NITROGEN EXCRETION BY ANCHOVY (*ENGRAULIS MORDAX* AND *E. RINGENS*) AND JACK MACKEREL (*TRACHURUS SYMMETRICUS*)[1]

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ABSTRACT

Teleost fish have been shown to excrete a variety of nitrogenous substances among which are ammonia, urea, and creatine. Previous reports show values for excretion of nearshore or bottom fish but not of pelagic species.

Two species of anchovy and jack mackerel were placed in chambers and their nitrogenous excretion products were measured. Ammonia, urea, and creatine accounted for 82% of the total nitrogen excreted by *Engraulis mordax* and the identified fraction was 83% ammonia, 16% urea, and 1% creatine.

The significance of pelagic fish as a source of ammonia and urea in California coastal waters is discussed.

On the basis of the major end product of their protein catabolism, animals are classified as ammonotelic, ureotelic, and uricotelic. Although these categories can be useful in evolutionary considerations (Baldwin, 1964), they are somewhat arbitrary in that the excreta of most animals contain a mixture of ammonia, urea, and uric acid. Mammals, elasmobranch fish, some amphibians, and some reptiles are considered to be ureotelic; teleost fish, some amphibians, and most invertebrates are ammonotelic; and birds and some reptiles are uricotelic (Baldwin, 1964). In ureotelic animals urea is produced via the ornithine cycle. It is, however, unlikely that this metabolic pathway is operative in nonureotelic organisms such as some teleosts, which excrete substantial quantities of urea. Brown and Cohen (1960) have shown that no marine teleost has the enzymes necessary for the first two steps in the ornithine cycle. The complete complement of ornithine enzymes has been found in the coelacanth however (Brown and Brown, 1967).

Arginase is present in the livers of teleost fish and hence dietary arginine has been suggested as a source of urea (Hunter and Dauphinee, 1924-1925; Hunter, 1929), but this suggestion is considered unlikely since arginine is an essential amino acid for this group of organisms (Forster and Goldstein, 1969). Purine catabolism also has been suggested as a means of urea formation via uricolysis (Brunel, 1937), and in support of this Goldstein and Forster (1965) found uricolytic activity in the livers of five species of marine and freshwater teleosts.

Delaunay (1929), Grafflin and Gould (1936), Grollman (1929), and Smith (1929) determined the composition of the urine of eight species of marine teleosts and their results were summarized by Scheer and Ramimurthi (1968). The proportions of various components of the total nonprotein urinary nitrogen varied greatly within, as well as between, species (ammonia varied from 0.5 to 9.6%, urea varied from 0.1 to 30.8%, creatine varied from 6.5 to 61.7%, and amino-N varied from 4.0 to 21.4%). In 1929 Smith used a divided chamber to permit separate determinations of the nitrogen released by the gills and by the kidneys, and his results showed that essentially all of the ammonia and urea released originated from the gills. In addition to these compounds, the branchial excreta consisted of amine or amine oxide derivatives while the less diffusible nitrogenous end products such as creatine, creatinine, and uric acid were excreted solely by the kidneys. It is therefore

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apparent that a release rate with ecological significance would have to consider both branchial and renal release.

Since the only data available from which one can calculate nitrogenous release rates for marine teleosts are for nearshore or bottom fish such as the sculpin, the starry flounder, and the blue sea perch (Wood, 1958), the following work was undertaken using significant pelagic species in order to assess the importance of marine teleosts as a source of ammonia, urea, and creatine in the euphotic zone.

METHODS

Experiments with the northern anchovy, *Engraulis mordax*, were conducted in August 1970, in the laboratories of the Fishery-Oceanography Center, La Jolla, California. Between experiments the fish were kept in a tank of flowing seawater and, unless specified otherwise, were fed frozen brine shrimp daily. For each experiment ten fish were placed in a 32-liter circular Plexiglas chamber similar to that described by Lasker (1970). During the first experiment the chamber was darkened and 24°C seawater flowed through it at a constant and determined rate. Beginning at the time the fish were introduced, effluent was sampled at 10-min intervals for 40 min. The fish had not been fed for 24 hr. For experiments 2 and 3 the flowing system was not used. The chamber was filled initially with seawater and during the experiments was exposed to room light. The temperature during experiment 2 was 24°C and water samples were taken at 10-min intervals for 40 min. The fish had been fed 30 min prior to their placement in the chamber. The temperature during experiment 3 was 21.5°C and water samples were taken at 10-min intervals for 70 min. The fish had not been fed for 48 hr and just after the 30-min sampling, 2.49 g of frozen brine shrimp were thawed and added to the chamber (the first and second portions of experiment 3 will be referred to as 3a and 3b). An appropriate control was run to determine the effect of the brine shrimp on the ammonia, urea, creatine, and total nitrogen concentrations.

Ten fish from the group used for experiments 1 and 2 and the ten used for experiment 3 were sacrificed for weight determinations. Wet weight determinations were made after blotting the specimens on filter paper, and dry weight was determined after they had been dried at 60°C for 96 hr.

Experiments with the Peruvian anchovy, *Engraulis ringens*, were conducted off the coast of Peru in April 1969, during the RV *Thompson* cruise 36. The methods of collection were described by Whitledge and Packard (1971). Release rates for urea and ammonia were determined for each of three fish in separate one-liter volumes of 0.45μ m Millipore^R filtered seawater at 15°C. Each experiment was run until the animal died (approximately 90 min).

Experiments with the jack mackerel, *Trachurus symmetricus*, were conducted off the coast of California in July 1970, during a cruise of the RV *Alpha Helix* for the Institute of Marine Resources Food Chain Research Group. Of three specimens caught with lure and line, two were placed in a 42-liter Plexiglas deck tank which was continually flushed with surface seawater, and the third, which had been injured when caught, was sacrificed for a weight determination. After approximately 5 hr the fish were transferred to a similar tank recently cleaned and filled with 19°C surface seawater which had been filtered through a 173 μm nylon mesh. Samples for ammonia and urea analyses were taken at the beginning and at the conclusion of the experiment 2 hr later. The fish were kept another 20 hr and released.

For samples from the *E. ringens* experiments ammonia was determined by a modified form of Johnston's (1966) rubazoic acid method and urea by a urease hydrolysis coupled with the rubazoic acid method. In all other experiments ammonia was determined by the phenolhypochlorite method (Solórzano, 1969) and urea by the urease method (McCarthy, 1970). All determinations were made in duplicate immediately after each experiment. Creatine concentrations were measured using a fluorescent complex with alkaline ninhydrin (Whitledge and Dugdale, in press). Total nitrogen was determined with the ultraviolet oxidation technique

of Armstrong, Williams, and Strickland (1966) as described by Strickland and Parsons (1968), but modified by the addition of sodium hypochlorite (chlorine bleach, 5.25% active ingredients). One ml sodium hypochlorite per 100 ml sample was found to increase the percentage of conversion of creatine to nitrate. If added in excess, the sodium hypochlorite will react with the hydrogen peroxide to release oxygen. The conversion of a standard solution of creatine to nitrate in the digester was 43.4%, but the addition of sodium hypochlorite increased this value to 95.0%. Urea standards showed 96-100% conversion without addition of sodium hypochlorite.

All chambers were washed with either fresh or distilled water immediately prior to each experiment and experimental periods were kept to a minimum in an effort to reduce possible effects of bacteria. Antibiotics interfere with both of the ammonia methods mentioned above, and could not be used to reduce bacterial activity. Wood (1958) showed that in fish excretion experiments running as long as 24 hr, bacteria on the surface of the fish do not affect the results and the concentrations of released nitrogen compounds were unchanged for an additional 24 hr.

The data were analyzed statistically using the Mann Whitney U and the Tukey-Siegel tests to compare the medians and variabilities respectively. Significant differences between experiments were at the 0.05 level.

RESULTS

The release rates for ammonia, urea, creatine, total nitrogen and the ammonia-urea ratios for all experiments are given in Table 1. The results of the *E. mordax* experiments represent the mean of the 10-min interval samples for each experiment. An example of the data obtained in one of these experiments is shown in Figure 1. At the conclusion of the first *E. mordax* experiment all of the fish had acquired darkened dorsal coloration and one was locked into the panic response described below for *E. ringens*. Immediately after release into the large holding tank, food was added and all except the one panicked fish, which died a few hours later, fed normally and regained normal coloration. During the other experiments with *E. mordax*, the fish behaved normally and retained their normal coloration. The fish in the *E. mordax* experiment 3b were restricted from feeding in their normal frenzied manner because of the size of the chamber and at the conclusion a small portion of the food remained uneaten. Creatine and total nitrogen values for the second *E. mordax* experiment indicate that

TABLE 1.—Excretion of nitrogenous compounds by *Engraulis mordax*, *E. ringens*, and *Trachurus symmetricus*.

Species		μg at N/mg dry wt/day				
		Ammonia	Urea	Creatine	Total nitrogen	Ammonia-N / Urea-N
Engraulis mordax						
starved one day	(1)	0.074	0.020			3.70
fed before experiment	(2)	0.185	0.036	0.003	0.273	5.14
starved 2 days	(3a)	0.055	0.021	0.002		2.62
feeding	(3b)	0.076	0.023	0.003		3.45
Engraulis ringens	(1)	0.240	0.083	0.118	0.507	2.90
	(2)	0.281	0.089	0.111	0.700	3.16
	(3)	0.171	0.057	0.104	0.346	3.00
Trachurus symmetricus		0.090	0.017			5.29

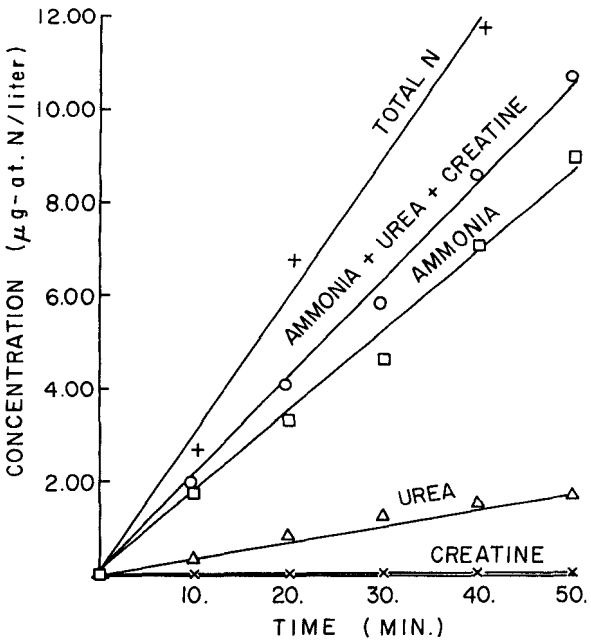

FIGURE 1.—Nitrogen excretion by 10 specimens of *Engraulis mordax* in experiment 2. Specimens were fed 30 min before experiment.

ammonia, urea, and creatine accounted for approximately 82.7, 16.0, and 1.3%, respectively, of the sum of the ammonia, urea, and creatine values. This sum was approximately 82% of the total nitrogen released. The fish used in the *E. mordax* experiments 1 and 2 had a mean wet weight of 13.9 g and a mean dry weight of 3.9 g per animal; those used in the third experiment had mean wet and dry weights, respectivly, of 15.2 g and 4.3 g per animal.

In the *E. ringens* experiments, the sum of the individually measured nitrogen compounds accounted for 69 to 96% of total nitrogen excreted. Relative amounts of ammonia, urea, and creatine averaged 44.6, 14.5, and 21.4%, respectively, while 19.5% was unidentified. Although the specimens of *E. ringens* appeared in good health for the first few hours after capture, their condition deteriorated rapidly after the experiment began. One lived for 83 min, another for 85 min, and the third for 105 min. The behavior pattern was a panic response in which the animals tried repeatedly to swim downward into the bottom of the container and eventually did considerable damage to their heads, resulting in broken blood vessels in their eyes and nasal regions. The dorsal coloration changed from a greenish-grey to jet black during the deterioration, and once an animal locked into this behavior pattern there was apparently no way to reverse it and death was inevitable. The mean wet weight and dry weight per fish for these experiments was 7.0 and 1.9 g, respectively, and nitrogen was found to be 10.9% of dry weight.

The results for the *T. symmetricus* represent a single value for both fish in the same chamber. Prior to, during, and in the 20 hr after the experiment the fish swam about the chamber in a calm manner. The wet weight of the sacrificed fish was 190.0 g.

DISCUSSION

The fish in the *E. mordax* experiment 2 were the most recently fed, and Figure 1 shows that urea, ammonia, and creatine were released at approximately constant rates over the experimental period. Table 1 shows that these release rates for ammonia, urea, and the ammonia-urea ratio were the highest of all the *E. mordax* experiments. The urea release rates for the other experiments (1, 3a, and 3b) were all similar, but the ammonia release rates and the ammonia-urea ratios appear to be related to the length of the starvation period.

For the *E. mordax* experiments, the statistical tests indicated that the ammonia release rates in experiments 1 and 3a and in experiments 1 and 3b were not significantly different within each pair with respect to central tendency. On the other hand there were significant differences between the pairs of ammonia release rates in experiments 1 and 2, 2 and 3a, and 2 and 3b. The variabilities for ammonia release rates for all of the experiments were similar. With regard to the urea release rates, only those for experiments 1 and 2 were significantly different with respect to location of central tendency and none of the experiments differed from each other with respect to variability.

These statistics imply that the effect of feeding is rapidly apparent in the ammonia release rates while it appears more slowly and to a lesser de-

gree in the urea release rates; this is clearly reflected in the ammonia-urea ratios. When the period of starvation was the greatest (experiment 3a) the ratio was the lowest, and when the starvation was least the ratio was the greatest. The ratio for experiment 3b presumably would have increased to a value comparable to that for experiment 2 when the time since feeding had become equal for both.

Upon thawing, the brine shrimp which were used to feed *E. mordax* liberated ammonia, urea, and creatine. If these substances were retained in large quantities by the shrimp, the results of experiments 2 and 3b could have been affected. Such interference is, however, unlikely since only the ammonia release rate increased with feeding in experiment 3. If this increased rate of release had resulted from ammonia liberated from the shrimp after ingestion by the fish, a comparable increase in the rate of urea release would have been expected since the quantities of urea liberated by the shrimp were approximately equal to those of ammonia.

It is important to note that since experiment 3 was conducted at a temperature 2.5°C lower than the other experiments, a correction of the measured rates should be made in order to compare them properly. Since an appropriate Q_{10} value was not available, the correction was not made. Presumably, however, a Q_{10} for an ammonia release rate would be similar if not identical to that for urea, and the ammonia-urea ratio would not be changed with a temperature correction. The lack of both a temperature correction and an appropriate relationship between body size and nitrogen excretion also makes the comparison of data between different species difficult.

The *E. ringens* experiments produced the highest release rates (particularly for creatine) and the lowest ammonia-urea ratios. This can probably be attributed to the high level of activity and/or the poor health of the specimens.

Wood (1958) ran experiments for 24 hr at 12°C, and from his Table 2 and an approximation of 28% wet weight = dry weight, one can calculate ammonia and urea release rates. These calculated mean release rates are 0.0141, 0.0179, and 0.0065 μg at ammonia-N + urea-N/mg dry weight/day, for the sculpin (*Leptocottus armatus*), the starry flounder (*Platichthys stellatus*), and the blue sea perch (*Taeniotoca lateralis*) respectively. These rates are nearly an order of magnitude lower than those reported here, but a temperature correction (assuming a Q_{10} of 2) would bring them within approximately a factor of five. The calculated ammonia-urea ratios for the sculpin, the starry flounder, and the blue sea perch are 3.09, 7.13, and 1.26 respectively. Since the fish used in Wood's studies were nearly ten times larger than the anchovies, were maintained for some time prior to the experiments on a diet of lingcod muscle, and for the experiments were enclosed in chambers barely larger than the fish, it is difficult to compare the results of the different sets of data.

Ammonia and urea are important plant nutrients and it is of interest to examine the significance of fish excretion as a source of these substances in the sea. Whitledge and Packard (1971) estimated that nitrogen excretion by the herbivorous *E. ringens* in the near surface waters of the Peru Current is an order of magnitude greater per unit volume of water than zooplankton excretion and they suggested, on the basis of these rates and measured rates of nitrogen uptake by phytoplankton, that fish excretion may be a major source of the ammonia utilized by phytoplankton in this area.

Off the coast of southern California the contribution of the fish community in the regeneration of ammonia and urea can also be estimated. Integrated values of phytoplankton nitrogen utilization at three stations in the euphotic zone off the coast of San Diego (Stations 1, 4, and 6, McCarthy[4] averaged 0.073 μg at ammonia-N/liter/day and 0.066 μg at urea-N/liter/day. For the area included in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) survey, the total biomass of the most common species of near-surface fish [northern anchovy (*Engraulis mordax*), Pacific hake (*Merluccius productus*), jack mackerel (*Trachurus symmetricus*), Pacific saury (*Cololabis saira*), and al-

[4] McCarthy, J. J. The uptake of urea by natural populations of marine phytoplankton. Manuscript in preparation.

bacore (*Thunnus alalunga*)] is estimated at 20-25 $\times$ 10^6 metric tons wet weight (Dr. P. E. Smith, personal communication). Using an area of 70 $\times$ $10^{10}m^2$, a depth of 140 m, an average excretion rate from Table 1 (*E. mordax*, experiments 1 and 2, and *T. symmetricus*), and a conversion factor (dry wt = 28% wet wt) approximate production rates of 0.0075 μg at ammonia-N/liter/day and 0.0015 μg at urea-N/liter/day can be calculated. These rates would account for 10% of the ammonia and 2% of the urea utilized by the phytoplankton.

Other investigators—Harris, 1959; Dugdale and Goering, 1967 and 1970; and Martin, 1968—have attempted to balance ammonia utilization by phytoplankton and excretion by zooplankton in Long Island Sound, the Bermuda region, the Peru Current and Narragansett Bay respectively. Further calculations can be made for the area off southern California to compare the significance of fish ammonia and urea excretion to that of zooplankton. A zooplankton standing crop estimate of 0.125 mg dry wt/liter was calculated from 10 years of data collected in the California Current as part of the CalCOFI program by multiplying the mean catch by a factor of 3 to compensate for the biomass of the smaller zooplankton lost through the 0.505 mm mesh (Dr. P. E. Smith, personal communication). Using average excretion rates for recently fed zooplankton (*Calanus helgolandicus, Calanus chilenis*, and *Clausocalanus* sp.) of 0.73 μg at ammonia-N/mg dry wt/day and 0.36 μg at urea-N/mg dry wt/day (McCarthy, 1971) average regeneration rates of 0.090 μg at ammonia/liter/day and 0.045 μg at urea-N/liter/day can be calculated. These rates would account for 123% of the ammonia and 68% of the urea utilized per day. If on the other hand, microzooplankton and zooplankton biomass data collected from April through September 1967 in the same approximate area as two of the three stations used for the phytoplankton utilization calculations are applied (Beers and Stewart, 1970; Mullin and Brooks, 1970) the calculated regeneration would be 0.020 μg at ammonia-N/liter/day and 0.010 μg at urea-N/liter/day. These rates account for 27% of the ammonia and 15% of the urea utilized by the phytoplankton. Hence, the fish contribution would amount to 8-27% of the ammonia and 3-13% of the urea released by both groups of organisms. There undoubtedly are, however, situations in which large fish or schools of fish (the mean density of an *E. mordax* school is estimated as the equivalent of 1,300 10-cm fish/m^3, Dr. P. E. Smith, personal communication) are more important than zooplankton in supplying ammonia and urea to a particular parcel of water.

Obviously these calculations are based on many simplified assumptions. Other than the fact that the zooplankton and fish biomass estimates are averages for larger areas and longer periods of time than can be represented by the phytoplankton utilization rates, perhaps the most poorly based assumption is the application of mean excretion rates for three zooplankton species and two fish species to the entire zooplankton and fish populations. More reliable estimates of excretion rates are needed for smaller species of zooplankton and larger species of fish.

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