

## **Energy sources for aquatic animals in the Orinoco River floodplain: evidence from stable isotopes**

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**Summary.** Stable carbon and nitrogen isotope ratios in autotrophs, aquatic invertebrates and fishes from the Orinoco River floodplain of Venezuela reveal that microalgae, including both phytoplankton and epiphytic (attached) forms, are predominant energy sources for many aquatic animals, even though aquatic vascular plants are much more abundant. Floating mats of the grass *Paspalum repens* and the water hyacinth *Eichhornia* spp. harbor particularly high densities of aquatic animals, but isotopic evidence indicates that few species are dependent on organic carbon originating from these plants. The stable isotopic evidence for the trophic importance of algae contradicts traditional interpretations of food webs in freshwater wetlands, which are generally thought to be based largely on detritus originating from vascular plants.

**Key words:** Orinoco River – Floodplain – Stable isotopes – Food webs – Algae

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Most investigations of food webs in freshwater wetlands have suggested that detritus originating from vascular plants is the predominant energy source for aquatic animals (e.g., Petr 1983; Junk 1984; Goulding et al. 1988; Mann 1988; Bayley 1989; Ward 1989). Much of the evidence for this general conclusion has come from observations of feeding and from analysis of stomach contents. In addition, ecosystem-level comparisons of primary and secondary production in wetlands have indicated that algal production is insufficient to sustain the secondary production of aquatic animals; food webs are thus assumed to be sustained largely by vascular plants, either through direct herbivory or, more importantly, through the consumption of vascular-plant detritus (Bowen 1987; Murkin 1989; Bayley 1989).

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There is considerable uncertainty in the evidence supporting a dominant role for vascular plants in wetland food webs. Direct observations of food ingestion and gut contents can be misleading because many aquatic animals assimilate only the most labile fraction of what they consume (Bowen 1987). Organic matter varies in its digestibility and nutritive value, and these differences are not well understood. Also, estimation of ecosystem-level primary production in wetlands is difficult, particularly for algae (Junk 1985; Bayley 1989; Murkin 1989).

Natural abundances of stable isotopes of carbon and nitrogen in consumers reflect assimilation rather than ingestion, and can serve as tracers of energy flow in ecosystems where the potential organic matter sources have distinct isotopic compositions (Peterson and Fry 1987). A particular advantage of stable carbon isotopes is that the isotopic composition of organic matter changes relatively little upon decomposition (Fry and Sherr 1984; cf. Benner et al. 1987), making it possible to identify the origins of fine particulate organic matter consumed by detritivores. Stable isotopes have been used as tracers in recent studies of energy sources for consumers in salt marshes and seagrass beds (Peterson and Howarth 1987; Fry et al. 1987; Sullivan and Moncreiff 1990), which have resulted in reconsideration of earlier interpretations of the trophic role of vascular plants in those ecosystems by revealing the importance of microalgae in the diets of many aquatic animals.

We report here measurements of stable carbon and nitrogen isotope ratios in the aquatic food web of the Orinoco River floodplain of Venezuela. We use the stable isotope measurements to investigate the relative importance of vascular plants and microalgae as energy sources for invertebrates and fishes. Our results indicate that both phytoplankton and attached algae are unexpectedly important sources of energy for many aquatic animals. The trophic importance of algae as an energy source in the Orinoco floodplain contradicts traditional interpretations of floodplain food webs, and has implications for the management of tropical floodplain fisheries (Araújo-Lima et al. 1986; Bayley and Petrere 1989) and for the conservation of biological diversity (Klopatek 1988).

## Study site

Our study site is located along the lower Orinoco River in Venezuela (Fig. 1). This area has been described in previous limnological and ecological studies (Hamilton and Lewis 1987; Twombly and Lewis 1987; Vásquez 1989; Rodríguez and Lewis 1990; Hamilton et al. 1990).

The floodplain of the Orinoco River, like many tropical floodplains, contains a mosaic of open water, floodplain forest, and floating mats of herbaceous plants (macrophytes). The potential autotrophic energy sources for consumers in floodplain waters thus include litter from forest trees, aquatic macrophytes, suspended algae (phytoplankton), and attached microalgae that grow on the submersed portions of vascular plants (epiphytic or periphytic algae). Seasonal fluctuations in water level of 10–15 m coincide with seasonal phases of growth and decomposition for vascular plants and algae. During inundation, litter from terrestrial plants is covered with water, and the macrophytes and algae flourish. Some woody plants drop their leaves during flooding, while others retain them. When the water level falls, most of the macrophytes die and decompose rapidly, although both macrophytes and algae may remain abundant in the greatly reduced areas of standing water. The plant ecology of similar floodplains in the Amazon Basin is described by Junk (1983).

As in most tropical floodplains, the plants that form floating macrophyte mats during inundation in the Ori-

noco floodplain include both  $C_4$  and  $C_3$  plants ( $C_4$  refers to the dicarboxylic acid pathway of photosynthetic carbon fixation, which is common among tropical grasses, and  $C_3$  refers to the Calvin pathway that is characteristic of most other plants). The  $C_3$  and  $C_4$  plants differ in carbon isotope fractionation during photosynthetic carbon fixation (Farquhar et al. 1989). The floating mats of  $C_4$  grasses are the only conspicuous  $C_4$  plants in the floodplain. In the Orinoco floodplain, the submersed roots and rhizomes of floating mats of both  $C_3$  and  $C_4$  plants harbor high densities of aquatic invertebrates and fishes, in contrast to the benthic and flooded forest habitats, where organism densities are low (M. Lasi, personal communication). This is also true of the Amazon floodplain, where greater food availability, refuge from predation, and the availability of oxygen have been suggested as alternative explanations for the rich fauna of floating macrophyte mats (Junk 1973 and 1984; Engle and Melack 1990).

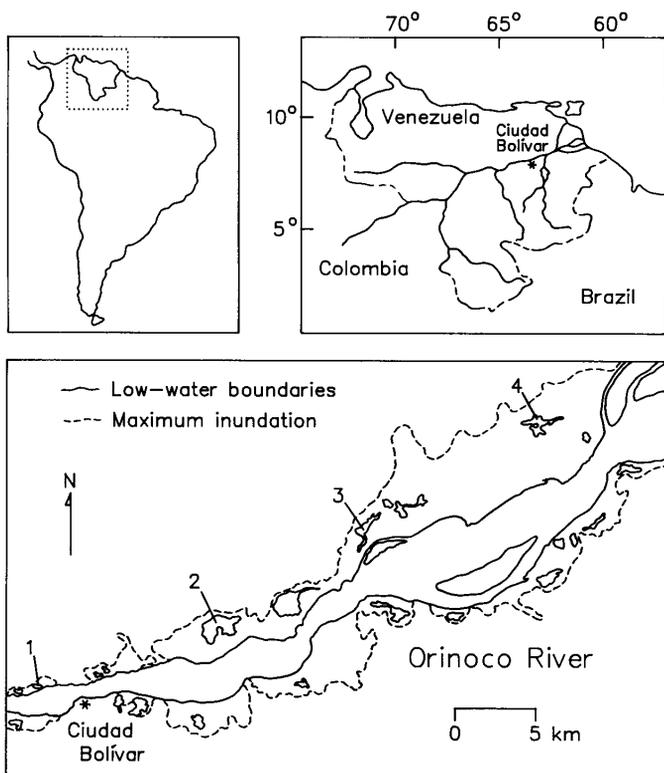
## Methods

Samples of autotrophs and invertebrates were taken from localized concentrations of distinct organic matter sources; sampling was designed to take advantage of the difference in carbon isotope ratios between  $C_3$  and  $C_4$  plants. Locations included floating mats of *Paspalum repens* (a  $C_4$  grass) and of the water hyacinth *Eichhornia* spp. (*E. azurea* and *E. crassipes*;  $C_3$  plants), central parts of the flooded forest, and open waters. Samples were collected in September–December 1988, during peak inundation and falling water. This is the phase of greatest primary and secondary production of the aquatic biota, and encompasses the maximum development and subsequent senescence of floating macrophyte mats.

Plankton was sampled by collection of 100 L of water from the center of the open-water areas (0.1–2.3 km<sup>2</sup>). We harvested zooplankton from the water sample with a 53- $\mu$ m mesh net, and then collected particulate material, which contained both suspended algae and organic detritus, with a continuous-flow centrifuge. The algal fraction was isolated by centrifugation of the particulate material in colloidal silica. The optimum density of the silica sol was determined by trial and error with step gradients to provide good separation of algae from the other material. Successive centrifugation of 10-mL subsamples of the slurry of concentrated particulate material eventually produced an almost pure sample of phytoplankton of sufficient size for stable isotopic analysis. The phytoplankton layer was removed, centrifuged several times through deionized water to remove the silica, collected on a pre-combusted glass-fiber filter, and dried at 60°C. The detrital layer was also collected and analyzed. Microscopic examination and carbon and chlorophyll measurements of both fractions confirmed that algae were successfully separated from detritus.

Epiphyton was washed from submersed plant parts by gentle agitation and brushing. The resulting slurry containing epiphyton was filtered through sieves of 800- and 275- $\mu$ m mesh, which removed large detrital particles and macroinvertebrates. Microalgae in the slurry were harvested by centrifugation in colloidal silica. Filters containing the epiphytic algal fraction were examined with a dissecting microscope before drying, and any remaining invertebrates and vascular-plant fragments were removed with forceps and needles.

Invertebrates were collected concurrently with the autotroph samples, and were separated by hand while they were alive. Copepods and cladocerans were induced to migrate through light gradients; the concentrated organisms were repeatedly collected, diluted, and induced to migrate again to yield nearly pure samples of these microcrustaceans (Straskraba 1964). Narcotization with



**Fig. 1.** Location of the study site. Samples were collected from the floodplain along the north bank of the Orinoco River. The principal lakes in the sampling area are numbered: (1) Orsinera, (2) Tineo, (3) Fundación, and (4) Tasajeras

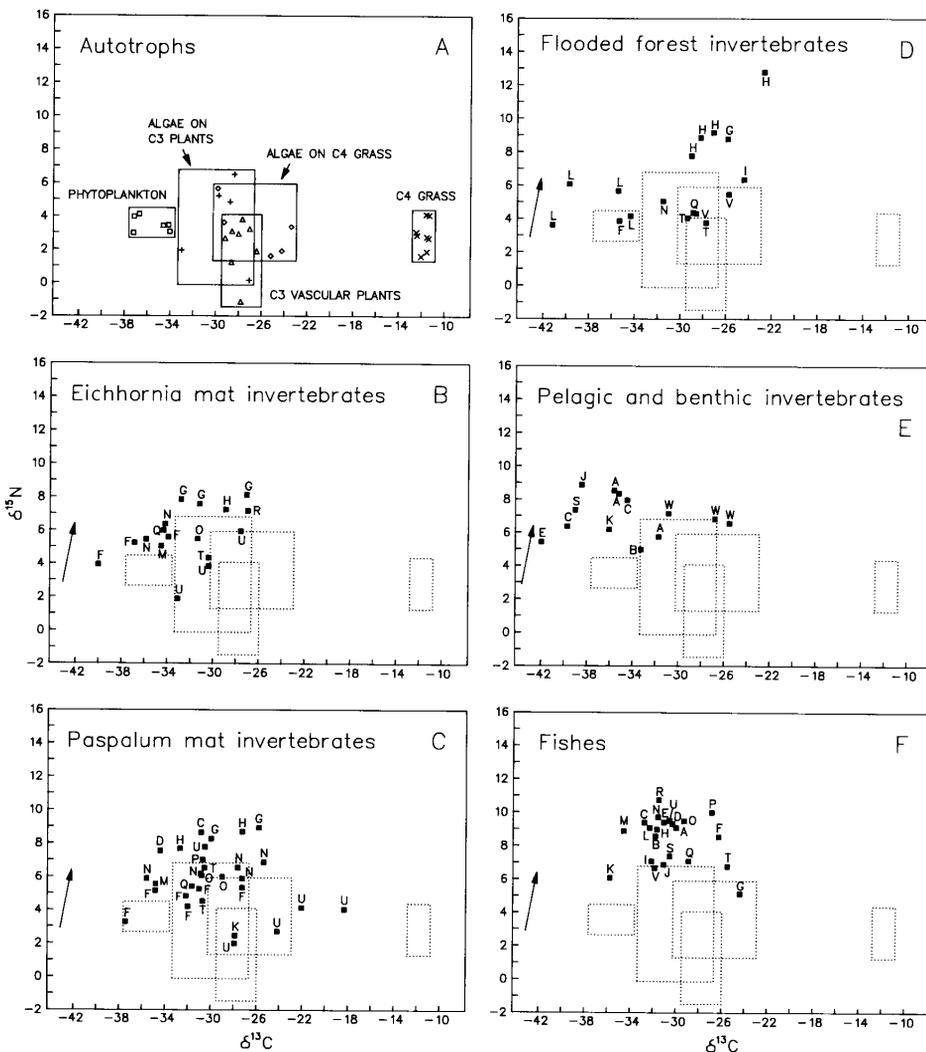
CO<sub>2</sub> was used to separate rotifers from microcrustaceans, which settled at different rates. After separation, invertebrates were held alive in filtered water overnight to allow for gut clearance before they were frozen, dried at 60°C, and ground to a fine powder. Shells were removed from small snails by dissection. Whole body samples were analyzed except for prawns, crabs, apple snails and bivalve molluscs, from which muscle tissue was removed for analysis, and for sponges, from which gemmules (resting stages) were collected for analysis. Most invertebrate samples were composites of numerous individuals.

An electrofishing boat was used to collect fishes from the borders of flooded forests and macrophyte mats (*P. repens*). The fishes were placed on ice, and a sample of the lateral musculature was later removed, dried and ground for isotopic analysis. Fish samples represent either single-species composites of 2–10 individuals (16 of 22 samples) or single individuals.

The carbon or nitrogen in samples of organic matter was converted to CO<sub>2</sub> or N<sub>2</sub> gas, which was analyzed for carbon or nitrogen isotope ratios by mass spectrometry at The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts. Results are expressed as  $\delta$  values, which are ‰ (parts per thousand) deviations from standard reference materials. The  $\delta$  value is higher (more positive) in a sample that is enriched in the heavy isotope (<sup>13</sup>C or <sup>15</sup>N). The mean  $\pm$  s.d. for the difference between duplicate subsamples of ground material was  $0.22 \pm 0.21\%$  for  $\delta^{13}\text{C}$  ( $N=42$ ) and  $0.26 \pm 0.23\%$  for  $\delta^{15}\text{N}$  ( $N=39$ ).

## Results

Autotrophs in the Orinoco floodplain varied widely in carbon isotopic composition (Fig. 2A). The disparate and narrow ranges of  $\delta^{13}\text{C}$  for the two groups of vascular plants reflect the two types of photosynthetic pathways (C<sub>3</sub> and C<sub>4</sub>); these plants utilize atmospheric carbon dioxide, which varies relatively little in isotopic composition. The phytoplankton was depleted in <sup>13</sup>C relative to vascular plants. The  $\delta^{13}\text{C}$  values of epiphytic algae living on either C<sub>3</sub> or C<sub>4</sub> plant surfaces were closest to, but more variable than, the  $\delta^{13}\text{C}$  values of C<sub>3</sub> vascular plants. The carbon isotopic composition of submersed autotrophs is known to be variable, principally because the isotope ratio of dissolved CO<sub>2</sub> varies according to the relative importance of atmospheric and respiratory CO<sub>2</sub> sources, and because diffusional limitation of CO<sub>2</sub> assimilation can reduce the expression of the enzymatic fractionation of carbon isotopes during carbon fixation (O'Leary 1981; Farquhar et al. 1989). The  $\delta^{13}\text{C}$  values for autotrophs in Fig. 2A are generally consistent with measurements reported for the Amazon floodplain



**Fig. 2A–F.**  $\delta^{15}\text{N}$  plotted against  $\delta^{13}\text{C}$  for autotrophs and aquatic animals in the Orinoco floodplain during inundation. Where a given plant or animal occurs more than once on the plots, each point represents a different site or sampling date. (A) The major groups of autotrophs. C<sub>3</sub> vascular plants include *Eichhornia* spp. and leaves of several tree species. The C<sub>4</sub> grass is *Paspalum repens*. Epiphytic algae were collected from submersed portions of vascular plants. (B–F) Aquatic invertebrates and fishes from the major habitats in the Orinoco floodplain (see Table 1 for identification of points). The arrow shows the average heavy isotope enrichment of an aquatic animal relative to its diet, and allows for extrapolation from consumers back to autotrophs

(Araújo-Lima et al. 1986; Hedges et al. 1986), although measurements for epiphytic algae have not been reported previously.

Aquatic invertebrates in floating mats of the macrophytes *Eichhornia* spp. (a C<sub>3</sub> plant) and *Paspalum repens* (C<sub>4</sub>) show similar ranges in isotope ratios (Fig. 2B–C). None of the aquatic invertebrates dwelling in the rhizomes and roots of the C<sub>4</sub> grass mats appears to feed primarily on organic carbon originating from the grass. However, 3 of the 5 small gastropod samples collected from *P. repens* were enriched in <sup>13</sup>C relative to the other invertebrates, which could be explained by a partial contribution of the C<sub>4</sub> carbon to their diets. We also sampled two terrestrial invertebrates that were observed feeding directly on leaves of *P. repens* above the water level: an unidentified grasshopper had  $\delta^{13}\text{C} = -12.0\%$ , and slugs (probably *Omalonyx*) had  $\delta^{13}\text{C} = -13.9\%$ . In contrast to the aquatic invertebrates, these appear to derive their nutrition largely from the grass tissue.

Stable nitrogen isotope ratios in animals can serve as indicators of trophic level because animals tend to be enriched in <sup>15</sup>N by 3–4‰ relative to the dietary <sup>15</sup>N (DeNiro and Epstein 1981; Minigawa and Wada 1984; Fry 1988). A smaller enrichment of about 1‰ occurs for <sup>13</sup>C (Fry and Sherr 1984). With the exception of a leguminous tree species that probably has nitrogen-fixing symbionts, the  $\delta^{15}\text{N}$  values of the autotrophs in Fig. 2A range between 0–6.5‰. We have plotted  $\delta^{15}\text{N}$  against  $\delta^{13}\text{C}$  so that the trophic level enrichment in consumers can be seen; the arrow on the plots depicts the expected enrichment for one trophic transfer.

Most invertebrates in the macrophytes were enriched in <sup>15</sup>N relative to the ranges for autotrophs, as expected because of the trophic level enrichment for <sup>15</sup>N. Comparison of the degree of <sup>15</sup>N enrichment to the length of the arrow on the figure suggests that these invertebrates occupy only about 2 trophic levels in the food web.

The carbon and nitrogen isotopic composition of flooded forest invertebrates that were collected from leaf litter and from stands of dead wood resembled that of the mat invertebrates, with a few exceptions (Fig. 2D). Wood-burrowing mayfly larvae (coded as L), which are filter-feeders that tunnel into dead wood to avoid predators (Sattler 1967), were the most depleted in <sup>13</sup>C, suggesting reliance on phytoplankton. One particularly large specimen of the freshwater prawn *Macrobrachium* (coded as H) may have been largely a carnivore or scavenger, as indicated by its exceptional enrichment in <sup>15</sup>N.

Zooplankton in the open-water areas, sponges that grow on submersed tree branches that border the open waters, and a benthic mayfly (*Campsurus* sp.) were depleted in <sup>13</sup>C, suggesting reliance on phytoplankton carbon (Fig. 2E). However, the large benthic bivalve *Prisodon* (coded as W) was more enriched in <sup>13</sup>C and may therefore assimilate substantial amounts of detrital material originating from vascular plants.

Fishes varied surprisingly little in carbon and nitrogen isotopic composition (Fig. 2F), even though they possess a wide range of morphological and anatomical adaptations for feeding (Table 1) (Goulding 1980; Goulding et

**Table 1.** Invertebrates and fishes that represent the coded points in Fig. 2. Trophic category is based on information from the literature: Herb. = primarily herbivorous or detritivorous; Carn. = primarily carnivorous; Omni. = omnivorous

Code	Identification	Trophic Category
<i>Invertebrates:</i>		
A	Sponge gemmules (Porifera: <i>Drulia brownii</i> )	Herb.
B	Rotifers and some copepods (Rotifera, Copepoda)	Herb.
C	Copepods and some cladocerans (Copepoda, Cladocera)	Herb.
D	Copepods (Copepoda)	Herb.
E	Cladocerans and some copepods (Cladocera, Copepoda)	Herb.
F	Clam shrimp (Conchostraca: <i>Cycletheria hislopi</i> )	Herb.
G	Prawns, <1.5 cm long (Decapoda: <i>Macrobrachium</i> spp.)	Herb.
H	Prawns, >1.5 cm long (Decapoda: <i>Macrobrachium</i> spp.)	Herb.
I	Crabs (Decapoda)	Herb.
J	Water mites (Hydracarina)	Carn.
K	Mayfly larvae (Ephemeroptera: Baetidae)	Herb.
L	Wood-burrowing mayfly larvae ( <i>Asthenopus curtus</i> )	Herb.
M	Damselfly nymphs (Odonata: Coenagrionidae)	Carn.
N	Dragonfly nymphs (Odonata: Libellulidae)	Carn.
O	Giant water bugs (Hemiptera: Belostomatidae)	Carn.
P	Water striders (Hemiptera: Veliidae)	Carn.
Q	Water boatmen (Hemiptera: Corixidae)	Omni.
R	Back swimmers (Hemiptera: Notonectidae)	Carn.
S	Phantom midge larvae (Diptera: <i>Chaoborus</i> sp.)	Carn.
T	Adult water beetles (Hydrophilidae, Gyrinidae)	Omni.
U	Small snails (Mesogastropoda, Basommatophora)	Herb.
V	Apple snails (Ampullariidae: <i>Pomacea</i> sp.)	Herb.
W	Bivalve clams (Mutelidae: <i>Prisodon</i> sp.)	Herb.
<i>Fishes:</i>		
A	<i>Schizodon</i> sp. (Anostomidae)	Herb.
B	<i>Leporinus fasciatus</i> (Anostomidae)	Herb.
C	<i>Moenkhausia intermedia</i> (Characidae)	Carn.
D	<i>Acestrorhynchus microlepis</i> (Characidae)	Carn.
E	Unidentified <i>Tetragonopterinae</i> (Characidae)	Omni.
F	<i>Triportheus angulatus</i> (Characidae)	Omni.
G	<i>Mylossoma duriventre</i> (Characidae)	Omni.
H	<i>Geophagus surinamensis</i> (Cichlidae)	Carn.
I	<i>Steindachnerina argentea</i> (Curimatidae)	Herb.
J	<i>Steindachnerina metae</i> (Curimatidae)	Herb.
K	<i>Curimata incompta</i> (Curimatidae)	Herb.
L	<i>Curimatella bolivarensis</i> (Curimatidae)	Herb.
M	<i>Psectrogaster ciliata</i> (Curimatidae)	Herb.
N	<i>Rhinosardinia amazonica</i> (Clupeidae)	Carn.
O	<i>Boulengerella lucia</i> (Ctenoluciidae)	Carn.
P	<i>Rhaphiodon vulpinus</i> (Cynodontidae)	Carn.
Q	<i>Pseudodoras niger</i> (Doradidae)	Carn.
R	<i>Anchoviella guianensis</i> (Engraulidae)	Carn.
S	<i>Loricariichthys brunneus</i> (Loricariidae)	Herb.
T	<i>Hypostomus plecostomus</i> (Loricariidae)	Herb.
U	<i>Pimelodus blochii</i> (Pimelodidae)	Omni.
V	<i>Semaprochilodus laticeps</i> (Prochilodontidae)	Herb.

al. 1988). The isotope ratios for most of the fishes cluster in a range that would be expected to result from diets ultimately based on phytoplankton and epiphytic algae. None of the species appears to depend largely on carbon originating from the C<sub>4</sub> grass, even though most of the fishes were captured along the borders of the grass mats. Our observation that most of the fishes are depleted in <sup>13</sup>C relative to potential sources of vascular-plant carbon is consistent with the conclusions of Araújo-Lima et al. (1986), who analyzed a variety of fishes harvested commercially from Amazon waters. Several of the fishes that we sampled differ in isotopic composition from the rest. The species most enriched in <sup>13</sup>C were *Mylossoma duriventre* (coded as G), a generalist that probably eats fruits and seeds; *Hypostomus plecostomus* (T), a benthic feeder; *Triportheus angulatus* (F), a surface feeder; and *Rhaphiodon vulpinus* (P), a piscivore. These four species do not seem to share a common trophic characteristic. The two species most depleted in <sup>13</sup>C are curimatids (M and K), which are known to ingest fine particulate organic material from surfaces and are assumed to be detritivores (Goulding 1980).

## Discussion

The isotope ratios provide an unambiguous indication that few of the aquatic animals of the Orinoco floodplain are nutritionally dependent on carbon produced by the C<sub>4</sub> grass mats, despite the abundance of the mats and of animals within the mats. The possibility remains that the grasses are particularly inedible, and that C<sub>3</sub> vascular plants support the food webs. However, several observations argue against a predominant dependence of food webs on C<sub>3</sub> vascular-plant carbon. Many consumers are more depleted in <sup>13</sup>C than the range for C<sub>3</sub> vascular plants, and their isotopic composition, after correction for trophic enrichment, indicates at least a partial algal contribution. The overall similarity in isotopic composition between consumers in the C<sub>3</sub> and C<sub>4</sub> macrophyte mats would not be expected if carbon from one or both of these macrophytes were an important energy source, but can be explained by a common dependence on algal carbon. Also, there is no evidence that *Paspalum repens* is particularly inedible. In fact, based on standard assays, this species appears to be a better nutritional source than most vascular plants (Howard-Williams and Junk 1977). Our observation that some terrestrial invertebrates feed directly on *P. repens* also shows that it is potentially edible. *Eichhornia crassipes* is known to be consumed directly by a number of terrestrial invertebrates as well (Pieterse 1978).

The δ<sup>13</sup>C values of some of the mat invertebrates indicate reliance on phytoplankton as a principal food source. Many of the mat invertebrates are adapted to filter-feeding. Slowly flowing waters, which are characteristic of the floodplain during inundation, carry plankton through macrophyte mats, where it becomes available to consumers (Junk 1973; Hamilton et al. 1990). The macrophyte mats may provide a suitable habitat for these species because they serve as a site for attachment and as a refuge from predators.

The stable isotopic evidence presented here leads to the conclusion that microalgae are important in supporting aquatic food webs in the Orinoco floodplain, despite the much greater abundance of living and detrital vascular-plant carbon. Quantitative information on the contribution of different classes of autotrophs to the total primary production is lacking for the Orinoco floodplain, but is available for the central Amazon floodplain. Bayley (1989) compiled data from a variety of studies to evaluate total primary production for a reach of the Amazon floodplain above Manaus that resembles our study site in terms of the seasonality and the proportional coverage by forest, macrophyte mats, and open water. In an area where about half of the original flooded forest remains, macrophytes, forest litter, phytoplankton and epiphyton produce organic carbon in the proportions 69, 24, 5.4, and 1.5%, respectively. Allochthonous organic carbon inputs from the river were also estimated and found to be relatively unimportant. The author noted that the estimate of epiphyton production is based on sparse data and is probably an underestimate because only epiphyton in macrophyte mats was considered. Nevertheless, he concluded that the above proportions are likely to be at least approximately correct. Bayley also estimated total fish production, which is about 1% of the total primary production. Assuming that these estimates are correct and that the trophic transfer efficiency is about 10%, the fish production requires efficient utilization of essentially all of the carbon produced on the floodplain, even if there is only one intermediate trophic level between autotrophs and fishes. Production by phytoplankton and epiphyton appears incapable of supporting much of the total fish production.

It is difficult to reconcile the findings of the present study with the conclusions of Bayley (1989) and others working on the Amazon floodplain who have argued for the importance of vascular-plant carbon in the support of food webs (e.g., Irmiler 1975; Howard-Williams and Junk 1976; Goulding 1980; Junk 1984; Soares et al. 1986). However, our findings do agree with the stable carbon isotope study of Araújo-Lima et al. (1986), in which detritivorous fishes from the Amazon floodplain were shown to rely largely on organic carbon originating from phytoplankton. We hypothesize that algal production in floodplain environments must be much higher than currently estimated, and that algae provide a superior source of nutrition that is selectively ingested or assimilated by a wide variety of aquatic animals, even when vascular-plant carbon is much more abundant in the environment.

Our results add to a growing body of evidence that points to algal production as an important source of energy for consumers in diverse aquatic ecosystems dominated by vascular plants (seagrass beds: Kitting et al. 1984 and Fry et al. 1987; salt marshes: Peterson and Howarth 1987 and Sullivan and Moncreiff 1990; Amazon floodplain: Araújo-Lima et al. 1986). Compared to seagrass beds and salt marshes, tropical floodplains represent a more extreme case of domination of an aquatic ecosystem by vascular plants, and yet microalgae still appear surprisingly important in food webs. For most

aquatic animals, the vascular plants may be more important in providing shelter from predators and substrata for the growth of epiphytic algae than as a source of organic carbon to sustain food webs.

We caution that our findings should not be taken to suggest that the floodplain forest and floating macrophyte mats are unimportant to aquatic animals in tropical floodplains. The existence of a mosaic of forest, macrophyte mats, and open waters is likely to be critical to the maintenance of high biotic diversity and production in these ecosystems, even though the vascular plants may not support much of the secondary production directly.

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