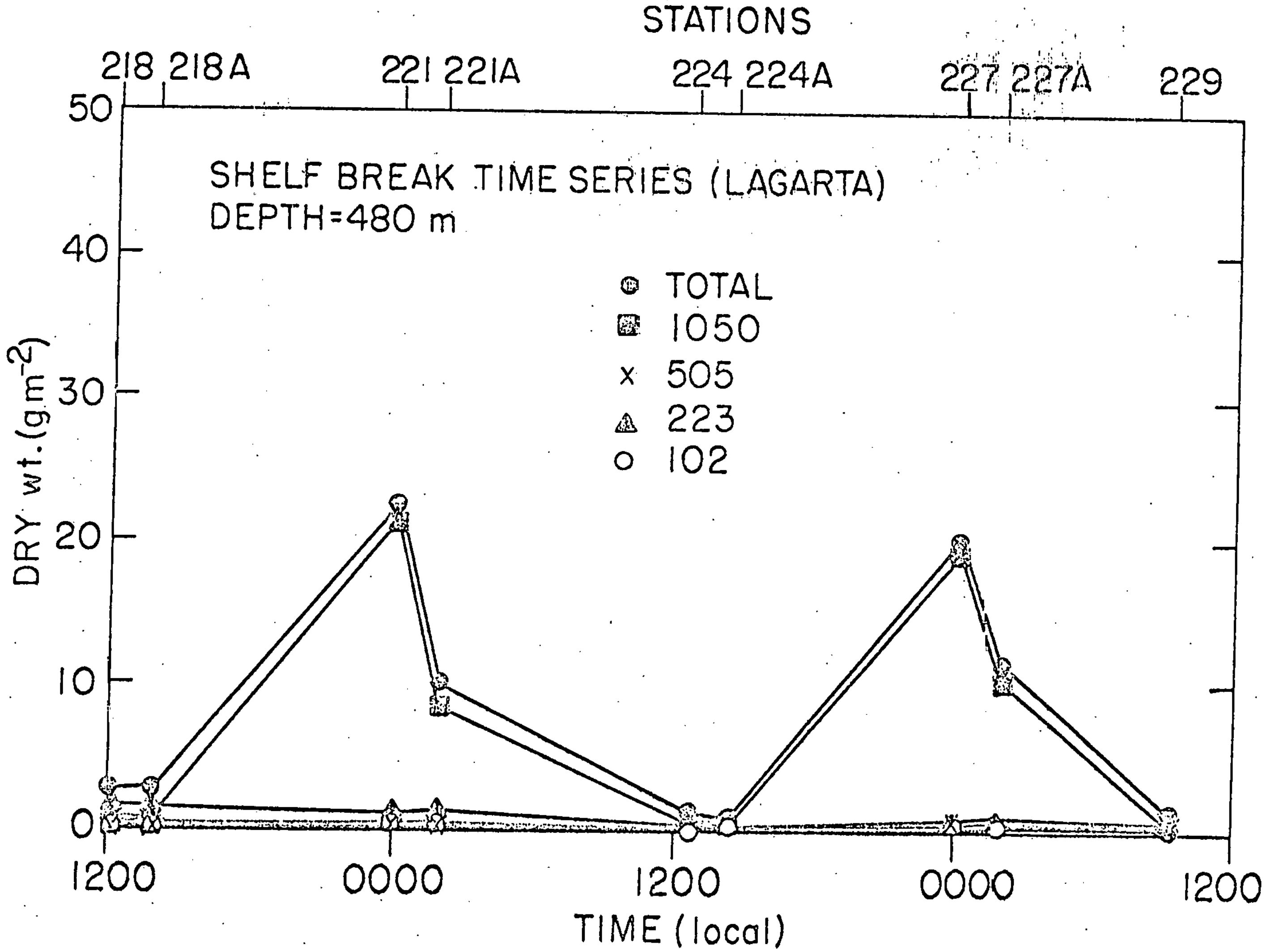

STATIONS
191
190
189
188
187
186
185
184
183
182
● TOTAL
■ 1050
× 505
▲ 223
○ 102
DRY wt. (g m-2)
20
16
12
8
4
0
200
150
100
50
0
DISTANCE OFFSHORE (km)


STATIONS
201
200
199
198
197
196
195
194
193
192
20
16
12
8
4
0
DRY wt. (g m⁻²)
● TOTAL
■ 1050
x 505
▲ 223
○ 102
150
100
50
0
DISTANCE OFFSHORE (km)

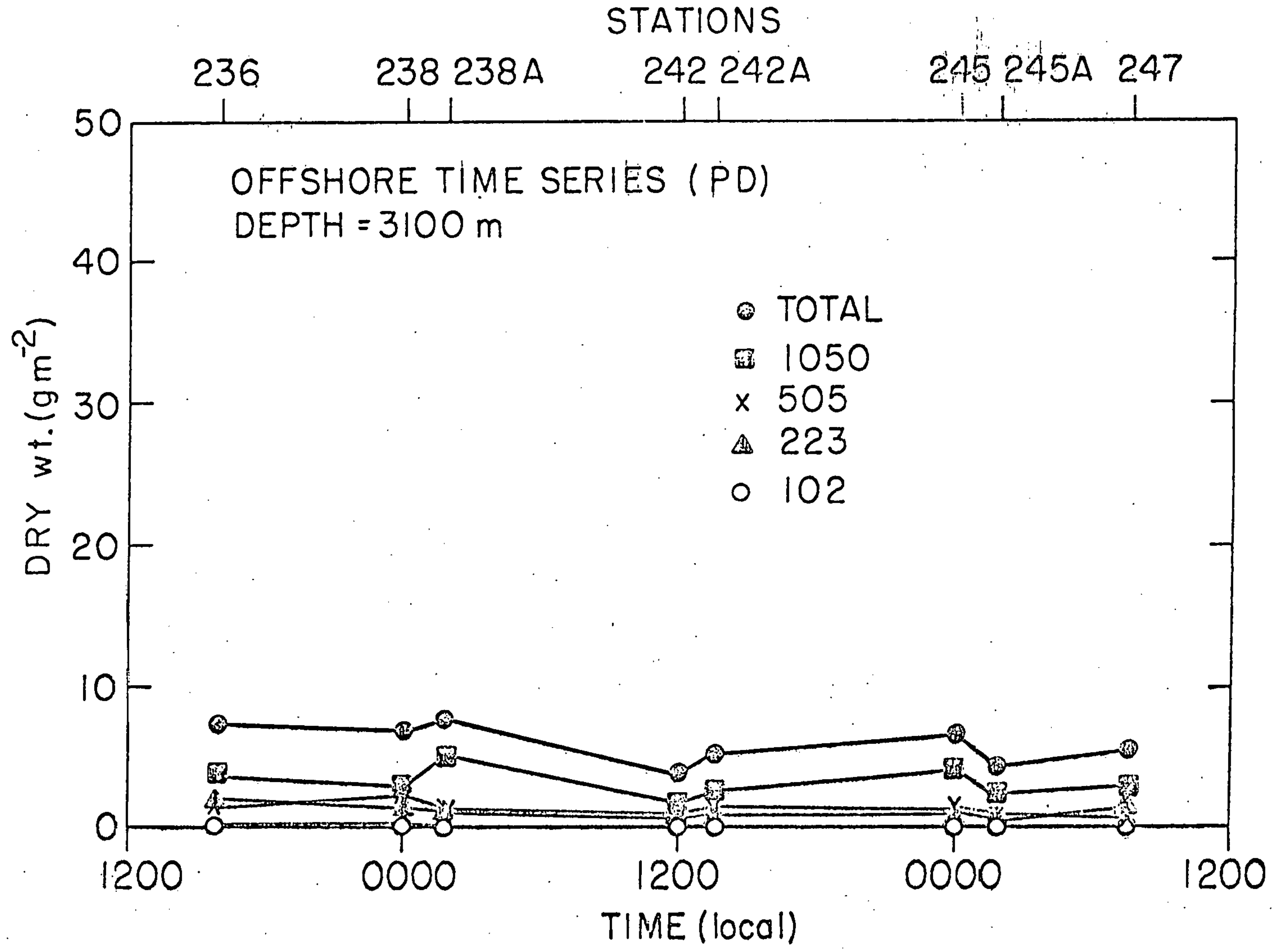

N
STATIONS
S
230
231
232
233
234
235
20
16
12
8
4
0
DRY wt. (g m^{-2})
TOTAL
1050
102
223
505
100
50
0
DISTANCE ALONGSHORE (km)



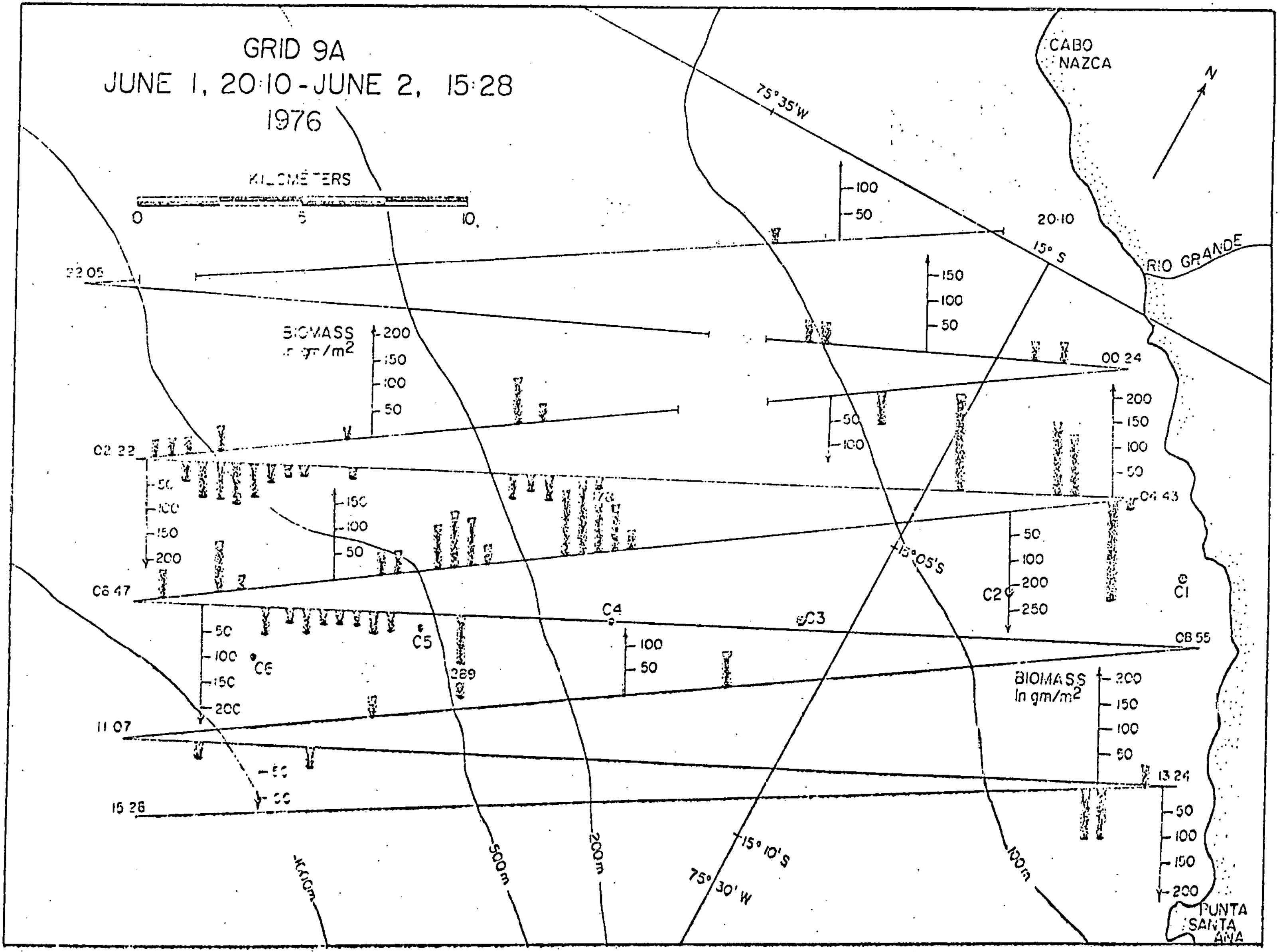
MAM 77 MELVILLE

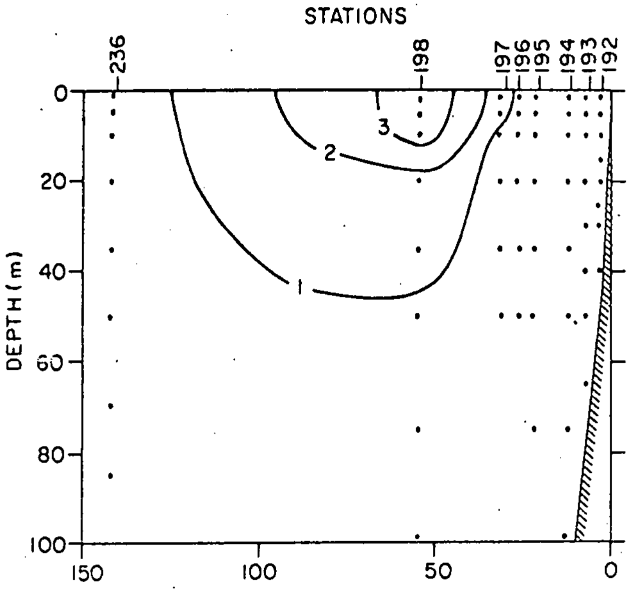


MAM 77 MELVILLE

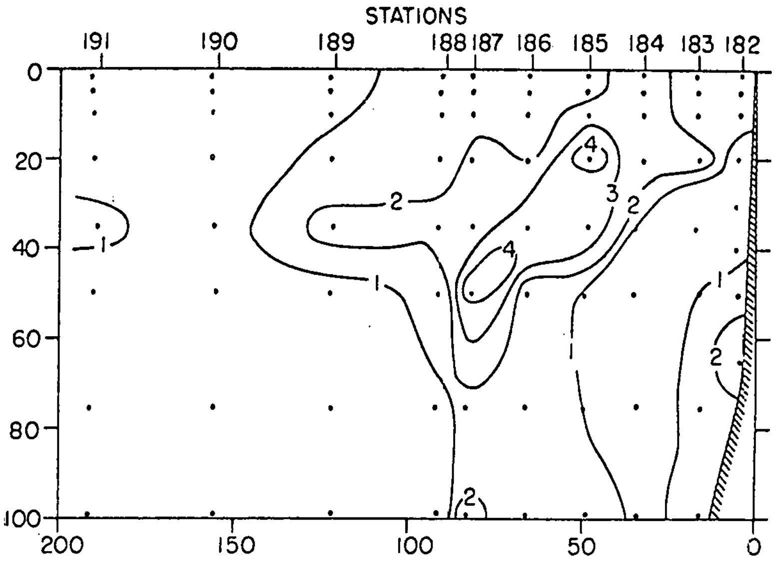


MAM 77 MELVILLE

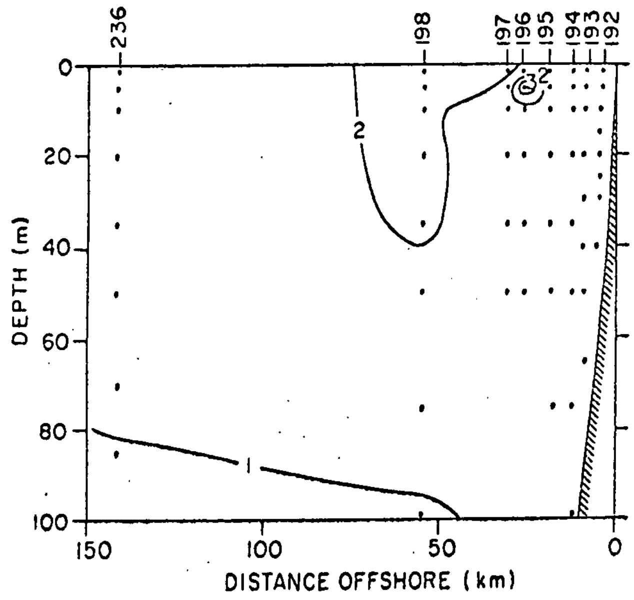

GRID 9A
JUNE 1, 20:10 - JUNE 2, 15:28
1976
KILOMETERS
0
5
10
CABO NAZCA
N
RIO GRANDE
PUNTA SANTA ANA
75°35'W
75°30'W
15° S
15°05'S
15°10'S
1000m
500m
200m
100m
BIOMASS in gm/m2
200
150
100
50
250
20:10
22:05
00:24
02:22
04:43
06:47
08:55
11:07
13:24
15:28
C1
C2
C3
C4
C5
C6
178
289



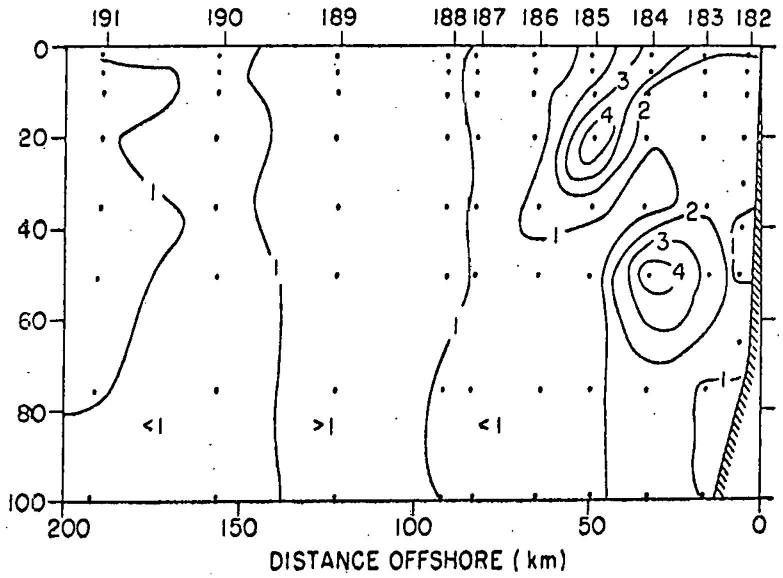
15° S AMMONIUM



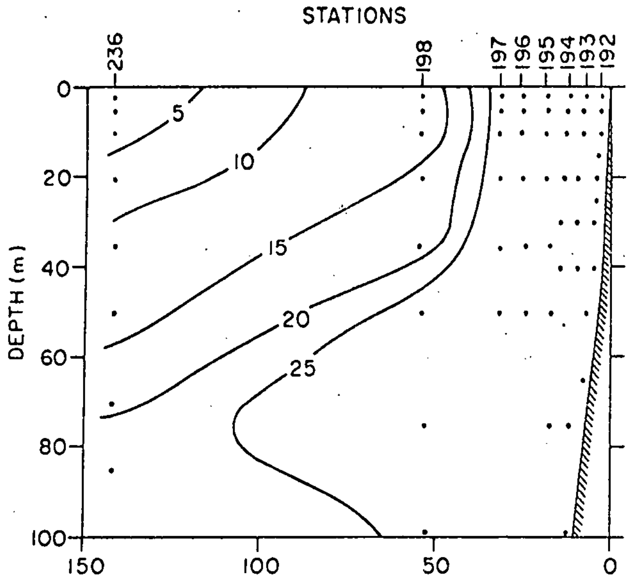
10° S AMMONIUM



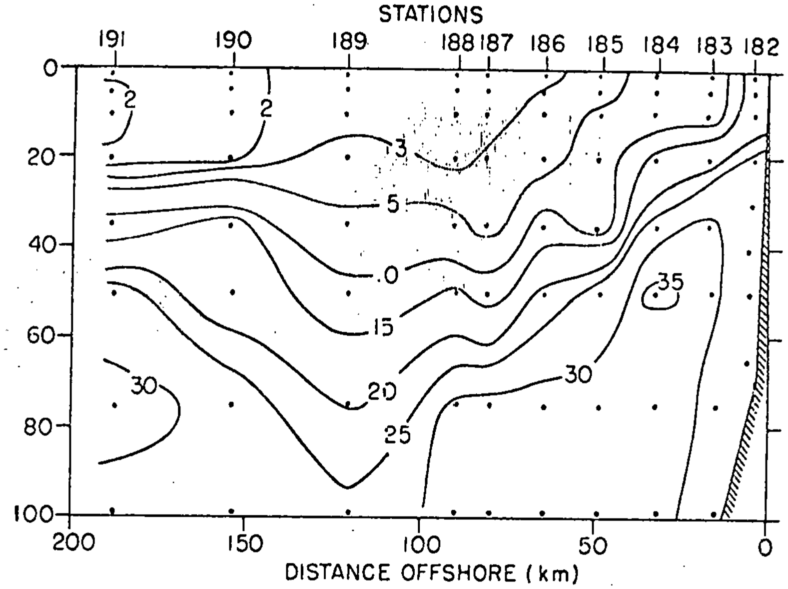
15° S UREA



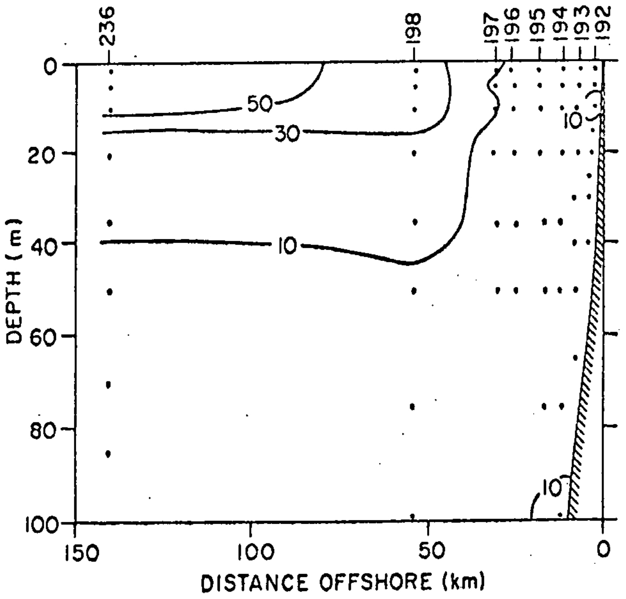
10° S UREA



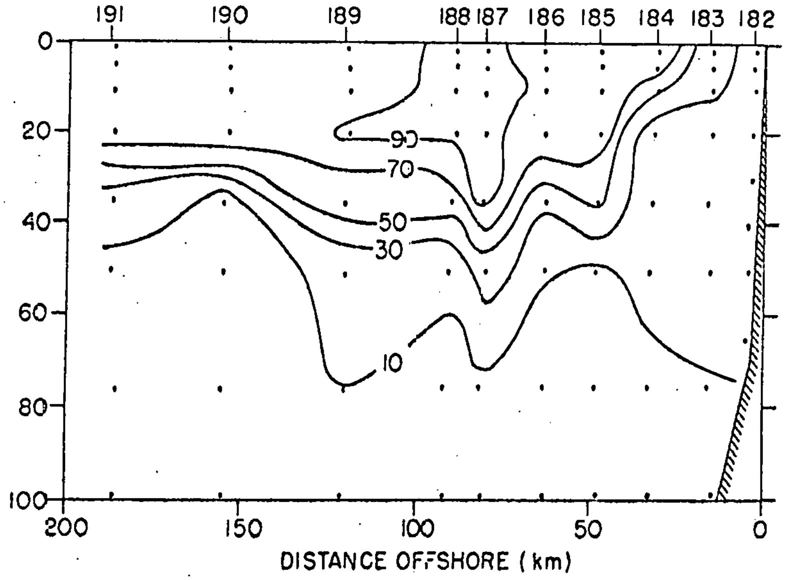
15° S TOT N



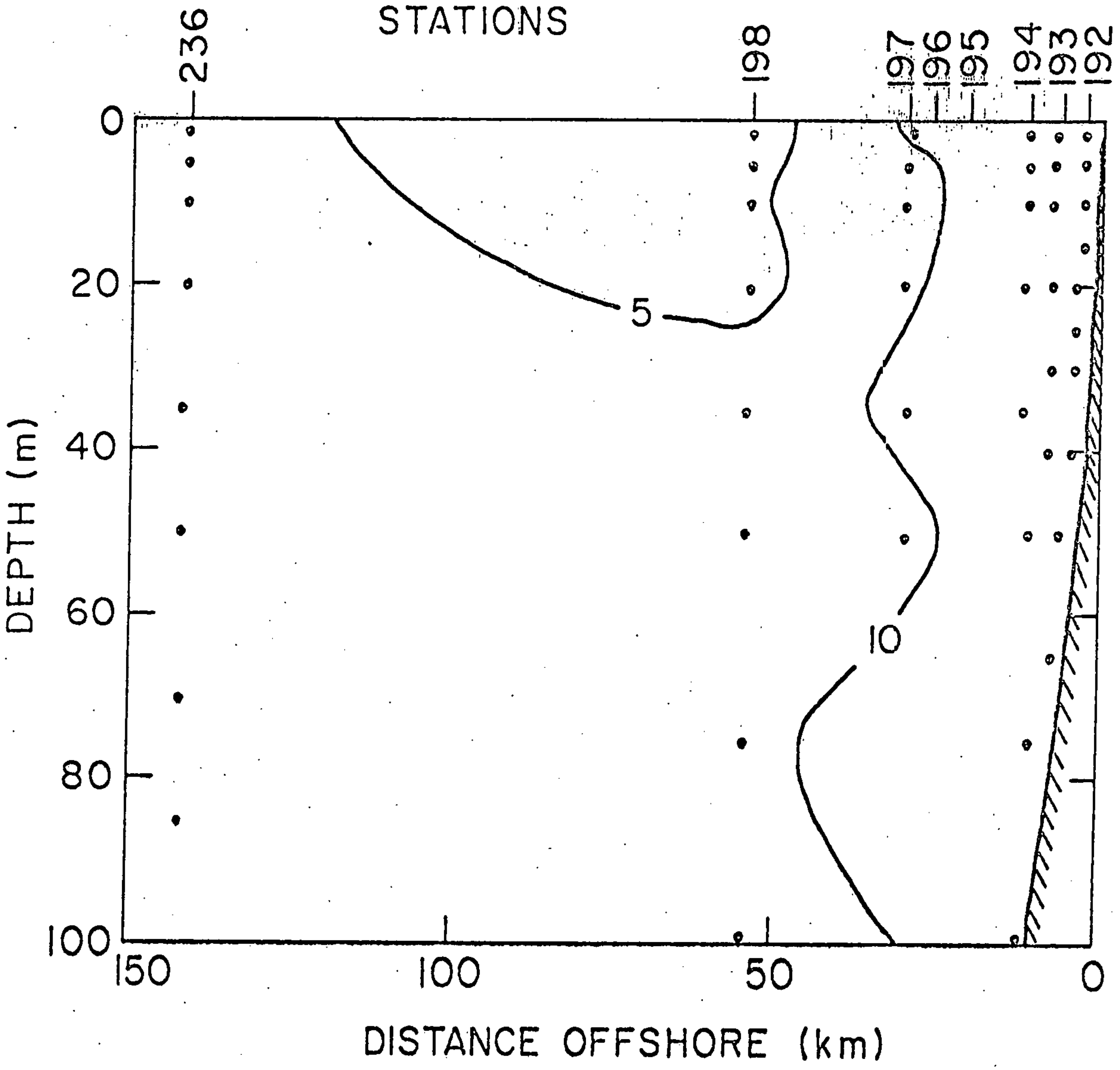
10° S TOT N



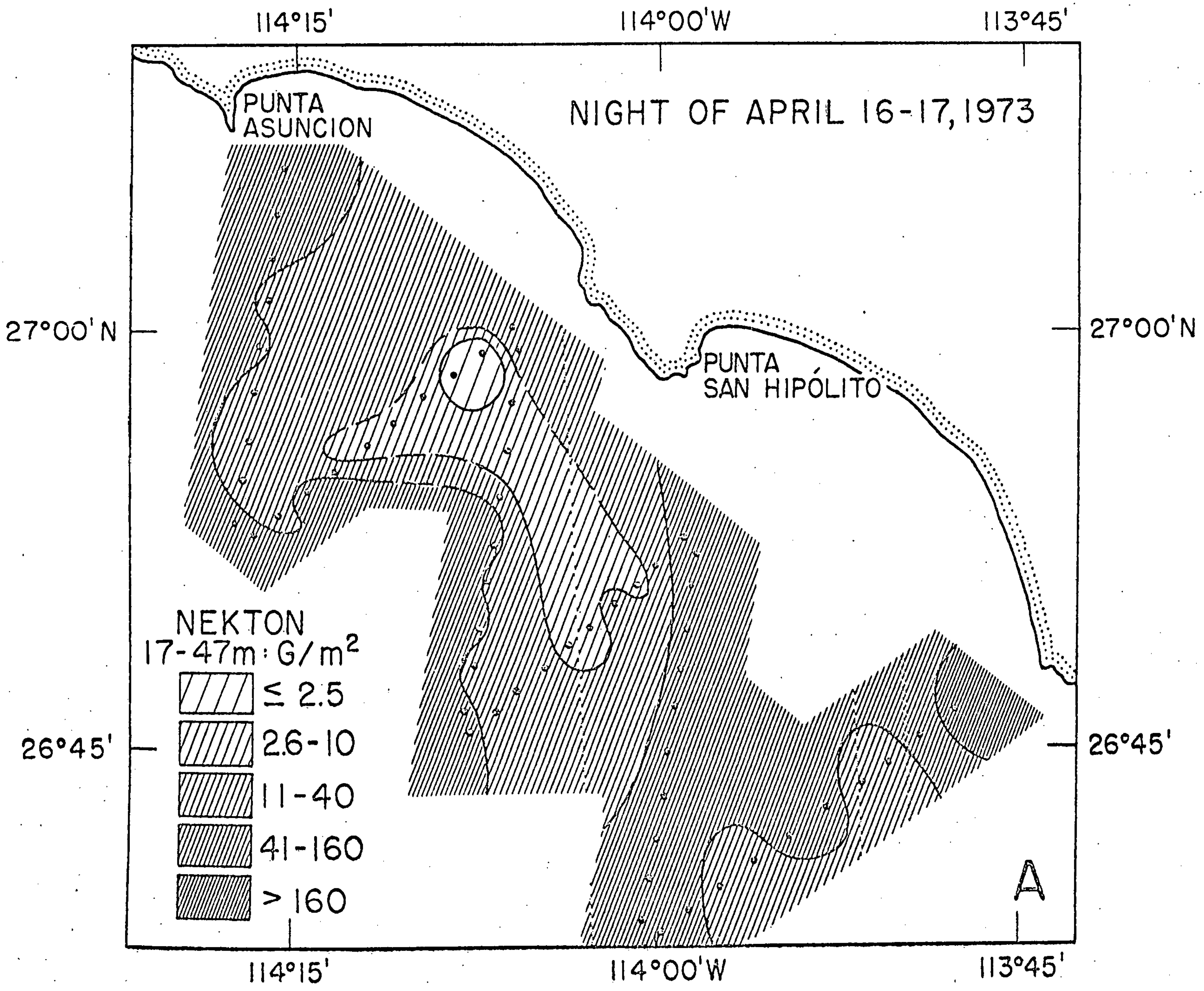
15° S PERCENT REGENERATED N

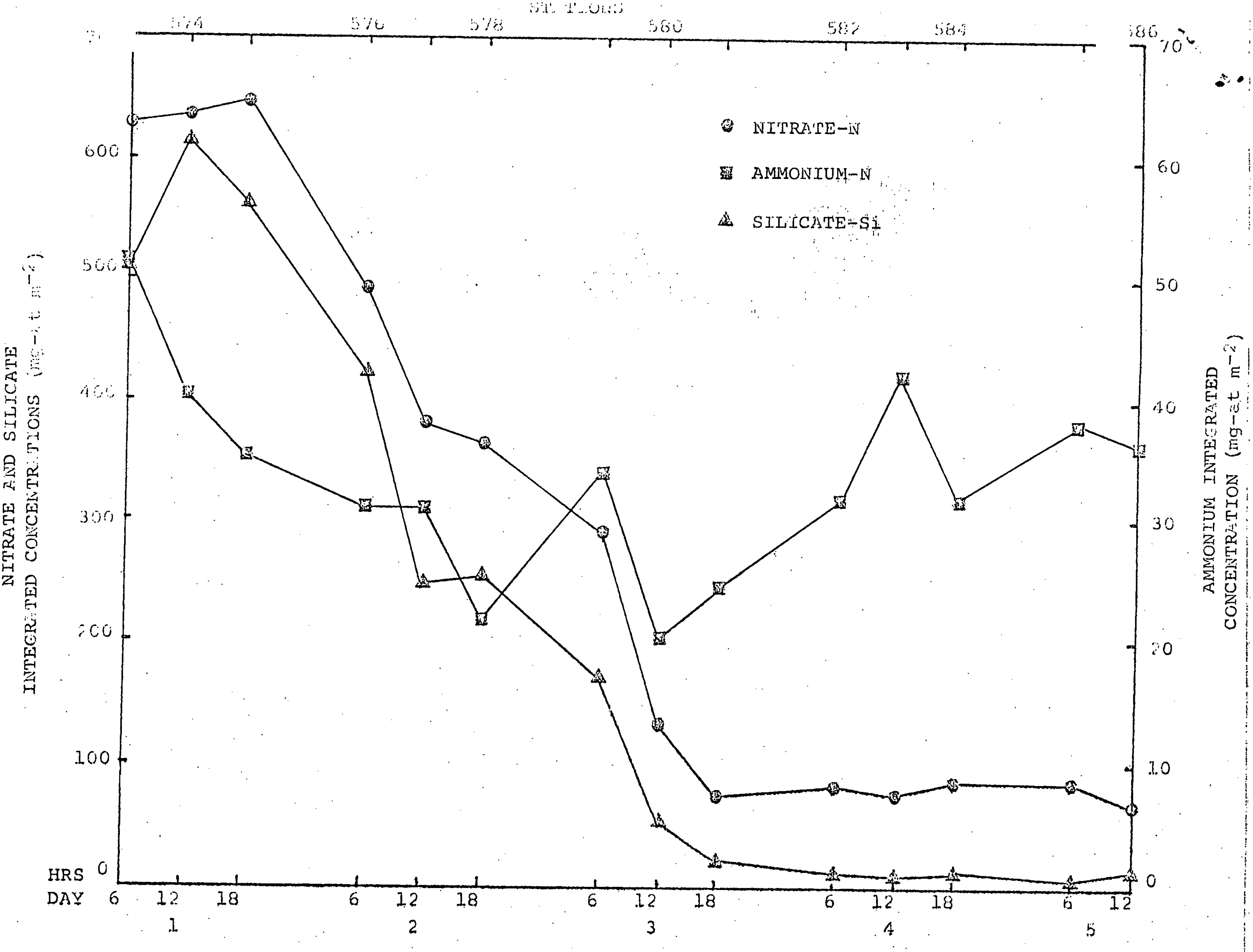


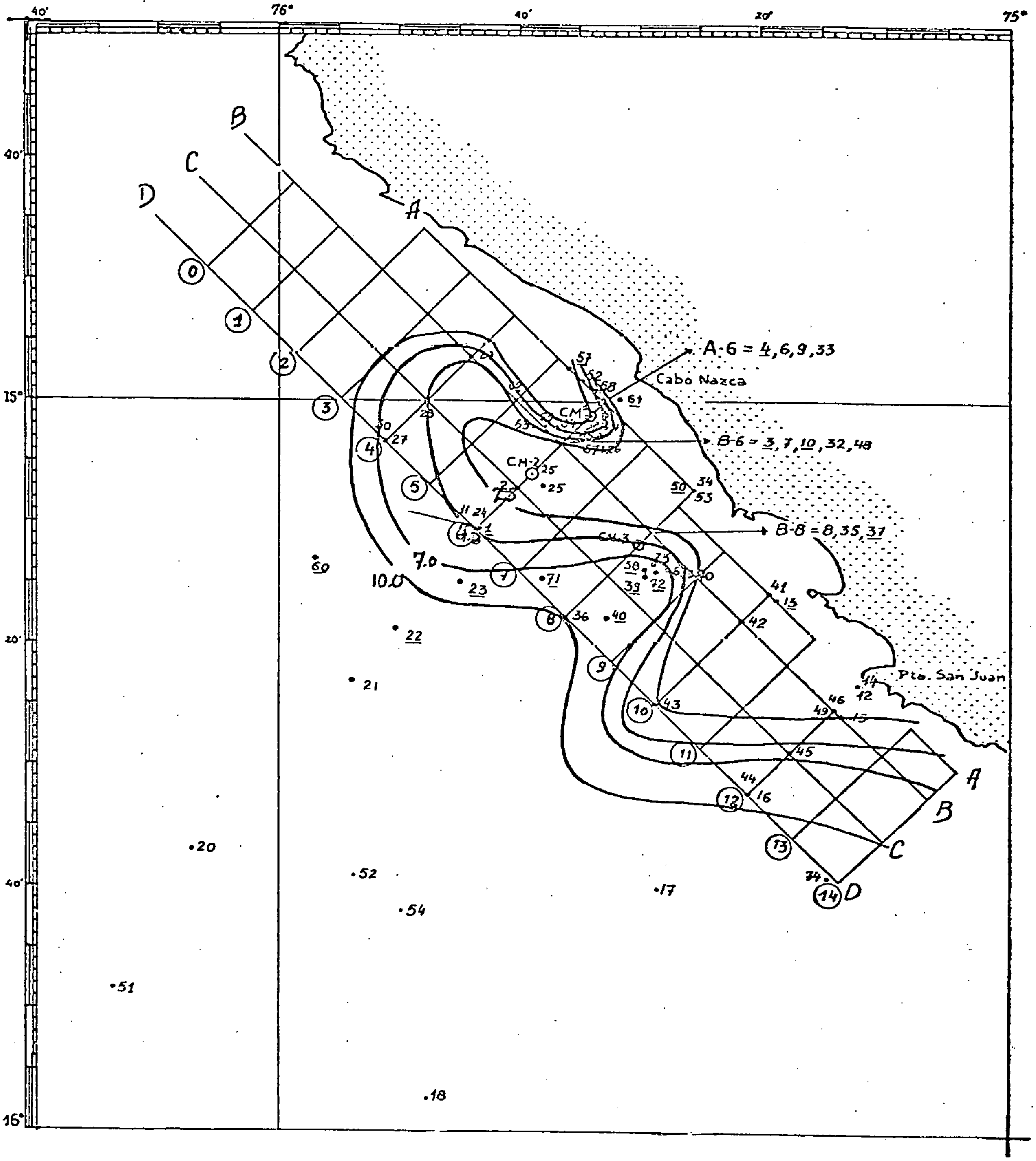
10° S PERCENT REGENERATED N



15°S DON MAM 77 MELVILLE


114°15'
114°00'W
113°45'
PUNTA
ASUNCION
NIGHT OF APRIL 16-17, 1973
27°00'N
27°00'N
PUNTA
SAN HIPÓLITO
NEKTON
17-47m: G/m²
≤ 2.5
2.6-10
11-40
41-160
> 160
26°45'
26°45'
A
114°15'
114°00'W
113°45'


STATIONS
574
576
578
580
582
584
586
NITRATE-N
AMMONIUM-N
SILICATE-Si
NITRATE AND SILICATE INTEGRATED CONCENTRATIONS (mg-at m^{-2})
600
500
400
300
200
100
0
AMMONIUM INTEGRATED CONCENTRATION (mg-at m^{-2})
70
60
50
40
30
20
10
0
HRS
DAY
6
12
18
6
12
18
6
12
18
6
12
18
6
12
1
2
3
4
5



40'
76°
40'
20'
75°
40'
15°
20'
40'
16°
A
B
C
D
A-6 = 4,6,9,33
Cabo Nazca
B-6 = 3,7,10,32,48
B-8 = 8,35,37
Pto. San Juan
CM-1
CM-2
CM-3
7.0
10.0
1.5
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
61
50
34
53
41
15
42
36
40
71
58
39
72
60
23
22
21
20
52
54
51
18
17
43
44
16
45
46
49
12
74
27
30
28
24
25