

Regeneration of Nitrogen by Zooplankton and Fish
in the Northwest Africa and Peru Upwelling Ecosystems

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TABLE OF CONTENTS

	Page
A. Introduction	1
B. Methods	3
C. Northwest Africa	4
D. Peru	7
E. Discussion	11
F. References	16

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A. INTRODUCTION

The availability of nutrients and light are the dominant controlling factors of the levels of primary production in the ocean. In the lower latitudes where most coastal upwelling areas are located, the amount of light is seldom below the critical level to inhibit productivity so nutrients are often the limiting factor in phytoplankton growth (KOBLENTZ-MISHKE, et al., 1970). Nutrients utilized in primary productivity are derived from two sources in upwelling areas. Nutrients are introduced to the euphotic zone from depth by the physical processes that create upwelling and nutrients are recycled by biological organisms that inhabit the area. Nitrate introduced into the euphotic zone by upwelling supports "new productivity" while ammonium and other excretory products regenerated by zooplankton and nekton supports "regenerated productivity" (DUGDALE and GOERING, 1967).

Intuitively one would think that the process of upwelling would provide the major amount of nutrients used in production processes and regeneration would contribute only a small amount. However, estimates of regenerated and new production using ^{15}N isotope techniques have shown that recycled ammonium may fulfill nearly half of the daily nitrogen requirement of phytoplankton and upwelled nitrate may provide the other half (DUGDALE and GOERING, 1970; WHITLEDGE, 1972). Ammonium is a

preferential source of nitrogen to fulfill phytoplankton nitrogen requirements (CONWAY, 1973) so in oceanic areas where relatively high concentrations of ammonium occur the regenerated productivity is nearly equal to new productivity. The process of upwelling with the high vertical advection provides an efficient mechanism to maintain a regenerated nitrogen pool in the euphotic zone even if the organisms excrete the ammonium at depths deeper than those at which phytoplankton growth occurs. The upwelling process itself returns this ammonium to the productive euphotic region.

Regeneration studies on zooplankton and nekton have been carried out in the upwelling areas of Northwest Africa on the JOINT-I cruise and Peru on the PISCO cruise. The two areas contain nekton populations that can potentially graze on phytoplankton. The Peru upwelling ecosystem is inhabited by the anchoveta, Engraulis ringens JENYNS, the dominant nekton component. CUSHING (1971) estimated that the anchoveta population is 10 times that of all other species in all seasons. The estimated stocks of anchoveta during the middle 1960's were in the range of 20 million metric tons. This large biomass of fish therefore is likely to exert a large influence through grazing and excretion. The Northwest Africa upwelling area fish are composed of several demersal and pelagic species. The amount of fish stocks off Northwest Africa is uncertain

but a rough estimate based on catch data (GULLAND, 1970) suggest that they are about an order of magnitude smaller than Peru stocks.

B. METHODS

For excretion experiments off Northwest Africa, specimens of Diplodus senegalensis CADENAT, Pagellus couperi DIEUZEIDE, Cantharus cantharus LINNAEUS, and Pomadasys incisus BOWDICH were captured by a bottom trawl. The animals were allowed to acclimate for several hours in a holding tank supplied with surface seawater. Healthy specimens were then transferred to an experimental tank that had previously been cleaned, rinsed with ethyl alcohol, flushed and filled with seawater. Additional experiments were carried out on animals that had been starved for one and two days. Samples for nutrients, dissolved organic nitrogen and urea were collected every ten minutes for as long as three hours. Zooplankton for the JOINT-I experiments were collected with vertical net tows of a 102 μ mesh net and were later fractionated into four size classes.

The Peruvian anchoveta were captured in a 9 m² dip net attached to the ship's crane. The specimens were kept in a holding tank for two hours before they were used in experiments. Individual fish were placed in one liter plastic tubes and incubated in tanks with circulating surface seawater. The excretion data was calculated from

the change in concentration of ammonium in the plastic tubes.

The zooplankton biomass was estimated during PISCO cruise using 100 m vertical net tows with 240 μ mesh netting (WALSH, et al., 1971).

The laboratory studies on Engraulis mordax GIRARD were conducted in a 32 liter circular chamber similar to that described by LASKER (1970). The specimens in these experiments had been in captivity for at least two weeks. Nutrient samples were collected from the chamber when the fish were introduced and every 10 minutes thereafter for 70 minutes. The experiments were stopped before the oxygen concentration went below 50 per cent saturation.

C. NORTHWEST AFRICA

The biomass of pelagic fish stocks in the Northwest Africa upwelling region estimated using acoustic and trawl methods was 60 g wet wt m^{-2} , about 20 percent of the anchoveta biomass off Peru. THORNE, et al., (in press) suggest that Sardina pilchardus WALB contributes most of the biomass (50 g wet weight m^{-2}) over the mid-shelf area and large concentrations Trachurus (80 g wet weight m^{-2}) were located at the shelf break and upper continental slope. The demersal fish stocks were dominated by the family Sparidae inshore, and at midshelf a mixture of Sparidae, Sciaenidae, Congridae and Pomadasidae families were found having a mean biomass of 2.2 g wet weight m^{-2} (HAEDRICH, et al., 1974).

Biomasses for cephalopods and shrimp (Plesionika spp.) were also found to be 0.9 and 1.4 g wet weight m^{-2} respectively.

The Northwest African fish nutrient excretion rates were approximately linear with time. The ammonium excretion of freshly caught Diplodus senegalensis CADENAT ranged from 1.03 to 1.44 $\mu\text{g N mg dry wt}^{-1} \text{ day}^{-1}$. Specimens starved one day had a mean excretion rate of 0.90 and those starved 2 days had a mean rate of 0.64 $\mu\text{g N mg dry wt}^{-1} \text{ day}^{-1}$. The highest ammonium excretion rate, 4.6 $\mu\text{g N mg dry wt}^{-1} \text{ day}^{-1}$, was observed for Sardinella (WHITLEGE, 1972). The urea excretion rates appeared similar in the well-fed and starved specimens. Excretion rates were measured on some organisms other than fish that were captured in the trawl nets. The ammonia excretion of cephalopods, determined in a manner similar to the fish excretion experiments off Northwest Africa, had a mean rate of 0.7 $\mu\text{g N mg dry wt}^{-1} \text{ day}^{-1}$. The excretion rates of shrimp was not measured but the rate was estimated to be about 2 $\mu\text{g N mg dry wt}^{-1} \text{ day}^{-1}$ based on published excretion rates of 2 $\mu\text{g N mg dry wt}^{-1} \text{ day}^{-1}$ of Euphausia pacifica HANSEN (JAWED, 1969) and a 2.9 $\mu\text{g N mg dry weight}^{-1} \text{ day}^{-1}$ excretion rate of the red crab (Pleuroncodes planipes STIMPSON) (WALSH, et al., in press).

Using the geographic distribution of the fish biomass, (THORNE, et al., in press; HAEDRICH, et al., 1974) and excretion measurements for pelagic and demersal specimens, the regeneration of ammonium by Northwest Africa fish was

calculated for the shelf area (< 200 m) to be 3.0 mg-at m⁻² day⁻¹ (Table 1) and 1.8 mg-at m⁻² day⁻¹ (Table 2) for the offshore area (> 200 m).

The zooplankton biomass over the shelf in Northwest Africa was found to be a mean value of 2.7 g dry wt m⁻², and 10.4 g dry wt m⁻² for the offshore area. This distribution of zooplankton dry weight biomass is different from wet weight biomass values (BLACKBURN, 1975) and may be due to wet weight to dry weight differences resulting from changes in the taxonomic composition. Nutrient excretion studies on the zooplankton captured in the 102 μ mesh nets were combined with biomass data to estimate zooplankton regeneration over the shelf and the offshore areas. The inshore region over the shelf was calculated to have a mean of 5.1 mg-at m⁻² day⁻¹ of ammonium regenerated by zooplankton while the offshore area had regeneration of 5.4 mg-at m⁻² day⁻¹ (SMITH and WHITLEDGE, in press). Of the total estimated ammonium regeneration over the shelf, zooplankton accounted for 63 per cent of the recycled nitrogen and nekton contributed the remaining 37 per cent.

Phytoplankton uptake of nitrate and ammonium in the shelf region, as measured by ¹⁵N-labeled substrates by DUGDALE and MACISAAC (personal communication), was estimated to be 10 and 11 mg-at m⁻² day⁻¹. The release of 8.1 mg-at NH₄-N m⁻² day⁻¹ in the shelf area by pelagic animals produces 73 per cent of the measured ammonium nitrogen uptake and 38 per cent of the combined nitrate-ammonium nitrogen

uptake. Other sources such as benthos (ROWE, et al., in press) and bacteria which are not included in this estimate, apparently supply the remaining 27 per cent of the measured phytoplankton ammonium requirement.

The size of an individual zooplankter increased offshore of the shelf as did the total zooplankton biomass. Zooplankton contributed 75 per cent of the total ammonium regenerated over the slope and the fish contributed the remaining 25 per cent. Uptake of nitrate and ammonium by phytoplankton in the offshore region was 19 and 11 mg-at m⁻² day⁻¹ (DUGDALE and MACISAAC, personal communication). Offshore the ammonium input can account for 65 per cent of the measured ammonium uptake and 24 per cent of the combined nitrate-ammonium nitrogen uptake. The difference between phytoplankton uptake of ammonium and the apparent ammonium production by zooplankton and fish probably cannot be contributed by the benthos or bacteria because the water is much deeper over the slope and the euphotic zone is relatively isolated from the bottom compared to the shelf region. Other zooplankton species not adequately sampled with the 102 μ nets (euphausids, etc.) could produce the difference in the offshore area since they have been reported in abundance in the area (CASANOVA, 1974).

D. PERU

The excretion and regeneration studies performed on PISCO cruise concentrated on the Peruvian anchoveta, Engraulis ringens JENYNS. The mean ammonium excretion rate

for E. ringens was $1.7 \mu\text{g NH}_4\text{-N mg dry wt}^{-1} \text{ day}^{-1}$.

A similar value was obtained for the ammonium excretion of E. mordax GIRARD in laboratory studies. The mean Peruvian anchoveta specimen dry weight was 1.7 g and contained 11.0 per cent of dry weight as nitrogen (MCCARTHY and WHITLEDGE, 1972). The mean per cent body nitrogen excreted per day was 9.1.

To assess the significance of regeneration and upwelling as sources of nutrients for primary production in the Peru upwelling area the quantity of regenerated nutrients was calculated for comparison with nutrient demands. The regeneration estimate of anchoveta in the Peru upwelling region was made by combining fishery catch statistics with nutrient excretion measurements collected on the PISCO cruise. Using an area of $82,317 \text{ km}^2$ (WOOSTER and REID, 1963) and a depth of 40 m for the normal depth of an anchoveta school (JORDAN, 1971), the volume of the upwelling region can be computed as $3.3 \times 10^{12} \text{ m}^3$. Anchoveta biomass estimates for the Peru region are all near 20×10^6 metric tons (GULLAND, 1968; RYTHER, 1969; CUSHING, 1971) but normal losses by fishing and bird predation would decrease the anchoveta biomass to about 12×10^6 metric tons in March 1969 when PISCO data were collected. Using these figures and assuming the fish are evenly distributed over the entire upwelling area in a 40 m layer there would be 3.6 g wet wt of anchoveta m^{-3} at the end of March. This biomass is about 5 times the estimated pelagic biomass off Northwest Africa. Using a

factor of 0.255 for wet weight to dry weight conversion (WHITLEDGE, 1972) there are 0.9 g dry weight fish m^{-3} ; equivalent to 0.5 fish m^{-3} . The ammonium excretion rate of 1.7 $\mu\text{g N mg dry wt}^{-1} \text{ day}^{-1}$ corresponds to a regeneration rate of 4.5 mg-at $\text{NH}_4\text{-N } m^{-2} \text{ day}^{-1}$ in the 40 m layer or 1.9 mg-at $m^{-2} \text{ day}^{-1}$ in the euphotic zone of approximately 17 m depth.

The mean zooplankton biomasses measured were 39.1 mg dry weight m^{-3} for day samples and 46.1 mg m^{-3} for night samples (WALSH, et al., 1971). These values are similar to the mean zooplankton biomass for Northwest Africa. Zooplankton ammonium excretion measurements of 10.4 $\mu\text{g N mg dry wt}^{-1} \text{ day}^{-1}$ collected on Calanus chilensis RODSKY on PIQUERO cruise to Peru (MCCARTHY, 1971) were used in regeneration estimates for zooplankton. At least 50 per cent of the biomass of zooplankton collected in all net tows using 100 μ mesh was larger than 505 μ (UNIVERSITY OF CALIFORNIA, 1971). The calculated ammonium regeneration rate of zooplankton using the mean and maximum biomasses were 3.1 and 12.1 mg-at N $m^{-2} \text{ day}^{-1}$ respectively in the upper 100 m and 0.5 and 2.0 mg-at $m^{-2} \text{ day}^{-1}$ in the upper 17 m. The mean biomass over the entire 100 m water column was used in the budget table because all the regenerated ammonium would eventually (less than 10 days) enter the euphotic zone as a result of vertical advection.

Zooplankton biomass samples were not collected in discrete depth intervals on the PISCO cruise so previous

estimates of zooplankton regeneration in Peru (WALSH, 1975; WHITLEDGE, 1972) were calculated on a per unit volume basis. This procedure assumes a homogeneous distribution of zooplankton and certainly underestimates the ammonium production by zooplankton in the euphotic zone.

Nitrogen uptake by phytoplankton was estimated using rates of uptake of ^{15}N -labeled ammonium and nitrate (UNIVERSITY OF WASHINGTON, 1970). The mean ammonium uptake measurements from 24 samples collected throughout the study area from the surface to the 1 per cent incident light level was $6.5 \text{ mg-at } \text{NH}_4\text{-N m}^{-2} \text{ day}^{-1}$. The mean measured nitrate uptake on stations where ammonium was measured was $13.9 \text{ mg-at } \text{NO}_3\text{-N m}^{-2} \text{ day}^{-1}$.

The requirements of primary productivity and inputs from regeneration of inorganic nitrogen compounds are summarized in Table 3. Regeneration by zooplankton and nekton supply $7.6 \text{ mg-at m}^{-2} \text{ day}^{-1}$ which is 117 per cent of the $6.5 \text{ mg-at m}^{-2} \text{ day}^{-1}$ required by phytoplankton.

The anchoveta and zooplankton in the Peru upwelling ecosystem contribute 59 and 41 per cent respectively for a total of 117 percent of the phytoplankton ammonium requirements, while the nekton and zooplankton off Northwest Africa produced about 27 and 46 per cent for a total of 73 per cent of the ammonium required. The much higher nekton biomass and similar zooplankton biomass in the Peru ecosystem compared to the Northwest Africa upwelling ecosystem makes the anchoveta an important component in the Peru upwelling

ecosystem (WHITLEDGE and PACKARD, 1971). Comparing ecosystems, the relative amount of primary production, supported by ammonium excretion of the anchoveta is more than two times the amount supported by Northwest African fish. The ammonium input by zooplankton and nekton off Peru produce 37 per cent of the combined nitrate-ammonium uptake by phytoplankton.

E. DISCUSSION

The large contribution of nutrients to primary productivity in the Peru upwelling system by the anchoveta implies that the anchoveta must consume a large portion of the primary production to maintain rapid growth and excretion rates. If growth and excretion are assumed to be the two main pathways of assimilated nitrogen and the other miscellaneous losses are small, it is possible to estimate ingestion (Fig. 1) as $(\text{Growth} \ \& \ \text{Excretion}) / (\text{Assimilation Efficiency})$. The anchoveta spawn during the austral winter in the months June through September and the young fish enter the fishery at about six months of age (PAULIK, 1970). The average increase in fish biomass is calculated to be about $1.0 \text{ g wet wt m}^{-3} \text{ month}^{-1}$. Converting to a daily basis the anchoveta nitrogen biomass increases $0.06 \text{ } \mu\text{g-at l}^{-1} \text{ day}^{-1}$. This 6 month rate was assumed to approximate a linear increase based on von Bertalanffy growth curves for the anchoveta (SCHAEFER, 1967) and monthly growth curves for the Pacific sardine (Sardinops caerulea GIRARD) (LASKER, 1970).

Table 4 presents the calculated daily nitrogen ingestion and per cent primary production grazed using an 83 per cent assimilation efficiency found for the Pacific sardine (LASKER, 1970).

Other ingestion estimates were calculated using growth rates of the Pacific sardine (Sardinops caerulea GIRARD) (LASKER, 1970) and Panama anchoveta (Cetengraulis mysticetus GÜNTHER) (SMAYDA, 1966). A fourth ingestion estimate for the anchoveta was derived from an ingestion estimate of the Japanese anchovy (Engraulis japonicus TEMMINCK et SCHLEGEL) (LEONG and O'CONNELL, 1969; TAKAHASHI and HATANAKA, 1960). The four ingestion estimates ranged from 0.88 to 1.01 $\mu\text{g-at N l}^{-1} \text{ day}^{-1}$. These grazing rates represent 54 to 61 per cent of nitrogen production. The phytoplankton nitrogen eaten per unit of anchoveta body nitrogen each day was 8.2 to 9.2 per cent.

The ingestion calculations are very sensitive to the volume of the upwelling area. The biomass, growth, assimilation efficiency and excretion rates are comparable to previously reported or commonly accepted values. However, estimates of the areal extent of the Peru upwelling region range from 6×10^4 to $5 \times 10^5 \text{ km}^2$. The three estimates of RHYTHER (1969), WOOSTER and REID (1963), and JORDAN (1971) are all in the range of 6 to $9 \times 10^4 \text{ km}^2$ but the area given by CUSHING (1971) is more than five times the others. JORDAN (1971) places the anchoveta mainly within 90 km of the coast with a total upwelling area of $8.6 \times 10^4 \text{ km}^2$.

The larger area estimated by CUSHING (1971) would increase the upwelling volume and decrease the anchoveta biomass m^{-2} so that the ingestion rate of the anchoveta per unit volume would be lowered to about 10 per cent of the daily phytoplankton nitrogen production. This would allow zooplankton to be included as an intermediate step in the food web provided that phytoplankton productivity remained as high throughout CUSHING's large area as was measured in the near-shore region on the PISCO cruise. Zooplankton production estimates were not made on the PISCO cruise but zooplankton biomass from settling volumes indicates that the anchoveta could live only one day on zooplankton as its only source of nourishment. It is unlikely that the generation time of zooplankton would be short enough to supply all the food necessary for the anchoveta.

From this analysis of ingestion it seems possible that anchoveta could switch from a phytoplankton to a zooplankton diet as seasonal changes in the upwelling occur. This corresponds to the more recently available literature on anchoveta feeding (ROJAS De MENDIOLA, 1971; ROJAS De MENDIOLA and OCHOA, 1973) which can be interpreted that the anchoveta is really an omnivore in contrast to previous reports which showed the anchoveta was probably a herbivore (ROJAS De MENDIOLA, 1958). The data collected during the first part of the PISCO cruise shows the high nutrient and chlorophyll concentrations confined to within 60 km of the coastline. Offshore of that point low open ocean concentrations of

nutrients and chlorophyll were present. This small region of productive waters would at that time compare favorably with the volume of the upwelling area used by RYTHER (1969) and would concentrate the anchoveta biomass in the productive nearshore region. With the anchoveta biomass in a small area more than 50 per cent of the phytoplankton productivity would be needed to satisfy their food requirements so the Peru upwelling ecosystem is probably a two-step food chain during this time.

During the last part of April on the PISCO cruise high nutrient and chlorophyll concentrations were measured offshore to at least 100 km on the R/V T. G. THOMPSON and 110 km on the R/V GOSNOLD and later in the year high chlorophyll concentrations as far as 260 km offshore have been observed (GUILLEN and IZAGUIRRE De RONDAN, 1973). During the austral fall or winter the upwelling ecosystem apparently may be as large as CUSHING (1971) suggested and there might be enough food to support the phytoplankton-zooplankton-anchoveta food chain. The offshore enlargement of the high nutrient and high productivity areas that are associated with seasonal changes in the upwelling system conform with the model of WALSH (1975) so it appears that both grazing calculations using excretion data and an ecosystem model predict that the Peruvian anchoveta can consume both zooplankton and phytoplankton.

The similarities of regeneration processes in the Peru and Northwest African upwelling regions are apparent

in the data showing a substantial percentage of primary production is derived from regenerated nitrogen even though relatively large amounts of nitrate are introduced in the euphotic zone by upwelling. The differences however revolve around the organisms responsible for recycling the largest percentage of nitrogen in each system. In Peru the anchoveta produces the largest amounts of ammonium while zooplankton and micronekton in Northwest Africa appear to fulfill that role. This shift in dominance in regeneration of nutrients from fish to zooplankton populations when going from a low latitude to a higher latitude upwelling area may be another indicator that nekton are replaced by zooplankton as phytophagous organisms in the more variable environments as suggested from other analyses (WALSH, 1976).

This research was supported by Grant GX 33502 of the National Science Foundation as part of International Decade of Ocean Exploration Coastal Upwelling Ecosystem Analysis (CUEA) program. Preparation of the manuscript was also partially supported by the United States Energy Research and Development Administration. I would like to acknowledge the helpful comments by Creighton Wirick and Dr. Maurice Blackburn and the valuable discussions with Drs. David Cushing and John Walsh concerning the thoughts presented in this paper.

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FIGURE LEGEND

Fig. 1 Simplified pathway of ingested nitrogen
through zooplankton or nekton

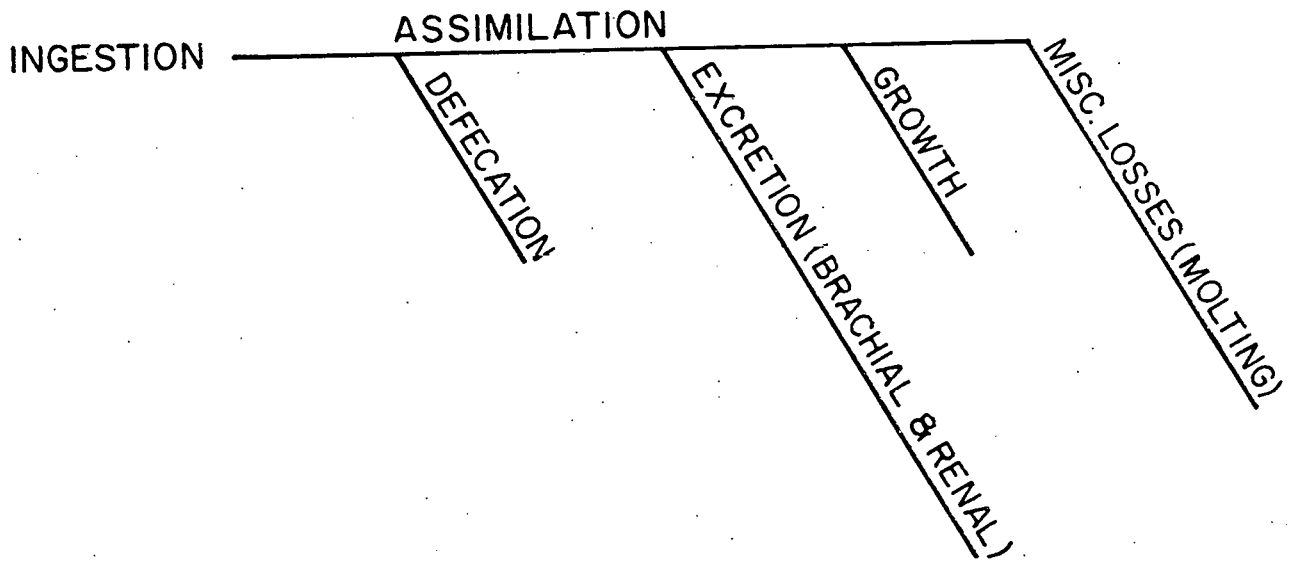


TABLE 1

Ammonium and Nitrate Budget for Northwest
Africa Shelf (< 200 m), mg-at m⁻² day⁻¹

Excretory Input

Pelagic Fish	2.9	
Demersal Fish & Cephalopods	0.06	
Shrimp	0.03	
Total		3.0
Zooplankton	3.9 - 7.6	
Mean Zooplankton		<u>5.1</u>
<u>TOTAL AMMONIUM INPUT</u>		8.1

Phytoplankton Uptake

Ammonium	11.	
Nitrate	10.	
<u>TOTAL UPTAKE</u>		21.

TABLE 2

Ammonium and Nitrate Budget for Northwest
Africa Slope (> 200 m), mg-at m⁻² day⁻¹

Excretory Input

Pelagic Fish	1.8	
Demersal Fish	~ 0	
Total		1.8
Mean Zooplankton		<u>5.4</u>
<u>TOTAL AMMONIUM INPUT</u>		7.2

Phytoplankton Uptake

Ammonium	11.	
Nitrate	19.	
<u>TOTAL UPTAKE</u>		30.

TABLE 3

Nitrogen budget in the euphotic zone
of the Peru upwelling region,
mg-at m⁻² day⁻¹

Excretory Input

Anchoveta	4.5		
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Zooplankton	3.1		
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TOTAL AMMONIUM INPUT		7.6	
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Upwelled nitrate	23.8		
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		<u>TOTAL INPUT</u>	31.4
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Phytoplankton Uptake

Ammonium	6.5		
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Nitrate	13.9		
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		<u>TOTAL UPTAKE</u>	20.4
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TABLE 4 Daily anchoveta growth, ingestion, and phytoplankton grazing, losses per unit volume of water in the Peru upwelling region. Estimates are based on data from LASKER (1970), TAKAHASHI AND HATANAKA (1960), AND SMAYDA (1966).

	Peru anchoveta growth estimate ^a	Pacific sardine growth estimate ^b	Japanese anchovy ingestion estimate ^c	Panama anchoveta growth estimate ^d
Anchoveta biomass µg-at nitrogen l ⁻¹	10.8	10.8	10.8	10.8
Daily anchoveta nitrogen growth µg-at l ⁻¹ day ⁻¹	0.06 ^a	0.15 ^b	0.10	0.08 ^d
Daily anchoveta total nitrogen excretion µg-at l ⁻¹ day ⁻¹	0.67	0.67	0.67	0.67
Daily anchoveta nitrogen assimilation µg-at l ⁻¹ day ⁻¹	0.73	0.82	0.77	0.76
Daily anchoveta nitrogen ingestion µg-at l ⁻¹ day ⁻¹	0.88	1.01	0.93	0.91
Daily phytoplankton nitrogen production µg-at l ⁻¹ day ⁻¹	1.63	1.63	1.63	1.63
Per cent daily phytoplankton nitrogen grazed	54.0	60.8	57.1	55.9
Per cent anchoveta body N ingested day ⁻¹	8.2	9.2	8.6 ^c	8.4
Per cent anchoveta growth day ⁻¹	0.56	1.40	0.92	0.77
Per cent growth efficiency (growth/ingestion)	6.7	15.2	10.6	9.1