REGENERATION OF NITROGEN BY THE NEKTON AND ITS SIGNIFICANCE IN THE NORTHWEST AFRICA UPWELLING ECOSYSTEM

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ABSTRACT

Nitrogen and phosphorus excretion rates were measured for octopus and six species of fish in the northwest Africa upwelling region near lat. 21°40'N. The nekton excretion rates ranged from 0.44 to 4.61 μg NH_4-N/mg dry weight per day and the whole body C:N (by atoms) of the specimens was 4.85. The calculated nitrogen turnover time in the well-fed specimens was about 65 days. The estimated rates of ammonium regeneration over the shelf (<200 m) for all the nekton was about 3 mg-at/m² per day which was 27% of the phytoplankton ammonium uptake requirements. On the slope (>200 m) the nekton regenerated 1.8 mg-at/m² per day which was 11% of phytoplankton ammonium uptake. The ammonium production by bacterioplankton, zooplankton, nekton, and sediments accounted for 226% of the ammonium utilized in the nearshore shelf region and 83% in the offshore region.

Ammonium is an important source of nitrogen for phytoplankton growing in the sea. Estimates of nutrient uptake using ^{15}N tracer experiments have indicated that ammonium regeneration may be responsible for 44 to 83% of nitrogen utilized by phytoplankton in the North Pacific gyre (Eppley et al. 1973) and up to 50% in the Peru upwelling system (Dugdale and Goering 1970). The source of ammonium in the marine environment may be recycled through any of several animal groups. Ammonium regeneration in Long Island Sound was found to be predominantly from zooplankton and benthos (Harris 1959), while in Georgia coastal waters, phosphate regeneration (and presumably ammonium regeneration) was produced by zooplankton that are large enough to be sampled adequately by nets (Pomeroy et al. 1963).

The regeneration of nitrogen by zooplankton has been examined in several coastal upwelling ecosystems. The red crab, *Pleuroncodes planipes*, copepodites, and adult *Acartia* regenerated about 16% of total phytoplankton nitrogen uptake (Whitledge in press) in the Baja California upwelling system while zooplankton in the Peru upwelling ecosystem regenerated about 15% of total nitrogen uptake (Whitledge 1978). In the northwest Africa upwelling region off Cape

Blanc (Fig. 1), the zooplankton were shown to recycle 33% of nitrogen productivity over the shelf (Smith and Whitledge 1977).

The focus in most regeneration studies has been zooplankton because fish and benthic organisms have relatively smaller biomasses in many oceanic areas. However, the biomass of the anchoveta in the Peru upwelling ecosystem was estimated to be 15 times greater than the zooplankton biomass (Dugdale and Goering 1970), and the fish regenerated 22% of the phytoplankton total nitrogen uptake and 59% of the ammonium uptake (Whitledge 1978). Since the fish in the Peru upwelling system produce a significant quantity of recycled nitrogen, another major fishing area, the northwest Africa upwelling system, was studied to examine the relative importance of nutrients regenerated by fish in comparison with that by zooplankton (Smith and Whitledge 1977), benthic processes (Rowe et al. 1977), and bacterioplankton (Watson 1978). In addition, the biology of many species of fish has not been investigated with respect to changes of nitrogen excretion rates over time and under various conditions so an attempt was made to increase our understanding of this elimination process.

METHODS

Near-bottom fish specimens of *Diplodus senegalensis*, *Pegellus couperi*, *Cantharus cantharus*, and *Pomadasys incisus* were captured in bottom
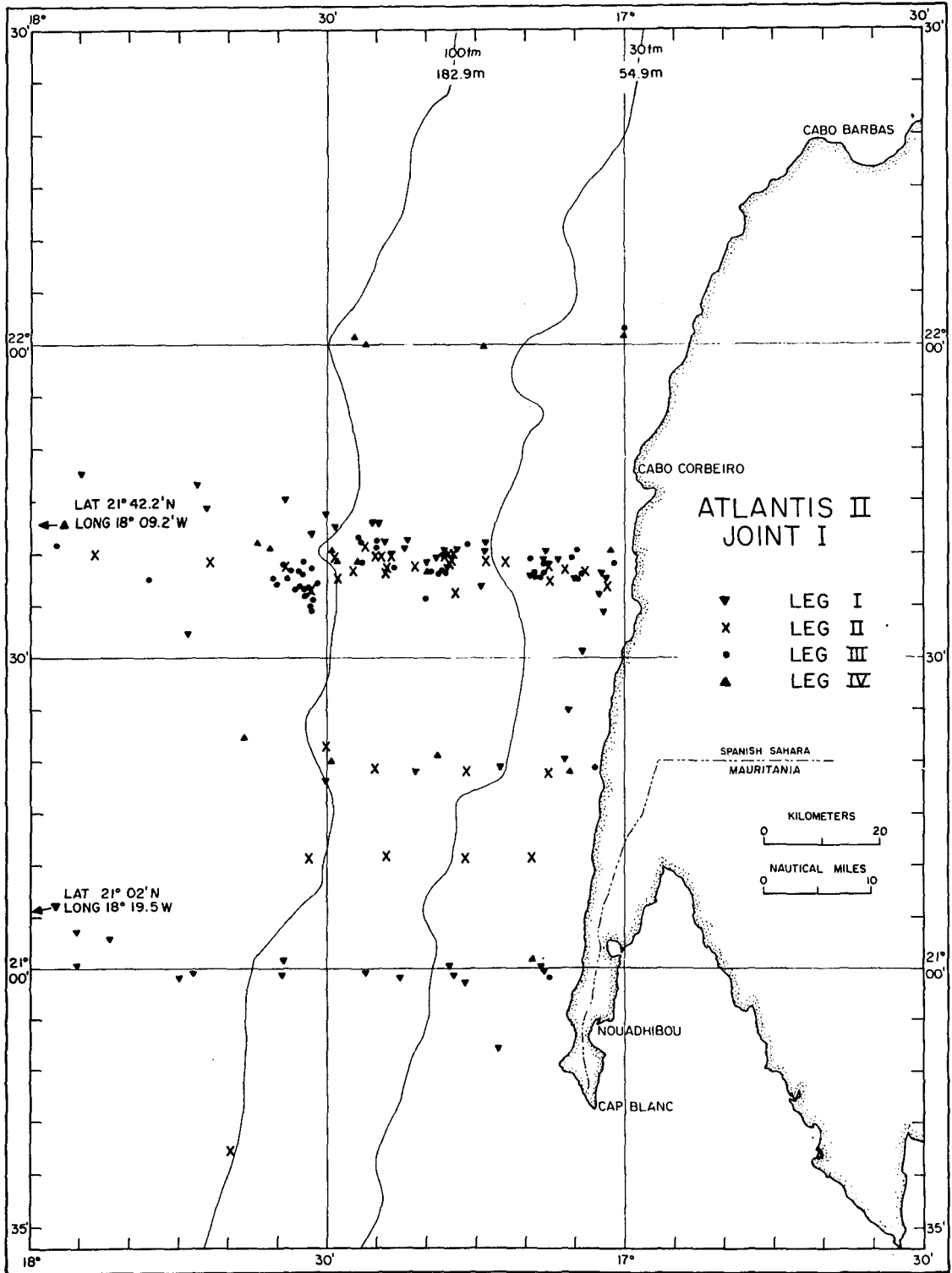
FIGURE 1.—Station locations in the upwelling region off northwest Africa.

trawls. The fish were transferred immediately to a holding tank aboard the RV *Atlantis II* and were maintained as long as a week with daily feeding. Specimens were held at least 6 h before experiments were initiated. Excretion measurements were collected on several specimens after the holding tank had been cleaned, rinsed with ethyl alcohol, flushed, and filled with seawater. The tank was covered with black polyethylene sheeting to reduce light and to prevent contamination by particulate matter. After the animals were placed in the tank and the experiment was initiated, water samples were collected every 10 min for periods of up to 3 h. Most of the experiments were started in the late evening so the temperature of the experimental tanks was within 1°-2°C of ambient surface seawater. There was no heating effect by sunlight so the temperature ranged from 14.5° to 16°C for all the experiments with <0.5° change in temperature during any of the experiments. "Fresh" specimens were examined within 12 h of capture. Specimens that had been starved for 1 and 2 d were used to estimate nonfeeding excretion rates. After all water samples had been collected, the specimens were blotted on towels and weighed. The animals were subsequently dried in a circulating oven at 70°C until a constant dry weight was obtained. The whole dried fish were ground into a powder for determination of percentage body nitrogen and carbon.

Excretion samples were analyzed for ammonium, urea, nitrate, silicate, phosphate, dissolved organic nitrogen, and dissolved organic phosphorus. The samples were freshly run and were filtered through a 0.45 μm glass-fiber filter to remove particulate matter. The chemical methods used were similar to those described by Freiderich and Whitledge (1972) except for urea and dissolved organic nitrogen and phosphorus which were determined by the methods of DeManche et al. (1973) and Armstrong et al. (1966).

RESULTS

Excretion Measurements

Eight excretion experiments were performed on a total of five species of demersal fish. In addition, excretion measurements were taken from two blue sharks, *Prionace glauca*, and several octopi, *Octopus vulgaris*. The typical tank concentrations of nitrogen compounds measured during the experiments are shown in Figure 2. The rate of ammonium excretion was approximately twice as large as the rate for urea. The rate of excretion for ammonium was more nearly linear than that for urea, although the nonlinearity for urea is probably within the precision limits of the method. The sum of ammonium and urea represents the identified nitrogen excretion in the experiments. The difference between this sum of ammonium and urea and total nitrogen excretion (as measured after ultraviolet irradiation) is probably composed of organic nitrogen compounds such as dissolved amino acids, trimethylamine oxide (Grollman 1929; Wood 1958), or creatine (Whitledge and Dugdale 1972). All experiments conducted showed a nearly linear increase in ammonium concentrations over the short duration of the experimental periods. Likewise the increases in urea and total excreted nitrogen were nearly linear but were more variable than ammonium.

A summary of all nitrogen excretion experiments is shown in Table 1. Well-fed demersal species such as *Diplodus senegalensis* excreted from 1.03 to 1.44 μg NH$_4$-N/mg dry weight per
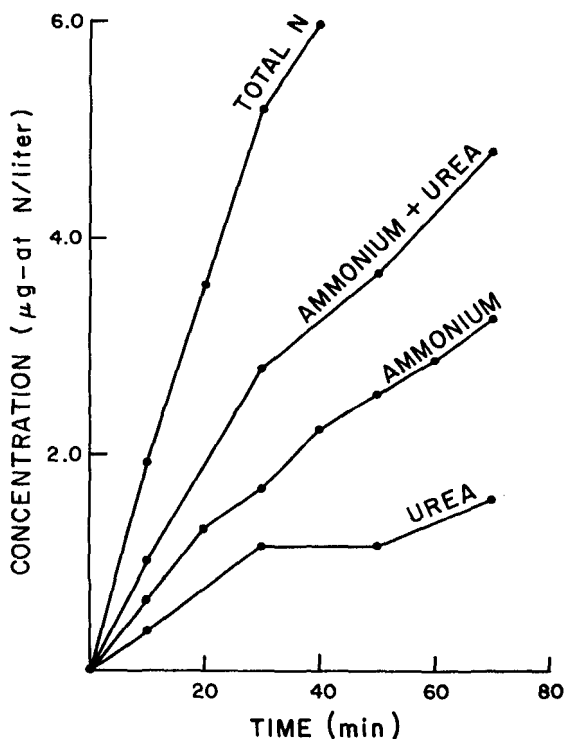
FIGURE 2.—Tank concentrations of ammonium, urea, and total nitrogen as measured by ultraviolet irradiation during an excretion experiment.

TABLE 1.—Excretion rate measurements of specimens from northwest Africa.

No. of individuals	Specimens	Experimental condition	μg N/mg dry wt per day			μg P/mg dry wt per day	
			NH₄	Urea	DON	PO₄	DOP
12	*Diplodus senegalensis*	fresh	1.44	0.76	2.6	0.23	0.09
9	*Diplodus senegalensis*	starved, 1 d	0.90	0.26	—	0.15	0.04
6	*Diplodus senegalensis*	starved, 2 d	0.64	0.35	2.0	0.22	0.18
2	*Pagellus couperi* and						
1	*Cantharus cantharus*	fresh	0.91	—	1.0	0.12	0.04
2	*Pagellus couperi* and						
1	*Cantharus cantharus*	starved, 1 d	0.64	0.08	—	0.05	—
1	*Pomadasys incisus* and						
9	*Diplodus senegalensis*	fresh	1.22	0.33	1.6	0.18	0.05
2	*Prionace glauca*	fresh	0.44	0.55	0.93	0.08	0
4	*Octopus vulgaris*	fresh	0.78	0.11	—	0.42	—
5	*Sardinella* spp.	fresh	4.61	4.78	—	1.68	—

day and 0.31 to 0.76 μg urea-N/mg dry weight per day. Specimens starved 24 h excreted 0.90 and 0.26 μg NH_4-N and urea-N/mg dry weight per day. A 2-d starvation lowered ammonium excretion to 0.64 while urea was 0.35 μg urea-N/mg dry weight per day. These rates are somewhat higher than the means of 0.17 and 0.05 μg N/mg dry weight per day for ammonium and urea measured at 12°C for Pacific staghorn sculpin, *Leptocottus armatus*; starry flounder, *Platichthys stellatus*; and blue sea perch, *Taeniotoca lateralis* (Wood 1958). After temperature corrections are made using a Q_{10} of 2.0 these rates are still larger than those measured by Wood (1958). Although linear temperature adjustments can be estimated, the food conversion efficiency can be variable and cannot be estimated by simple increases in rates as temperature increases (Pandian 1970); therefore, excretion rates can be expected to be somewhat nonlinear also. Feeding studies on the Atlantic menhaden showed that ingestion rates are equivalent to 0.30-1.2 μg N/mg dry weight per day for filter feeding on *Thalassiosira rotula* (Durbin and Durbin 1975). Using an assimilation efficiency of 80% and growth rate of 5% assimilation, the nitrogen excretion rates should be about 0.23 μg N/mg dry weight per day. This rate is about 20 to 33% of the rates calculated for the smaller specimens in this study.

The other demersal species, *P. coupei* and *C. cantharus*, excreted 0.91 μg NH_4-N/mg dry weight per day when specimens were fresh and 0.64 μg NH_4-N/mg dry weight per day when starved 48 h. The pelagic *Sardinella* spp. showed an ammonium excretion rate of 4.61 μg NH_4/mg dry weight per day. Ammonium excretion by the blue shark was 0.11 μg N/mg dry weight per day while urea excretion rates were slightly higher (0.13 μg N/mg dry weight per day) than values for the demersal fish.

Measured quantities of orthophosphate in excretion samples were smaller than ammonium but displayed an approximate linear increase with time. Dissolved organic phosphorus (DOP) was often excreted in quantities similar to orthophosphate. The sum of orthophosphate and DOP, representing total phosphorus excretion, is a linear function of time over the relatively short experimental period (Fig. 3). Phosphorus excretion rates (Table 1) were smaller after the fish had been starved 1 d. However, specimens starved 2 d showed high phosphorus excretion rates. Ammonium was decreased after 2 d of starvation, indicating elemental excretion ratios may change as starvation proceeds. Nitrate, nitrite, and silicate were excreted in insignificant or zero concentrations in all experiments. Control chambers starting with the same initial water as the experimental tanks showed no con-
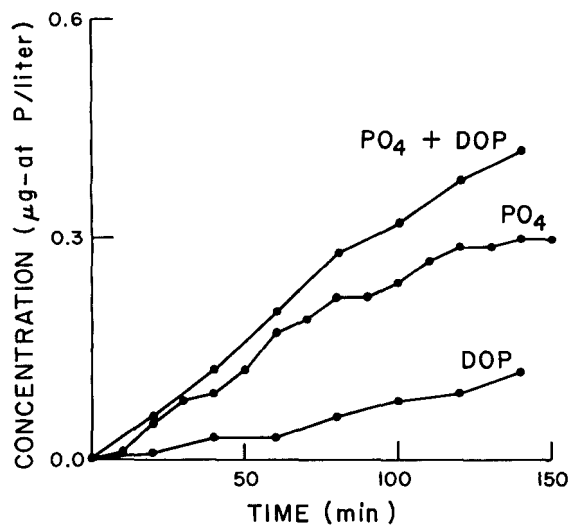

FIGURE 3.—Tank concentration of orthophosphate and dissolved organic phosphate during an excretion experiment.

centration changes of any of the measured parameters greater than the standard precision of the chemical methods ($\approx$5%).

Other Measurements

The wet and dry weights were determined for all specimens except for *P. glaucas* where only wet weights were estimated by displacement volume. The wet and dry weights determined for all other specimens (Fig. 4) were linearly related by the least squares equation, dry weight = 0.284 wet weight + 1.5, with an r^2 of 0.96.

The percentage body carbon content in all dried specimens ranged from 33.7 to 48.9. The mean and standard deviation for the 34 samples was 41.6±4.24% C. Fresh *D. senegalensis* specimens contained a mean of 42.59% C (Table 2) while specimens starved 1 and 2 d had 43.08 and 36.6% C. The mean percentage body nitrogen determined for all specimens was 9.35 with a standard deviation of ±1.49%. Fresh *D. senegalensis* specimens contained 10.36% N while specimens

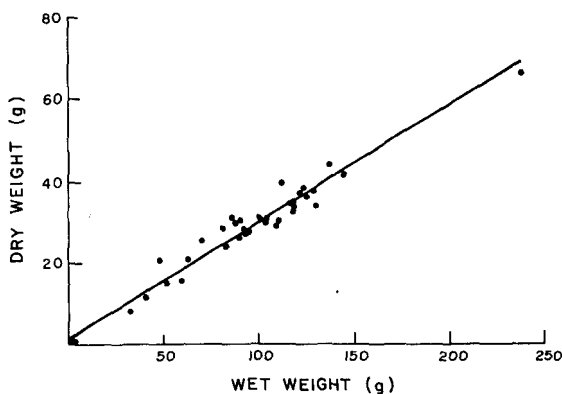starved 1 and 2 d had 9.79 and 7.41% N. Carbon to nitrogen ratios (by atoms) calculated from these data were 4.85 for fresh *D. senegalensis* and 5.18 and 5.90 for specimens starved 1 and 2 d. These ratios show a larger loss of nitrogen than carbon during starvation and the ratios bracket the value of 5.17 measured as the mean C:N of 10 Peruvian anchoveta, *Engraulis ringens*, and correspond to the C/N values reported for phytoplankton and zooplankton (Walsh and Howe 1976). When changes in body nitrogen content are calculated from changes in C/N values and are compared with measured nitrogen excretion losses, assuming defecation is approximately equal to excretion (an assimilation efficiency of 50%), then about 67% of the observed C/N changes in *D. senegalensis* are explained.

The absolute rates of nitrogen loss by excretion were calculated for the various nitrogen fractions. The sum of ammonium and urea losses were then compared with body nitrogen content to determine percentage body nitrogen loss per day which ranged from 1.2 to 1.5%. These nitrogen loss rates would require from 65 to 85 d for turnover of body nitrogen. These nitrogen turnover estimates are quite reasonable for fish of this size range so the nitrogen excretion rates should not be grossly overestimated due to the stress of capture and handling. Of course, loss of scales, mucus, and reproductive losses would decrease this turnover time and, if they were known, would represent a refinement of this estimate.

Nekton Biomass

Nekton biomass was determined in the study area by acoustic mapping surveys on the RV *Atlantis II* and bottom trawls during the cruise period. Results of the acoustic surveys that were

FIGURE 4.—Wet weight vs. dry weight plot for all fish specimens.

TABLE 2.—Mean and standard deviation of experimental measurements for *Diplodus senegalensis, Octopus vulgaris,* and *Prionace glauca.*

Specimens[1]	Dry wt (g)	Body C (% of dry wt)	Body N (% of dry wt)	Body C/N (by atoms)	NH₄ excretion/day (g)	Urea excretion/day (g)	Sum NH₄ + urea excretion/day (g)	Total N excretion/day (g)	Body N excreted/ day as NH₄ and urea (%)	Turnover time of body N (d)
D. senegalensis fresh	29.42 (6.13)	42.59 (3.84)	10.36 (1.08)	4.85 (0.77)	0.0359	0.0100	0.0459	—	1.53	65.4
D. senegalensis starved 1 d	27.27 (6.41)	43.08 (4.40)	9.79 (1.07)	5.18 (0.73)	0.0245	0.0071	0.0316	—	1.17	85.5
D. senegalensis starved 2 d	28.36 (4.87)	36.60 (3.57)	7.41 (0.52)	5.90 (0.75)	0.0182	0.0100	0.0282	0.0569	1.34	74.6
O. vulgaris fresh	318.5		11.04		0.248	0.035	0.283	—	0.805	124
P. glauca fresh	2,160	—	—	—	0.950	1.188	2.138	—	0.989	101

[1]Number of specimens as in Table 1.

coincident in time with the excretion experiments showed a mean pelagic biomass over the northwest Africa shelf of 40 to 60 g wet weight/m^2 (Thorne et al. 1977). Analysis of fish egg and larvae samples later indicated that the relative abundance of sardine to anchovy was about 4:1 (Blackburn and Nellen 1976) or mean densities of 32 g wet weight of sardines and 8 g wet weight of anchovy/m^2. Converting to dry weight the sardine and anchovy standing stock would be 8 and 2 g/m^2, respectively.

Demersal fish stocks on the shelf sampled by bottom trawling gear were more varied in composition than pelagic stocks. A composite estimate of demersal stocks taken in several trawls by three vessels included 2.2 g wet weight/m^2 of fish mainly represented by the families Sparidae, Sciaenidae, Pomadasyidae, and Congridae (Haedrich et al. 1976). In addition, at depths of about 50 m cephalopods were found in abundances of about 1 g wet weight/m^2, and at 200 m large numbers of the shrimp Plesionika spp. were collected, amounting to 1.44 g wet weight/m^2.

The biomass of pelagic fish in the slope area at depths >200 m was estimated by acoustic measurements to be about 80 g wet weight/m^2 and was thought to be composed of jack mackerel, Trachurus symmetricus (Thorne et al. 1977). Just offshore of the shelf break concentrations as large as 105 g wet weight/m^2 of fish were occasionally observed. Demersal fish biomass was smaller than found on the shallow shelf region and was estimated to be 3.3 g wet weight/m^2 from bottom trawls (Haedrich et al. 1976).

It should be noted that biomass estimates obtained from the acoustic survey for the pelagic populations and the trawl sampling for demersal nekton were often highly variable (Thorne et al. 1977). Several of the most abundant nekton species (e.g., Sardinella spp.) were migrating through the study area and a considerable amount of commercial fishing was occurring so the mean biomass values used in regeneration calculation are an attempt to use a reasonable value that was the best estimate of the nekton biomass assessment investigators.

Regeneration Rates

Regeneration rates were calculated from nekton biomass and fish excretion data for the shelf (<200 m) and slope region (>200 m) in the northwest Africa upwelling area. These regions were considered separately because of large differences in both the fish and zooplankton populations in these two areas. The sum of ammonium regeneration rates calculated for pelagic fish over the shelf amounts to 2.87 mg-at/m^2 per day (Table 3) while demersal fish regeneration rates were 0.09 mg-at/m^2 per day for a total of 2.96 mg-at/m^2 per day. The anchovy excretion rates were estimated from Engraulis ringens and E. mordax values (Whitledge 1978) and Plesionika spp. excretion rates were estimated using values for small sizes of Pleuroncodes planipes, a pelagic crab endemic to the eastern tropical Pacific.

The ammonium regeneration rates for the slope region were dominated by T. symmetricus (1.80 mg-at/m^2 per day) while demersal fish contributed only 0.04 mg-at/m^2 per day. The jack mackerel excretion rate used in the calculation was obtained from specimens examined in the eastern Pacific region (McCarthy and Whitledge 1972).

TABLE 3.—Regeneration of ammonium by fish over the shelf and slope areas of northwest Africa upwelling ecosystem.

	Wet wt g/m^2	Dry wt g/m^2	Ammonium excretion rate µg N/mg dry wt per day	Regeneration rate mg-at N/m^2 per day
Shelf (<200 m)				
Pelagic				
Sardine	32	8	4.6	2.63
Anchovy	8	2	[1]1.7	0.24
Demersal				
Sparids and				
flatfish	2.2	0.55	1.23	0.05
Cephalopods	1.0	0.17	0.71	0.01
Shrimp	1.4	0.22	[2]2.0	0.03
Total	44.6	10.94		2.96
Slope (>200 m)				
Pelagic				
Horse mackerel	80	20	1.26	1.80
Demersal				
Sparids	1.6	0.4	1.23	0.04
Total	81.6	20.4		1.84

[1]Estimated from Engraulis ringens and E. mordax rates.
[2]Estimated from Pleuroncodes planipes rates.

DISCUSSION

The significance of nutrient regeneration by fish is most apparent when the ammonium regeneration rates are compared with phytoplankton uptake rates measured by ^{15}N-labeled nitrate and ammonium. The mean ammonium and nitrate uptakes are estimated to be 11 and 10 mg-at/m^2 per day for the shelf region (MacIssac and Dugdale[2]). The ammonium regeneration rate for

the fish totals 2.96 mg-at/m^2 per day (Table 4), which is about 26.9% of the ammonium used by phytoplankton and 14.1% of total inorganic nitrogen utilized.

Results of zooplankton regeneration experiments obtained at the same time showed variations related to size of the organisms and depth of water. Smaller zooplankton were most abundant and had largest excretion rates inshore while the largest zooplankton biomass was located just offshore of the shelf break where the larger zooplankton with smaller excretion rates were found (Smith and Whitledge 1977). The mean ammonium regeneration rate calculated from zooplankton that were separated into four size classes of 102, 223, 505, and 1,000 μm was 4.7 mg-at/m^2 per day over the shelf, which is about 42.7% of the ammonium used in primary production and 22.4% of total inorganic nitrogen uptake.

The release of ammonium from the sediments off northwest Africa was estimated by placing bell jars on the bottom in the shallow inshore region (25 m) where divers could collect initial and final samples using plastic bottles (Rowe et al. 1977). The mean ammonium release rate from the two locations was 5.64 mg-at N/m^2 per day. This value represents 0.23 μg-at/l per day if mixing occurred over the entire water column in the nearshore region. The ammonium content of pore water in the upper few centimeters and at the seawater-sediment interface was quite large in the two nearshore stations compared with samples collected at 50 and 200 m. Likewise the gradients of ammonium production at the sediment-water interface was shown to decrease from >100 μg-at/l per cm at 25 m to <40 μg-at/l

per cm offshore of the shelf break. So using the concentration of ammonium in pore water and sediment-water interface gradients as indicators of ammonium flux from the sediments, the sediments were estimated to be releasing about 5.6 and 1.9 mg-at/m^2 per day at water depths of 50 and 200 m. These sediment-release values would provide 78.9% of ammonium used in primary production and 24.2% of the total inorganic nitrogen uptake over the inner shelf. A smaller portion of productivity evidently sinks to the sediments hence smaller benthic release rates are observed.

The input to the water column from the sediments nearshore at depths of 30 m or less are probably very significant in creating and maintaining a high concentration of ammonium found in the shallow waters (Fig. 5) that are often discolored due to a large air-derived suspended load. The ammonium-release rates from the sediment are larger than nearshore pelagic regeneration rates and the large aeolian sediment load (Sarnthein and Walger 1974; Rowe et al. 1977; Milliman 1977) was presumably large enough to inhibit phytoplankton nutrient uptake as a result of light attenuation and to discourage large biomasses of zooplankton (Codispoti and Friederich 1978). It is therefore probable that the primary productivity not eaten by the small-sized zooplankton falls to the bottom, so an appreciable quantity of ammonium is placed in the water column by zooplankton excretion and particulate organic matter decomposition on the bottom.

TABLE 4.—Nitrogen budget for northwest Africa upwelling ecosystem.

	Ammonium regeneration mg-at/m^2 per day	Percent of ammonium uptake	Percent of nitrate plus ammonium uptake
Shelf[1]			
Bacterioplankton	0.5	7	2
Zooplankton	7.82	104	33
Fish	2.96	39	13
Benthic sediments	5.64	75	24
Total	16.92	225	72
Offshore[2]			
Bacterioplankton	4.43	27	20
Zooplankton	5.35	33	24
Fish	1.84	11	8
Benthic sediments	1.88	12	8
Total	13.50	83	60

[1]Phytoplankton ammonium uptake = 7.5 mg-at/m^2 per day.
 Phytoplankton nitrate uptake = 16.0 mg-at/m^2 per day.
[2]Phytoplankton ammonium uptake = 16.2 mg-at/m^2 per day.
 Phytoplankton nitrate uptake = 6.2 mg-at/m^2 per day.
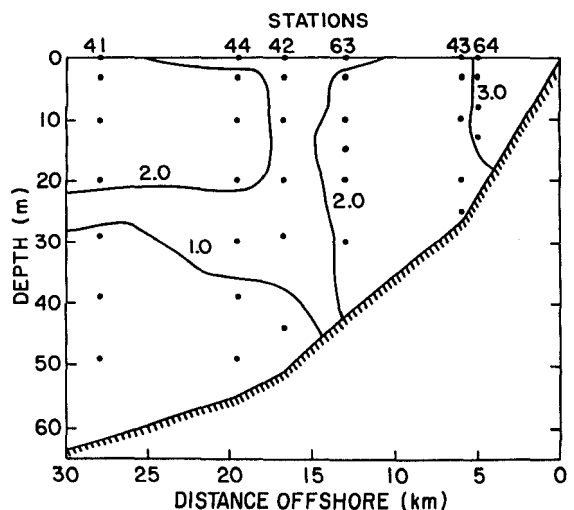 Source for footnotes 1 and 2: Dugdale and MacIsaac, unpubl. results.

FIGURE 5.—Distribution of ammonium (μg-at/l) observed in a transect of stations across to shelf at lat. 21°40'N.

Bacterioplankton studies in the northwest Africa upwelling ecosystem (Watson 1978) estimated the phytoplankton biomass in the water column to be much larger than bacterial biomass at stations <350 m water depth. The bacterial biomass in the sediments, however, was higher nearshore and lower offshore. The water column contained only 8% of the bacterial biomass on the inshore stations, so the bacteria are probably recycling only about 0.5 mg-at N/m^2 per day inshore. The offshore region has about 73% of the bacterial biomass in the water column compared with the sediments, so the bacterioplankton may regenerate as much as 4.4 mg-at/m^2 per day in the deeper waters of 200 m or greater. The bacterial processes that were occurring in the sediments were estimated from bell jar experiments (Rowe et al. 1977). The inshore bottom ammonium release rates (5.64 mg-at/m^2 per day) include bacterial, meiofaunal, and chemical processes occurring in the sediments, so these values were used rather than the purely bacterial rates of Watson (1978). The difference between the bell jar and bacteria-only rates is about 5.1 mg-at/m^2 per day. This difference is quite high to explain as a chemical rate so meiofaunal rates evidently are quite important. In offshore waters the sediment release rates are much lower than inshore based on near-bottom ammonium gradients and decreased ammonium pore water concentrations.

The sparids in this study, Mediterranean Sea reef fish (Whitledge 1972), and the nearshore and bottom fish of British Columbia (Wood 1958) have apparently much smaller weight-specific ammonium excretion rates than fish such as the Peruvian anchovy, northern anchovy, jack mackerel, and sardinella. The increased metabolic rate needed by mackerels and clupeoids is probably a result of their large energy demands resulting from continuous swimming. Low metabolic rates in sluggish mammals have been shown to be related to their relatively infrequent movements (Whittow 1977) compared with highly active animals of similar body weight. As a result it could be predicted that respiration or excretion rates for fish should be related to both their body weight and index of locomotion such as swimming speed or daily swimming time.

The total amount of ammonium regenerated in the upwelling ecosystem off northwest Africa has spatial variability which cannot be ignored. Nevertheless, regeneration in organisms from bacterioplankton through benthos (Table 4) is

estimated to recycle significantly large amounts of nitrogen in the ecosystem and easily produce all of the ammonium used in primary productivity. In some shallow locations ammonium is produced in large quantities and biological uptake is reduced such that high concentrations of ammonium are often observed in the very nearshore water.

ACKNOWLEDGMENTS

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