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Nutrients, Recycling, and Biological Populations in Upwelling Ecosystems

by

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

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ABSTRACT

Nutrient recycling has been studied in the upwelling areas of Baja California, Northwest Africa, and Peru. Regeneration by biological populations in these areas contributes significant quantities of recycled nitrogen which is utilized in productivity processes. Each area has a different combination of organisms which leads to differences in the relative contributions of zooplankton, nekton, or benthos to the nutrient cycles.

Comparisons of ammonium regeneration rates of zooplankton and nekton-micronekton populations in the three upwelling areas show that zooplankton recycle relatively less nitrogen in the Baja California and Peru systems than nekton. In the Northwest Africa upwelling region, however, zooplankton, fish, and benthic inputs are all substantial. In recent years the Peruvian upwelling system has been altered with the decline of the anchoveta population and an increase in the importance of zooplankton in nutrient recycling. The distribution of recycled nitrogen (ammonium and urea) in transects across the shelf at 10°S and 15°S indicates that regeneration is relatively more important at 10°S in the region of the wide shelf. In both areas the distribution of ammonium and urea are not entirely coincident thereby indicating differences in their production and/or utilization.

INTRODUCTION

The upwelling areas in the world's oceans are located off the west coasts of the major continents and are typified by cold, nutrient-rich waters which maintain large phytoplankton populations, especially in the low latitudes where the quantity of light is always sufficient for photosynthesis. Upwelling transports nutrient-rich subsurface water into the euphotic zone where phytoplankton utilize the nutrients in photosysthesis. The uptake of nutrients in primary productivity derived from upwelling has been called "new production" to show that biological processes have not utilized this nutrient since it was introduced into the euphotic zone (Dugdale and Goering, 1964). The uptake of nutrients derived from herbivore excretion or bacterial regeneration has been termed "regenerated production" to show that the production was based on the uptake of nutrients that previously had been used in a biological process in the euphotic zone.

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 from the standpoint of increasing production efficiency of the ecosystem. This topic has only recently been examined in upwelling ecosystems and is the central focus of this paper.

NORTHWEST AFRICA

The JOINT-I experiment investigated the upwelling ecosystem off northwest Africa, in the area of Cape Blanc off Spanish Sahara (Barber, 1977). The region was of great interest because of the numerous countries that were utilizing the fishery resources of the area.

Zooplankton

The distribution of zooplankton across the shelf off Cape Blanc was determined using vertical tows of bongo nets equipped with 102 μm mesh netting. 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. 1). The inshore maximum was observed on a station at the 45 m isobath while the offshore maximum was found in water about 200 m deep. The total biomass was largest (13.19 g dry wt m^{-2}) offshore which was probably the result of large number of euphausiids. The inshore maximum of 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. When the excretion rates were combined with biomass values at each of the locations, the regeneration rates of zooplankton across the shelf (Table 1) were largest at the areas of high zooplankton biomass both inshore and offshore. The inshore rates were relatively larger than the offshore rates 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, resulted in 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 wt 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 wt m^{-2}, cephalopods were about 1 g wet wt m^{-2} and shrimp were about 1.44 g wet wt m^{-2} to give a total of 4.7 g wet wt m^{-2} for demersal biomass (Haedrich, Blackburn, and Brulhet, 1976). 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 2). 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 with ammonium accounting for more than 50% of excreted nitrogen. These rate measurements ranged from 0.42 to 4.62 µg NH_4-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 3). 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-at NH_4-N m^{-2} d^{-1} are released into the water column. 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, the southern shelf station which had a larger ammonium flux rate than the northern shelf station also had a larger ammonium gradient between the water column and the sediments. The sediment subsurface ammonium concentrations in pore water were about 150 μgat l^{-1} in the top 20 cm. 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 production. 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 4 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. 2). 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 was most likely the causal factor for the large observed ammonium concentrations (Huntsman and Barber, 1977).

The outer shelf region, near Station "O", had one of the lowest zooplankton biomasses of the transect and contains a mixture of large and small organisms. The zooplankton regeneration rate was about 70% of the inshore value. Because of the large pelagic nekton biomass in this region, the nekton rate was nearly twice as large as that observed inshore. The release of nitrogen from the offshore sediments was only 33% of the inshore rate and was based largely on the lower sediment bacterial biomass estimates offshore (Watson, 1978). Nutrient pore water concentrations also decreased offshore. 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 to about 10% of its previous level. This decrease in anchoveta biomass was probably accompanied by changes in other nekton stocks such as an increase in the biomass of sardine and hake. In addition, the decline in anchoveta biomass probably resulted in an increase in zooplankton biomass (Walsh, Whitledge, Esaias, Smith, Huntsman, Santander, and De Mendiola, 1980).

Zooplankton

The zooplankton stocks were determined for the Peru upwelling ecosystem at 10°S and 15°S using vertical bongo net tows (Dagg, Cowles, Whitledge, Smith, Howe, and Judkins, 1980). 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 (Table 5). The numerical counts were dominated by *Paracalanus* spp., *Oncea* spp., *Oithona* spp., and Appendicularia (Judkins, in press; and Geynrikh, 1973). Just beyond the shelf break which is located about 100 km offshore the >1050 μm size class showed an increased number of *Calanus* and reflects the same general distributional pattern of biomass that was found in March 1978 (Flint and Timonin, in press). Zooplankton dry weight biomass was larger on the 15°S transect where the shelf is only about 25 km wide. Larger zooplankton (e.g. Eucalanus inermis, Centropages brachiatus and Calanus chilensis) were found at most stations at 15°S. These three species comprised 31% of the biomass on the 15°S transect and 9.6% on the 10°S transect. Zooplankton dry weights over the shelf were similar at 10°S and 15°S. The 100 km wide shelf at 10°S was characterized with a mean ± standard deviation dry weight biomass of 2.30 ± 0.53 g m^{-2} (Table 5). At 15°S the 25 km wide shelf had a biomass of 3.76 ± 2.23 g m^{-2}, an increase of about 60%. In the offshore area at 10°S there was more biomass (3.23 ± 0.81 g m^{-2}) than over the shelf, however, at 15°S the mean dry weight biomass offshore was 9.53 ± 5.36 g m^{-2}, which is 295% of the shelf value.

Zooplankton excretion rate measurements were conducted on large organisms that were also being used in ingestion experiments. The excretory rate 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. These ranges are similar to values measured collected in the northwest Africa upwelling experiments. Size class excretion rates were also determined in 1976 at the same location (Table 6). The rates for Peru were nearly identical to those for northwest Africa 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

With the introduction of acoustic surveys of the pelagic fish stocks, the Peru upwelling ecosystem has been the focus of attention since the decline of the anchoveta biomass in 1972. Speculation exists on the quantity of anchoveta remaining and the possible increase of hake and sardine (Walsh et al., 1980). Acoustic methods were used to estimate the total pelagic nekton biomass in the study area at 15°S. 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 pelagic biomass of 127 g wet wt 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 wt 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 7) 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 for the silverside (5.2 μg N mg dry wt^{-1} d^{-1}) was comparable to the rate measured for Sardinella spp. off northwest Africa. The sardine and anchoveta were characterized by lower rates (2.2 and 1.7 μg N mg dry wt^{-1} d^{-1}.

Nutrient Regeneration Budget

A nitrogen budget was constructed for the shelf and offshore Peruvian upwelling areas at 15°S using the nekton ammonium excretion rates combined with mean nekton biomass estimates (Table 8). The calculation assumed all the inshore nekton biomass was anchoveta since a good estimate of sardine biomass was not available. The shelf nitrogen budget, which used the 3 inshore stations, estimated the zooplankton regeneration rates to be 4.11 mg-at m^{-2} d^{-1} (Table 5). The loss of ammonium from the sediments, based on S^{35} experiments, estimated the quantity of carbon utilized by the bottom community to be ∿ 91 g C m^{-2} y^{-1} (Rowe, personal communication). Converting to nitrogen using a C:N ratio of 5, about 4.16 mg-at N m^{-2} d^{-1} were released from the sediments. The sediments were relatively rich in carbon, i.e. the C:N ratio was greater than 5 so this could be an underestimate. The ammonium-N regeneration rate 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 estimated offshore pelagic nekton biomass and jack mackerel excretion rates. The demersal nekton regeneration rate was calculated from an estimated standing stock for hake (Gulland, 1970) and excretion rates for a starry flounder (Wood, 1958). The resulting regeneration rate for demersal stocks was very low (0.07 mg-at m^{-2} d^{-1}) which may be the result of an underestimated biomass of 60,000 metric tons for the whole Peru upwelling area (∿4.3 g dry wt m^{-2}). The zooplankton ammonium regeneration rate, calculated using the five offshore stations (Table 5), 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 benthic regeneration rate for the shelf sediments was used for the offshore budget because there were no strong across shelf gradients in the S^{35} 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. The cross shelf distribution of ammonium and urea at 15°S and 10°S (Figs. 3a-3d) each exhibited a maximum concentration about 50 to 100 km offshore. At 15°S the maximum concentration for ammonium and urea was located in the surface waters beyond the shelf break about 25 km offshore. The elevated concentrations of ammonium and urea occurred over the shelf at 10°S (shelf break at ∿ 100 km) near the bottom of the euphotic zone. Careful examination of the urea distributions at 15°S and 10°S revealed that the maxima were located inshore of their respective ammonium maxima. This could be the result of different utilization patterns 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 was larger for nekton than for zooplankton (Table 3). The nekton ammonium excretion over the shelf is nearly the same as for zooplankton (4.11/3.86 = 106%), while offshore the zooplankton ammonium regeneration was comparatively much larger (7.33/1.72 = 426%). So the urea maximum inshore was probably the result of regeneration by the anchovy and sardine populations while the more offshore ammonium maximum was 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. 3e and 3f) 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 was characterized by a total nitrogen concentration of more than 25 μg at 1^{-1} with a sharp gradient about 125 km offshore where the concentration decreased to less than 5 μg at 1^{-1}. The nearshore area at 10°S didn'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 more uptake-regeneration cycles while over the shelf. This suggests 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 total nitrogen concentration at 15°S consisted of less than 10% regenerated nitrogen in the nearshore area where nitrate concentrations were high (Fig. 3g), but the percentage increased to greater than 50 beyond the shelf break. In a similar fashion at 10°S the inshore water had a low percentage of regenerated nitrogen but increased to values greater than 90% in the surface layer at the shelf break (Fig. 3h).

Dissolved organic nitrogen (DON) as measured by the ultraviolet irradiation technique (Armstrong, Williams, and Strickland, 1966) exhibited a distribution with uniformly high concentrations nearshore as if the source of DON was in deep water and lower concentrations near the surface offshore where uptake may have occurred (Fig. 4). The distribution of DON was distinctly different than ammonium or urea 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, Kelley, Whitledge, Mac Isaac, and Huntsman, 1974). 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*, was probably the dominant herbivore during the upwelling season (Walsh, Whitledge, Kelley, Huntsman, and Pillsbury, 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 range in zooplankton biomass in March 1972 was 0.2 to 1.0 g wet wt m^{-3} (mean of 0.6 g wet wt m^{-3}) and was composed principally of stage V nauplii of *Calanus helgolandicus*. In April 1973 the zooplankton community consisted of 72% copepodites, 22% adult *Acartia* and 6% *Calanus* with a mean estimated biomass of 1.15 g wet wt m^{-3}. It appears then that the zooplankton biomass in the Baja upwelling system increased from about 1.15 to 6.38 g dry wt m^{-2} during the onset 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 when combined with the biomass, were used to estimate ammonium regeneration.

Micronekton

Using acoustic gear, the red crab, *Pleuroncodes planipes*, was estimated to have a pelagic wet weight biomass of 100 g m^{-2} (Blackburn and

Thorne, 1974) although earlier in the 1973 cruise a series of net tows resulted in biomass values of ∿ 5 g wet weight m^{-3}. During the previous year biomass values of 7 g wet wt m^{-3} were measured (Walsh et al., 1977). The March biomass of the red crab was about 7 g wet wt m^{-3} and the April biomass was ∿ 5 g wet wt 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 for this organism.

The red crabs also gather in large populations on the bottom, especially those 3 years or older (Boyd, 1962; Smith, Harbison, Rowe, and Clifford, 1975). Bottom photographs were used to estimate a density of about 8.2 red crab m^{-2} and the mean weight of these benthic crabs were 5.58 g $animal^{-1}$ (Walsh et al., 1977). The distribution of red crabs on the bottom was very patchy, but their biomass could be as high as 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 9). 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 had a larger zooplankton regeneration rate (6.28 mg-at N 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-N released m^{-2} d^{-1} by all of the Pleuroncodes. The drop in the red crab regeneration rate 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), resulting in an excess of 16% of ammonium produced.

DISCUSSION

Nutrient regeneration in a stable environment like the euphotic zone in an oceanic gyre is vital in maintaining 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 processes occur 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. 5). The ammonium increased during the latter part of the drogue study where it was measured at elevated concentrations. The 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. 6a). With some delay the phytoplankton start active uptake of the nitrate resulting in an increase in the biomass. As the newly upwelled water enters the euphotic zone 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. 6b). 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 the region where 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 interactions in various ecosystems (Dugdale and Whitledge, 1970; Walsh and Dugdale, 1971; Walsh, 1975; and Walsh, 1977) 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.

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 10). This 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.

Zooplankton rank 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, Stevenson, Eppley, and Brooks, 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 northwest Africa eco system and was slightly smaller in Peru, Cape Timiris off northwest 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 time lag 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.

For the nearshore summer upwelling areas off Washington and Oregon, Jawed (1973) 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 it was presumed that large concentrations of nitrate reduced the importance of ammonium in the ocean.

Of the three upwelling systems, the regeneration of ammonium by nekton is most important in the two areas where commercial quantities of small pelagic nekton exist. Since the decline in the anchoveta biomass, Peru has slightly smaller regeneration rates than northwest Africa while the clupeoid 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 that the clupeoid occupies 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 undertaken for any areas with large benthic fish populations.

The regeneration of nitrogen from sediments appears to be most important in northwest 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 be lost by sinking in Baja California, however, the older benthic red crabs are possibly using that as a principal food source.

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 coastal upwelling regions constituted 30 to 90% of the total (Sorokin, Korsak, Mamaeva, and Kogelschatz, in press). So the focus of zooplankton sampling may have missed a significant component in the upwelling ecosystem.

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, Renger, Venrick, and Mullin, 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 microzooplankton smaller than 183 μm or from vertical turbulent diffusion. Urea was also considered to be an important nitrogen source.

The regeneration of relatively large quantities of nitrogen by zooplankton and nekton populations implies that these organisms must be major consumers of primary (and secondary) productivity. The excretion rates measured for zooplankton and nekton can be used to estimate their ingestion rates if growth and excretion are assumed to be the two main pathways of assimilated nitrogen. A previous estimate indicates that from 54 to 61 percent of the daily phytoplankton nitrogen productivity was consumed by the Peruvian anchoveta in 1969 (Whitledge, 1978). Zooplankton ingestion was not estimated at that time because very few biomass or excretion rate data were available. The assimilation efficiency of both zooplankton and nekton used in calculations of ingestion (Table 11) is 70%. The growth rates are obtained from literature values of estimated secondary productivity in each of the upwelling areas or from laboratory rates of similar species. The zooplankton and nekton combined ingestion of primary productivity ranged from 62% in Peru (April 1977) to 76% in northwest Africa, while the Baja California value was 65%. The absolute ingestion rates were quite different than the percentage of productivity grazed. The smallest ingestion rate was estimated to be 12.20 mg-at N m^{-2} d^{-1} for Peru with 49% coming from nekton and northwest Africa was 16.62 mg-at m^{-2} d^{-1} with 31% of ingestion by nekton. Baja California had a value of 23.64 mg-at N m^{-2} d^{-1} grazed with nekton (red crabs) consuming 60% of that amount. So the zooplankton in Peru had ingestion rates of about 54 to 66% of the zooplankton rates in the two other systems and Peruvian nekton ingestion rates were 42 to 116% of the rate of northwest Africa and Baja California nekton. These values are a reflection of the low primary productivity measured on the C-line in Peru in 1977 and the relatively low biomass of zooplankton and nekton populations compared to the other upwelling systems. The trophic structure of the zooplankton indeed showed that no more than 50% of the zooplankton were filter feeders at any location across the shelf (Flint and Timonin, in press). In any event, this indicates that more productivity may be sinking to be incorporated in benthic processes or depleting oxygen concentrations to lower than normal values (Dugdale, Goering, Barber, Smith, and Packard, 1977). In 1978 it was estimated that 12% of primary productivity sinks to the bottom (Vinogradov, Shushkima, and Lebedeva, in press) when the lowest concentration of oxygen observed was 0.12 mℓ ℓ^{-1} (Bordovsky, Gasarova, Domanov, and Stunghas, in press). The 1976 observations of anoxic conditions must have been the result of increased sinking of organic matter and the amount sinking would probably have to be larger than 12% of primary production.

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Table 1. 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 2. 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 3. 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		Silicate-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	2.29	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

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

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

Table 4. 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*

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* Unpublished nitrogen uptake data of MacIsaac and Dugdale.

Table 5. 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 µm	102-223 µm	223-505 µm	505-1050 µm	>1050 µm	Total	102-223 µm	223-505 µm	505-1050 µm	>1050 µm	Total
10°S											
182	60	.408	3.047	.752	5.008*	9.215*	.91	7.01	.53	–	8.45
183	90	.383	1.308	1.058	2.594*	5.343*	.85	3.01	.74	–	4.60
184	100	.171	.558	.419	1.770	2.918	.38	1.28	.29	.67	2.62
185	100	.123	.586	.660	1.114	2.483	.27	1.35	.46	.42	2.50
186	100	.092	.676	.431	.895	2.094	.21	1.55	.30	.34	2.40
188	100	.120	.545	.376	.645	1.686	.27	1.25	.26	.25	2.03
189	100	.103	.655	.598	2.619	3.975	.23	1.51	.42	1.00	3.16
190	100	.105	.458	.432	1.363	2.358	.23	1.05	.30	.52	2.10
191	100	.072	.405	.174	2.692	3.343	.16	.93	.12	1.02	2.73
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
193	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

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* phytoplankton contamination in sample.

Table 6. Nitrogen release (μg N mg dry wt^{-1} d^{-1}) by zooplankton off Peru. Values are means ±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 7. 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})	
<u>Engraulis</u> <u>ringens</u> (7)	1.70	1.74±1.48	ref 1
<u>Sardinops</u> <u>sagax</u> (4)	1.52	2.19±0.24	
<u>Trachurus</u> <u>symmetricus</u> (1)	47.5*	1.26	ref 2
<u>Austromenidia</u> <u>regia</u> <u>regia</u> (14)	3.26	5.17±1.78	

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

Table 8. 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**

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* 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 9. 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*

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* From Whitledge and Conway (1977).

Table 10. 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
Upwelling Areas							
NW Africa							
Cape Blanc Shelf	72	33	15	-	-	24	
Cape Blanc Outer Shelf	61	24	29	-	-	8	
Cape Timiris Shelf	15	15	-	-	-	-	Herbland et al., 1973
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
Coastal Areas							
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
Open Ocean							
N. Pacific Gyre	44-83	44-83	-	-	-	-	Eppley et al., 1973

Table 11. Zooplankton and nekton ingestion rates and percent of daily phytoplankton grazed. Units are g dry wt m^{-2} and mg-at m^{-2} d^{-1}

	Northwest Africa	Peru	Baja California
Zooplankton			
Zooplankton biomass	3.78	4.41	6.38
Zooplankton growth	0.24	0.28	0.40
Zooplankton excretion	7.82	4.11	6.28
Zooplankton assimilation	8.06	4.39	6.68
Zooplankton ingestion	11.51	6.27	9.54
Nekton			
Nekton biomass	10.55	31.80	7.50
Nekton growth	0.10	0.29	0.47*
Nekton excretion	3.48	3.86	9.40
Nekton assimilation	3.58	4.15	9.87
Nekton ingestion	5.11	5.93	14.10
Total ingestion	16.62	12.20	23.64
Phytoplankton growth-N	23.5	21.7	39.5
% daily phytoplankton-N production grazed	71	56	60

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*Calculated using Pleuroncodes planipes rates (Blackburn, in press).

FIGURE LEGENDS

Figure 1. 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).

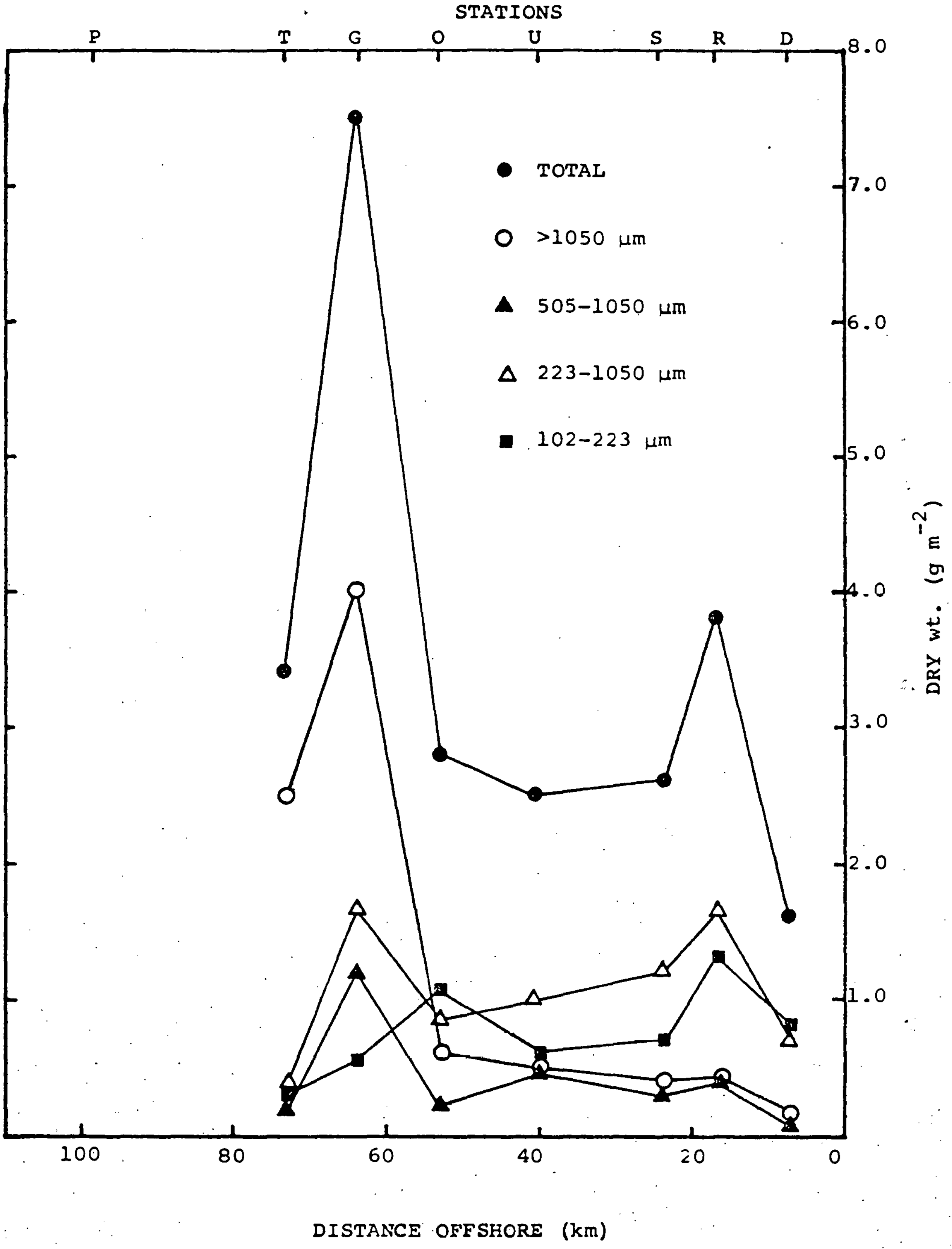
Figure 2. Concentration of ammonium (μg-at l^{-1}) on a cross shelf transect near 21° 40'N off northwest Africa.

Figure 3. 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 4. Concentration of dissolved organic nitrogen (μg-at l^{-1}) on a cross shelf transect near 15°S off Peru.

Figure 5. 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 6. 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).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8.0
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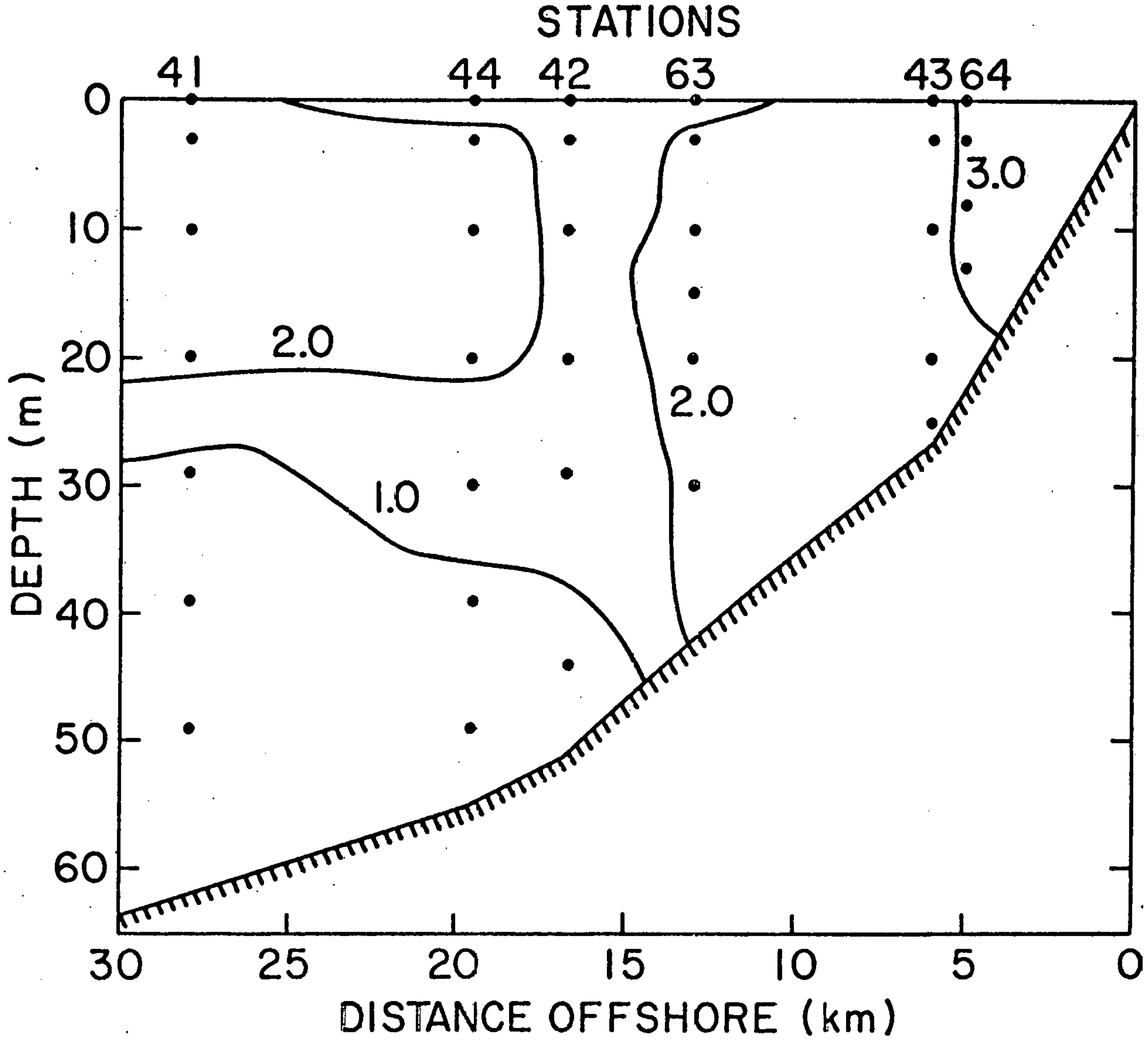
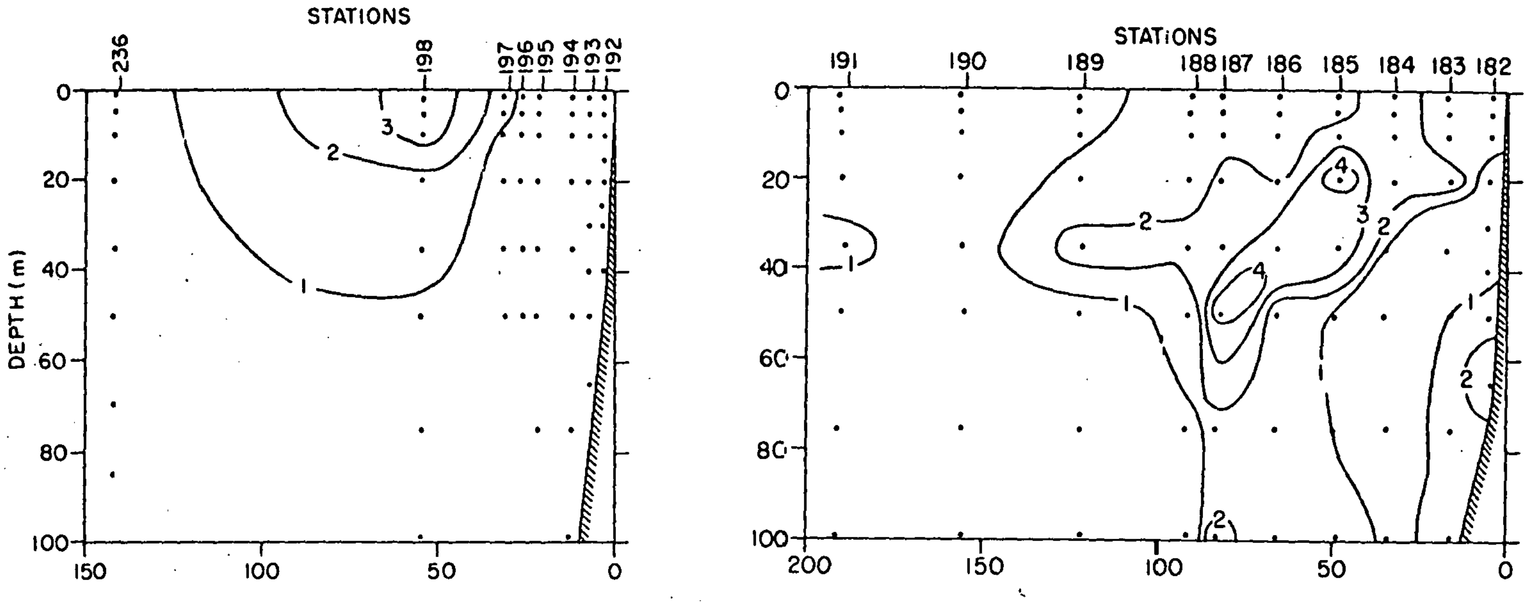
1.0
DRY wt. (g m⁻²)
100
80
60
40
20
0
DISTANCE OFFSHORE (km)

Fig. 1



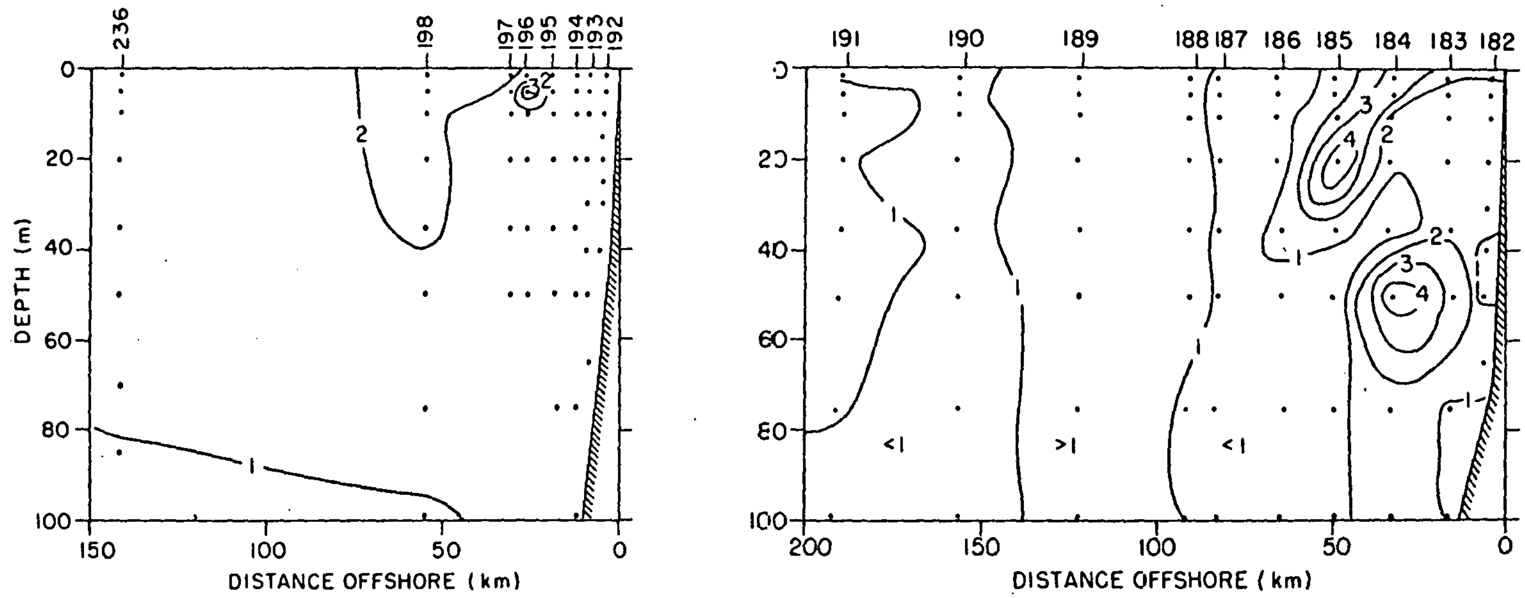
STATIONS
41
44
42
63
43
64
0
10
20
30
40
50
60
DEPTH (m)
2.0
1.0
2.0
3.0
30
25
20
15
10
5
0
DISTANCE OFFSHORE (km)

Fig. 2



15° S AMMONIUM

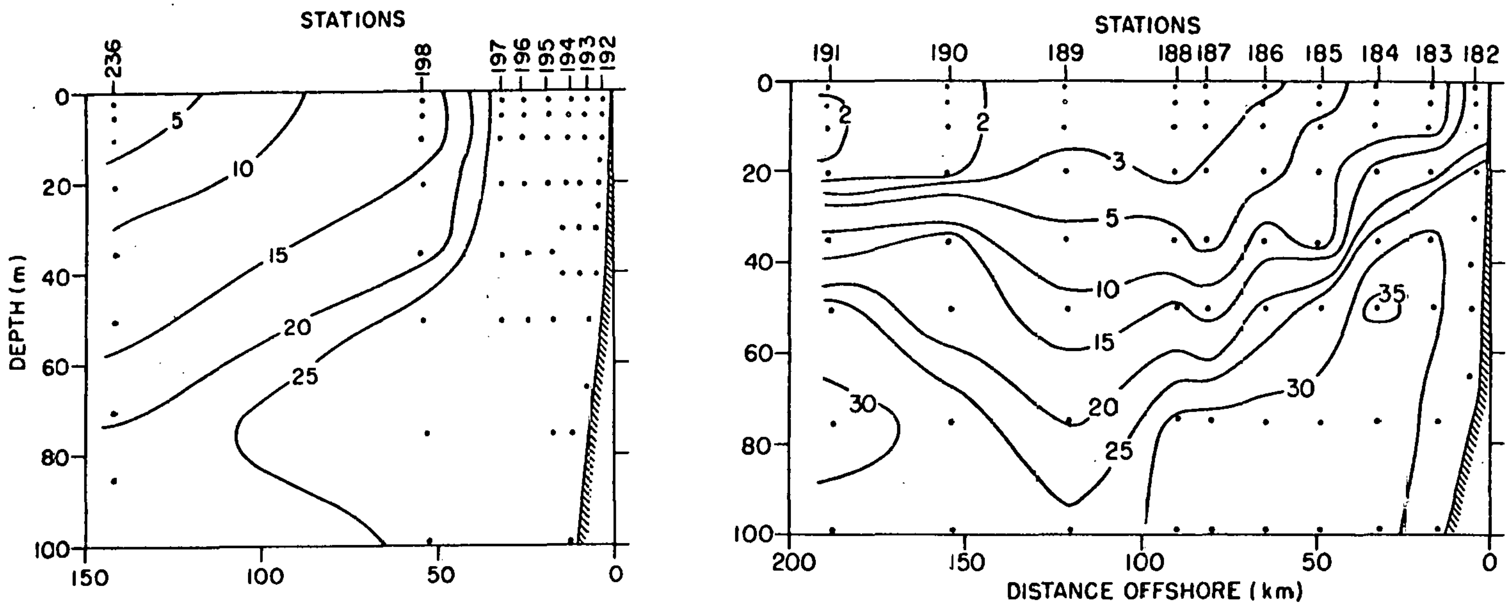
10° S AMMONIUM



15° S UREA

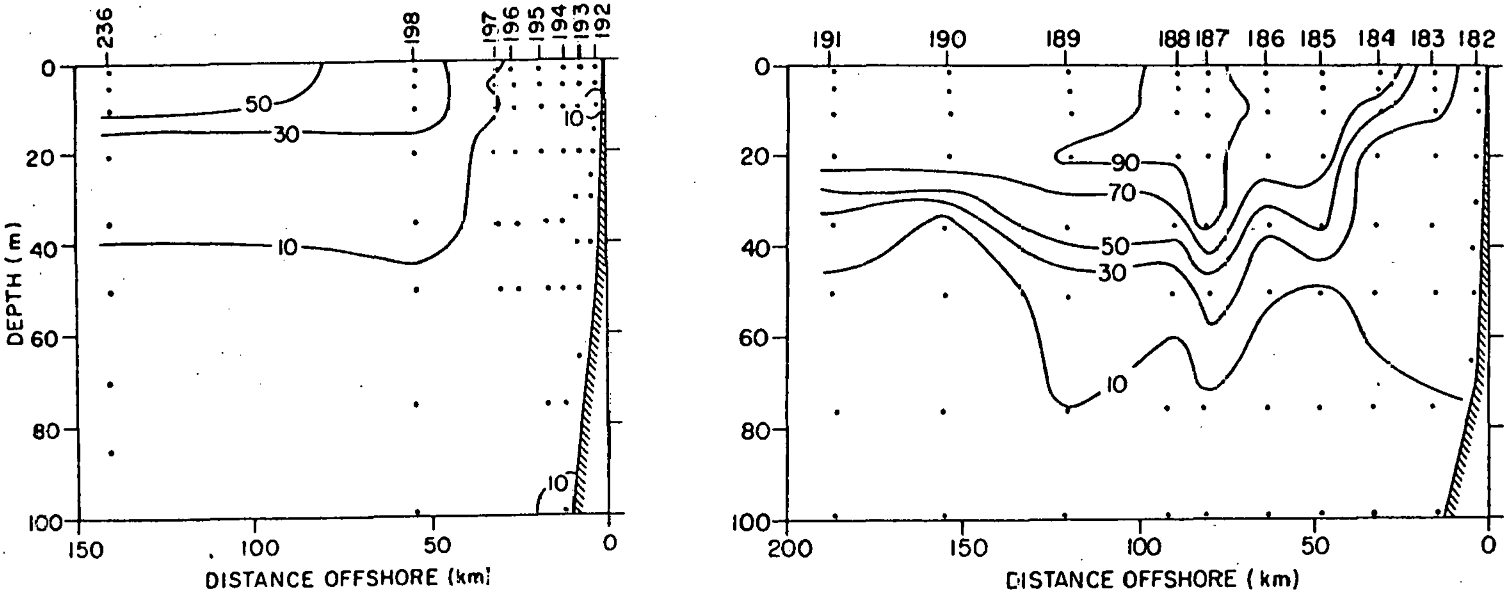
10° S UREA

Fig. 3a-d



15° S TOT N

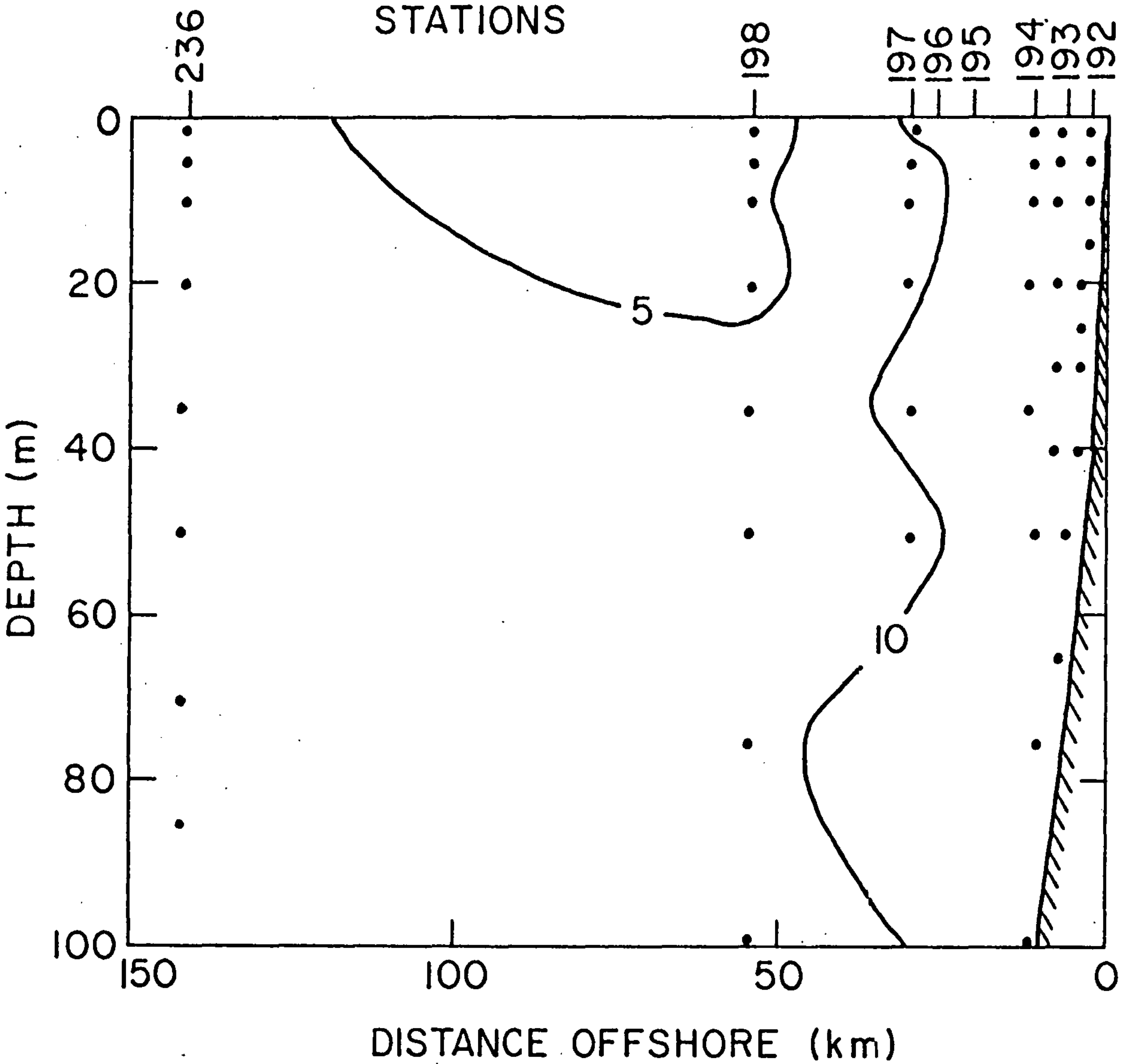
10° S TOT N



15° S PERCENT REGENERATED N

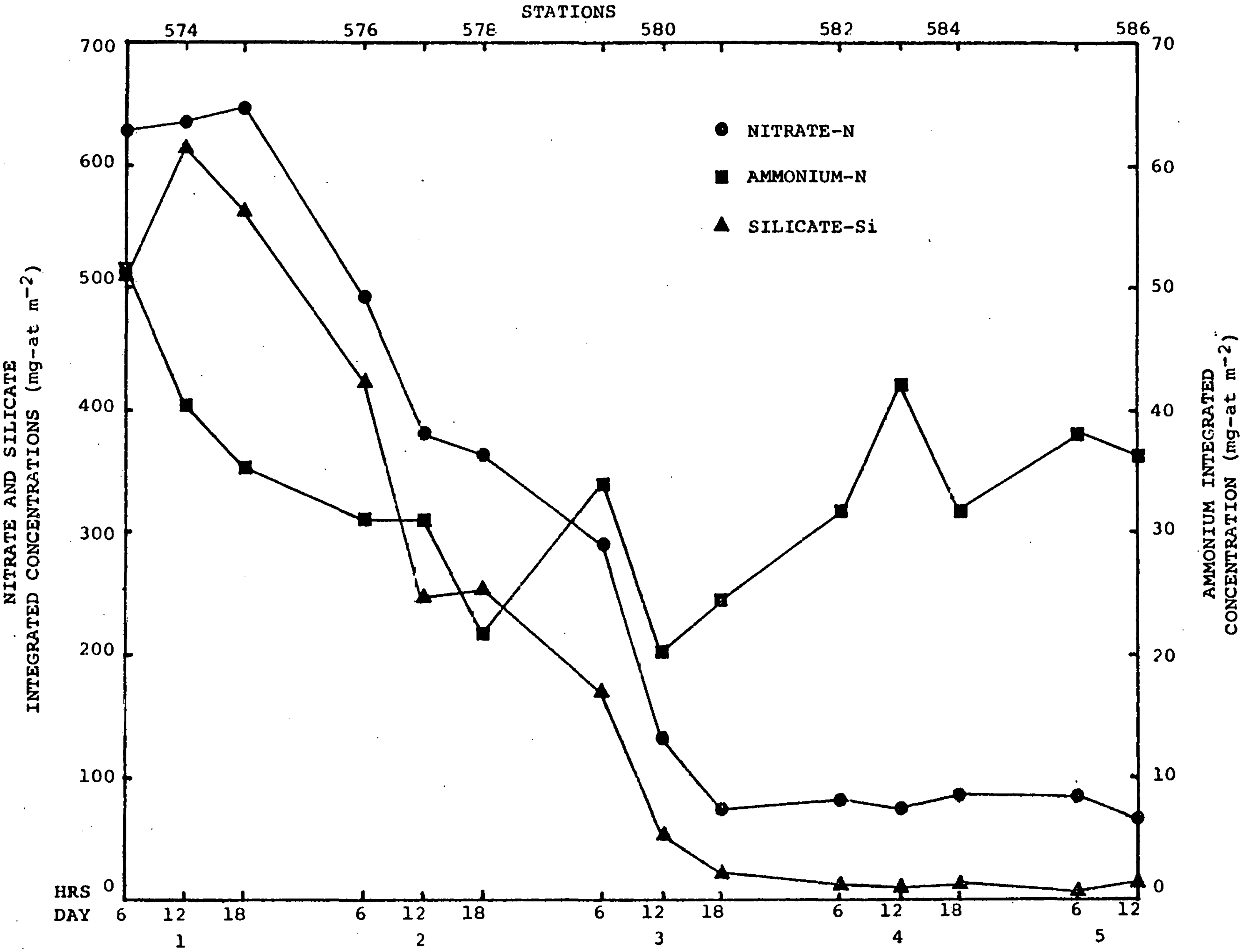
10° S PERCENT REGENERATED N

Fig. 3e-h



15°S DON MAM 77 MELVILLE

Fig. 4



STATIONS
574
576
578
580
582
584
586
NITRATE AND SILICATE INTEGRATED CONCENTRATIONS (mg-at m^{-2})
AMMONIUM INTEGRATED CONCENTRATION (mg-at m^{-2})
700
600
500
400
300
200
100
0
70
60
50
40
30
20
10
0
● NITRATE-N
■ AMMONIUM-N
▲ SILICATE-Si
HRS
DAY
6
12
18
6
12
18
6
12
18
6
12
18
6
12
1
2
3
4
5

Fig. 5

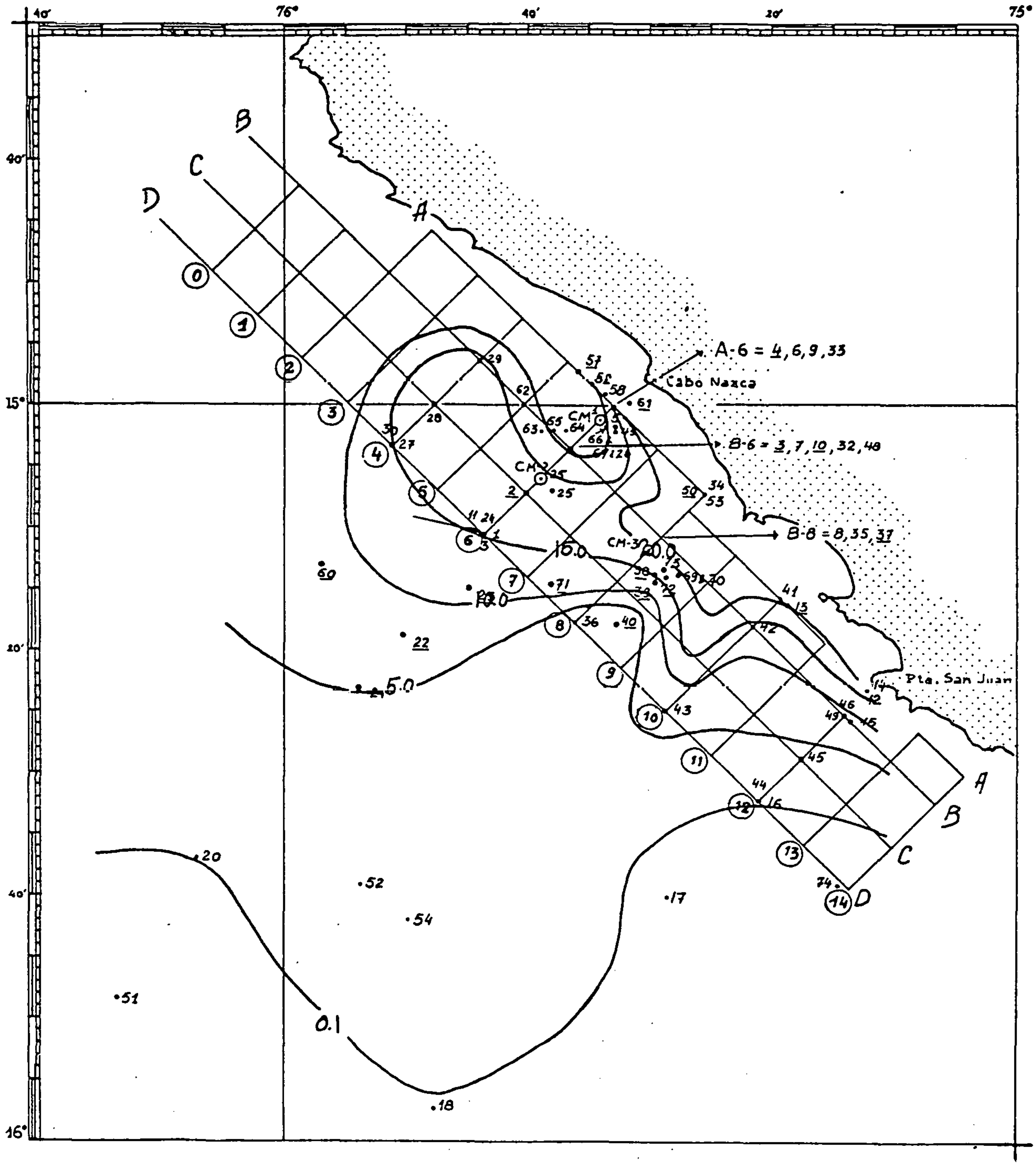

40'
76°
40'
20'
75°
40'
15°
20'
40'
16°
A
B
C
D
A
B
C
D
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
A-6 = 4,6,9,33
Cabo Nazca
B-6 = 3,7,10,32,48
B-8 = 8,35,31
Pta. San Juan
CM-1
CM-2
CM-3
20.0
10.0
12.0
5.0
0.1
29
28
27
30
62
63
65
64
66
57
58
61
2
25
50
34
53
11 24
1
3
71
69
22
21
36
40
38
39
41
13
42
43
44
16
45
46
49
15
14
12
74
20
52
54
17
51
18

Fig. 6a

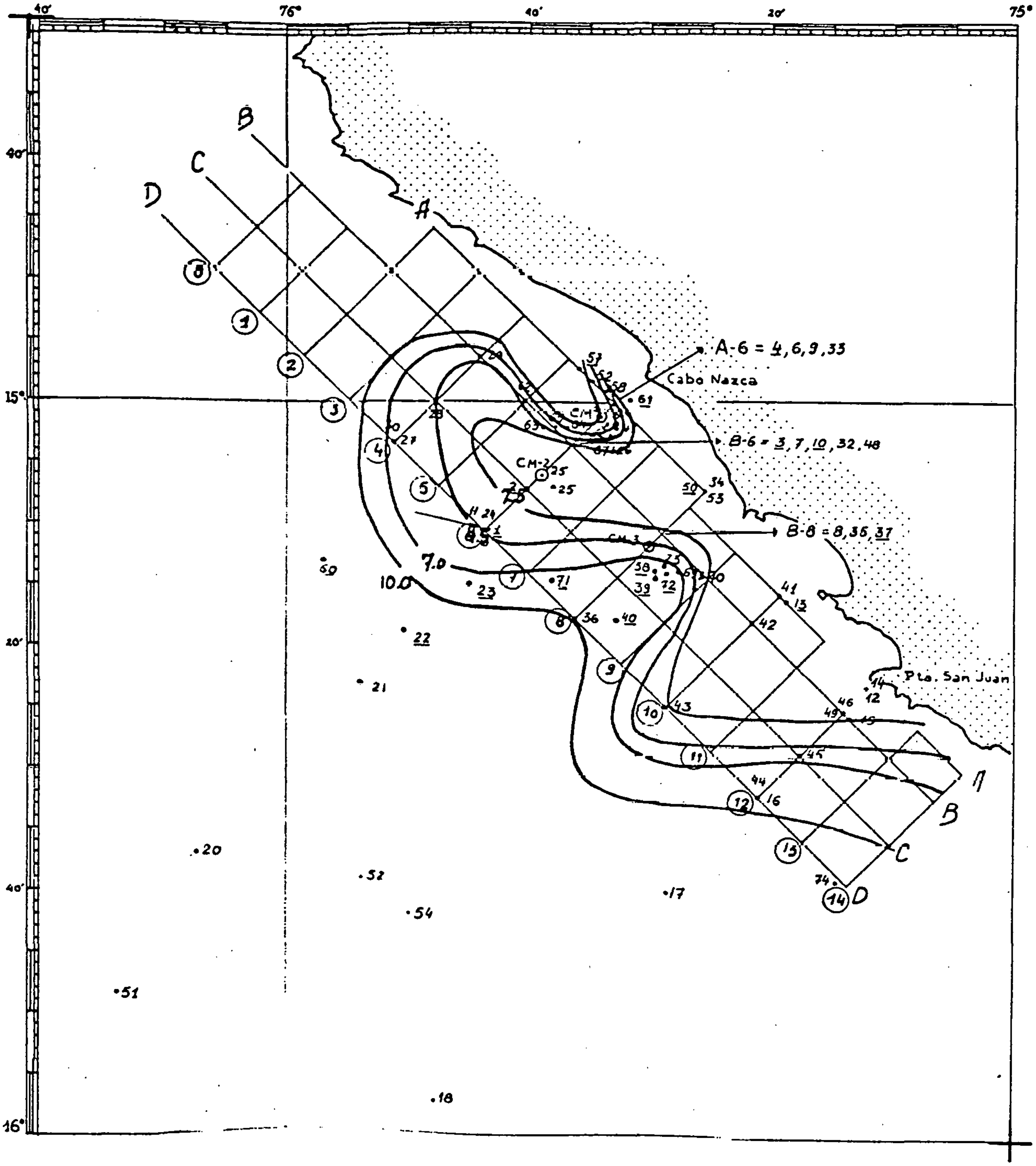

40'
76°
40'
20'
75°
40'
15°
20'
40'
16°
A
B
C
D
A-6 = 4,6,9,33
Cabo Nazca
B-6 = 3,7,10,32,48
B-8 = 8,35,37
Pto. San Juan
CM-1
CM-2
CM-3
7.0
10.0
25
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
20
21
22
23
24
25
27
28
29
34
36
38
39
40
41
42
43
44
45
46
49
50
51
52
53
54
57
58
61
63
69
71
72
73
74

Fig. 6b