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Energy Sources for Detritivorous Fishes in the Amazon

Carlos A. R. M. Araujo-Lima, Bruce R. Forsberg,* Reynaldo Victoria, Luiz Martinelli

Detritivorous fishes form an important part of the ichthyomass in the Amazon basin. Most of these fishes are contained in the orders Characiformes and Siluriformes (catfishes). The Characiformes constitute more than 30% of the total fish yield in the Amazon basin, whereas the catfishes are of minor importance. Stable isotope data indicate that Characiformes species receive most of their carbon through food chains originating with phytoplankton, while the Siluriformes receive a significant part of their energy from other plant sources.

The primary protein source for the human population in the Amazon basin is fish (1). More than 30% of the fish consumed in the Amazon basin are detritivores (2–4), and evidence shows that this percentage has risen in recent years (4, 5). Most of these detritivorous fishes are contained in the order Characiformes (families Prochilodontidae and Curimatidae), whereas the catfishes (Siluriformes) form a second minor group.

Effective management of these populations will require an understanding of factors controlling their production. A critical first step will be to identify the plant carbon sources that fuel the detritivore food chain. There are four general groups of autotrophs in the Amazon region that could support detritivorous fishes, either directly or indirectly: trees, phytoplankton, periphyton, and aquatic macrophytes. Both aquatic macrophytes (5, 6) and trees (7) have been suggested as the principal carbon source for detritivorous fishes in the Amazon. There is also some evidence that algae can be important in the detritivore diet (5, 7). These hypotheses, however, are largely based on visual analyses of stomach contents, which can be misleading. These fishes are bottom feeders, and the stomach analyses generally reveal a complex mosaic of food items in their diet, including microinvertebrates, al-
gae, bacteria, and detritus, usually dominated by detritus (5, 7, 8). It is not clear, though, which of these food items is digested and assimilated by the fish (8) and, with the exception of live algae, it is not possible to identify the autotrophic carbon source from which the material originated.

Stable isotope tracers offer an alternative and more direct approach to this question. Isotope analysis based on the use of $^{13}$C, an effective tracer of carbon flow through food chains (9), has been especially useful in identifying the plant carbon sources that support production at higher trophic levels (9). We present here the results of a $^{13}$C tracer study of carbon flow through fish detritivore food chains in the central Amazon basin. Our objective was to identify the principal autotrophic carbon sources supporting detritivorous fish production in the Amazon.

Plant ($n = 147$) and fish ($n = 56$) samples were collected during high- and low-water seasons in 1984 and 1985 (10). Suspended particulate organic carbon (POC), phytoplankton, periphyton, tree parts, and aquatic macrophytes were sampled at a variety of sites in the central Amazon basin (11) (Fig. 1). Fish samples were collected near Manaus and over most of the Amazon River system by the Manaus fishing fleet (Fig. 1). Preliminary processing of the samples was carried out at Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus (12), and isotope analyses were performed at Centro de Energia Nuclear na Agricultura (CENA) in Piracicaba (13).

The results of the isotope analyses are shown in Fig. 2. Some published values for Amazonian plants were also used in determining the means, ranges, and 95% confidence intervals for the plant end members (14). The C$_4$ macrophytes (principally Echinodroma pulchellula and Paspalum repens) were the heaviest (that is, most positive) plant end members with a mean $^{13}$C value of $-12.9$ per mil. The next heaviest plant groups were periphyton, C$_3$ macrophytes, tree wood, and tree seeds with mean $^{13}$C values of $-26.8$, $-27.6$, $-27.6$, and $-28.3$ per mil, respectively. A Student-Newman-Keuls (SNK) test indicated no significant difference after paired comparison of these four means ($P > 0.05$). Tree leaves were significantly lighter than tree wood and seeds (SNK test; $P < 0.05$) with a mean value of $-30.0$ per mil. The mean $^{13}$C value for POC samples containing more than 60% live phytoplankton was $-33.3$ per mil, and the mean for all POC samples was identical. The similarity of these two means suggests that POC in the lakes is derived primarily from phytoplankton. Since phytoplankton is the most negative plant end member, this result is unambiguous: the contribution of carbon from other plant end members must be relatively small.

The mean $^{13}$C values for the characiform detritivore species ranged between $-32.5$ to $-34.2$ per mil and were not significantly different (SNK test; $P > 0.05$). The siluriform catfishes were significantly heavier (SNK test; $P < 0.05$) with a mean $^{13}$C value of $-26.0$ per mil.

The $^{13}$C values for the catfishes fell in the middle of the plant end-member values. Since there are more than two plant end members, the carbon source for this fish group is uncertain. Catfishes could be receiving carbon primarily from periphyton or from an unknown mixture of plant end members. We can only conclude that neither phytoplankton nor C$_4$ macrophytes provide all the energy for this group. The results for the characiform species are easier to interpret since their $^{13}$C values fell close to the most negative end member, phytoplankton. In this case the result is unambiguous. The Characiformes must receive a large fraction of their carbon from phytoplankton and very little from the other plant groups (15, 16). The maximum contribution of tree leaves (the lightest alternative carbon source) to the carbon balance of Semaprochilodus taeniurus, and the other characiform species is 30 and 0%, respectively, whereas the contribution of C$_4$ macrophytes (the heaviest alternative carbon source) does not exceed 5% for any of the five species (17).

Although it was possible to identify the carbon source only for the characiform species, this result is important. The characiform detritivores are the most important group of food fish in the Amazon, accounting for over 99% (2) of the detritivorous fish yield and over 30% of the total fish harvest (2, 3). Thus, our results suggest that a large portion of the fish consumed in the Amazon is derived through food chains beginning with phytoplankton. Macrophytes, which have been proposed as a major energy source for detritus-based food chains, appear to be relatively unimportant.
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10. Nine fish and 37 plant species were sampled. The
    characiformes fish species were Semaprochilodus
taeniurus, Prionothoglanis gigas, Pseudorhombus
    laticeps, and Pterogymnotus riolii-
    lodes. The catfish species were Pterygoplichthys
    multiradiatus, Loricariichthys platynectes, Hoplosternum
    thoracatum, and Hemibarbus aculeatus. Only adult
    fishes were sampled.
11. POC samples were collected exclusively in lakes. We
    collected POC samples to estimate phytoplankton
    8°C values. POC samples with more than 60% phytoplankton
    were classified as pure phytoplankton
    samples. POC samples were not collected in the
    river because phytoplankton biomass is typically
    very low (T. K. Fisher, Comp. Biochem. Physiol. 62A,
    1 (1979); R. C. Witman, J. E. Richey, F.
12. Samples for isotopic analysis were prepared by comb-
    ination of 10 mg of dry matter with CaCO3 in
    screw-cap stainless steel tubes. The samples were
    burned overnight at 550°C and purified by passage
    through alcohol-dry ice traps. The purified sample
    was collected in a tube with liquid nitrogen, in a
    special vacuum line. A set of CEN's standards
    [pure charcoal from C3, and C4 plants, dried
    at 5°C and 2°C, respectively (DFB limestones] was
    prepared with each sample batch; thus, no correc-
    tion for oxygen was necessary, as its source was the
    same for the samples and the standards. All
    carbon-13 values represent the mean of two separate
    analyses from the same sample (SEM = 0.25
    8°C unit) and were reported relative to DFB limestone:
    
    $\delta^{13}C = \frac{\text{sample} - \text{standard}}{\text{standard}} \times 1000$

    Analyses were performed in a Micromass model
    602 E mass spectrometer fitted with double inlet
    and double collector systems.

    (Sixteen wood, 15 leaf, and 4 macrophyte values
    were included in the analysis.)

    14. Since the organic matter encountered in stomach
    analyses is largely unrecognizable, it is not clear
    whether these fishes are obtaining their energy
    directly from phytoplankton by consuming their
    sedimented remains or indirectly by consuming the
    remains of organisms at higher trophic levels. The
    8°C results in their phytoplankton and fish species, re-
    spectively, and $\delta^{13}C$ was the lower limit of the 95%
    confidence interval for the mean 8°C value of the
    alternative carbon source. An increase of 1 delta unit
    per trophic level was assumed to be due to fraction-
    ation ([M. De Niro and S. Epstein, Geochim. Cosmo-
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    15. We thank L. P.-Daniel for identifying the siluroid
    species, C. G. Fernandes and T. Pinheiro for help
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Expression of Bovine 17α-Hydroxylase Cytochrome P-450 cDNA in Nonsteroidogenic (COS 1) Cells

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Cortisol production requires the activity of only 17α-hydroxylase, whereas the formation of sex steroids requires both 17α-hydroxylase and 17,20-lyase activities. Studies in reconstituted enzyme systems have suggested that a single steroid hydroxylase, 17α-hydroxylase cytochrome P-450 (P-450(17α)), catalyzes both activities. By expression of bovine adrenocortical P-450(17α) in COS 1 (transformed monkey kidney) cells, which normally contain no detectable P-450(17α), it has now been established that a single polypeptide chain does catalyze both the 17α-hydroxylase and the 17,20-lyase reactions. This heterologous system supports 17α-hydroxylation of pregnenolone and progesterone with equal efficiency, but catalyzes about five times as much 17,20-lyase activity when 17α-hydroxypregnenolone is the substrate than when 17α-hydroxyprogesterone is the substrate. For these activities to be observed in COS 1 cells, newly synthesized apocytochrome P-450(17α) must bind heme and insert into the endoplasmic reticulum such that endogenous cytochrome P-450 reductase can support hydroxylation. Thus, COS 1 cells are a useful system for expression and study of various forms of cytochrome P-450.

STUDIES OF MICROSOMAL 17α-HYDROXYLASE CYTOCHROME P-450 (P-450(17α)) AS WELL AS OTHER EUKARYOTIC CYTOCHROMES P-450 HAVE BEEN COMPLICATED BY PROBLEMS ASSOCIATED WITH PURIFICATION FROM THEIR MEMBRANE (MICROSOMAL OR INTERNAL MITOCHONDRIAL) ENVIRONMENTS AND SUBSEQUENT RE-CONSTITUTION OF THEIR ACTIVITIES IN VITRO. THE SIMILARITIES IN PHYSICAL AND BIOCHEMICAL CHARACTERISTICS OF DIFFERENT CYTOCHROMES P-450 (1) TOGETHER WITH POTENTIAL ARTIFACTS GENERATED DURING SOLUBILIZATION, PURIFICATION, AND RECONSTITUTION PROCESSES (2) HAVE MADE IT DIFFICULT TO UNAMBIGUOUSLY ASSIGN ONE OR MORE ACTIVITIES TO AN INDIVIDUAL FORM OF CYTOCHROME P-450. PREPARATIONS OF PURIFIED ADRENOCORTICAL AND TESTICULAR P-450(17α) POSSESS 17α-HYDROXYLASE ACTIVITY NECESSARY FOR THE PRODUCTION OF CORTISOL, AS WELL AS 17,20-LYASE ACTIVITY REQUIRED FOR SEX STEROID FORMATION (3). HOWEVER, THE RATIO OF ACTIVITIES CHANGES DURING PURIFICATION PROCEDURES (3) AND IN VIVO UNDER DIFFERING PHYSIOLOGICAL CONDITIONS (4). ALSO, IN HUMANS, DEFICIENCIES ASSOCIATED WITH THESE ACTIVITIES HAVE BEEN REPORTED FOR EITHER 17α-HYDROXYLASE ACTIVITY (5) OR 17,20-LYASE ACTIVITY (6). AFTER IDENTIFYING AND CHARACTERIZING A COMPLEMENTARY DNA (cDNA) CLONE SPECIFIC FOR BOVINE P-450(17α) (7), WE WANTED TO CLEARLY CONDITION THE REPORTED DUAL ACTIVITIES ASSOCIATED WITH THE P-450(17α) POLYPEPTIDE CHAIN.

Our strategy was to analyze the activities