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Foodweb analysis of the Orinoco floodplain based on production estimates and stable isotope data

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Abstract. Stable isotope data and indirect methods for estimating consumer production were used in a foodweb analysis for the Orinoco River floodplain, Venezuela. The ratio of annual production to mean annual biomass ($P_a/\bar{B}$) was estimated from mass at maturity for all major categories of consumers. Field data on $\bar{B}$ then were used to estimate P_a for each major category. Carbon sources for all categories of consumers were identified through $\delta^{13}C$ analysis, and trophic shifts in $\delta^{15}N$ were used in assigning trophic levels to consumers. The ultimate C source for both invertebrates and fish was algae (phytoplankton and periphyton), even though macrophytes and litterfall from the floodplain forest composed 98% of potentially available C. Production of invertebrate consumers (benthos, rhizofauna, and zooplankton), which occurred almost entirely through 1st-level consumption, was estimated as 14 g C m^{-2} y^{-1}. Fish, which produced 11 g C m^{-2} y^{-1}, showed a mean $\delta^{15}N$ trophic shift of 1.8 units above the algal C source, suggesting that ~20% of fish production was directly accountable to consumption of algal C (1st-level consumption), and that most of the remainder was attributable to 1st-level carnivory. Data on production and trophic shifts implied trophic efficiency of 5% for invertebrates and 20% for fish. Although the food web is focused on a very small fraction of potentially available primary C (algae), this C source can account quantitatively for the observed production of both invertebrates and fish. The food web showed marked trophic compression (large consumers supported by trophic levels 1 and 2), which is the only means by which high production of large consumers can be sustained on a small fraction of the potentially available C.

Key words: food webs, tropical floodplains, primary and secondary production, trophic dynamics, fish production, energy flow.

A comprehensive analysis of C or energy flow through a food web requires information on availability of primary sources of organic matter and their rates of use by primary consumers, as well as the trophic positions and production rates for all major categories of consumers. Such an analysis is not yet available for any floodplain. One explanation lies in the biotic complexity of floodplains, which especially complicates the estimation of consumer production. In addition, identification of C sources for primary consumers and of trophic position for all categories of consumers has been virtually impossible until the recent use of stable isotopes for these purposes (Fry 1988, Kling et al. 1992, Cabana and Rasmussen 1994).

Production of aquatic consumers is best estimated through studies of growth rates and abundances of individual taxa. Such studies, which must be of sufficient duration to represent temporal changes in growth and abundance (e.g., Benke 1993), may not be feasible for ecosystems containing multiple community types of high diversity (e.g., benthic invertebrates plus zooplankton and fish). Direct production estimates of all major consumers may be especially difficult in the tropics where cohorts, which facilitate population analysis, often are indistinct because of extended reproductive seasons. A more tractable approach for estimating production in support of comprehensive foodweb analysis involving multiple community types, especially in the tropics, is through use of methods that do not require direct quantifi-

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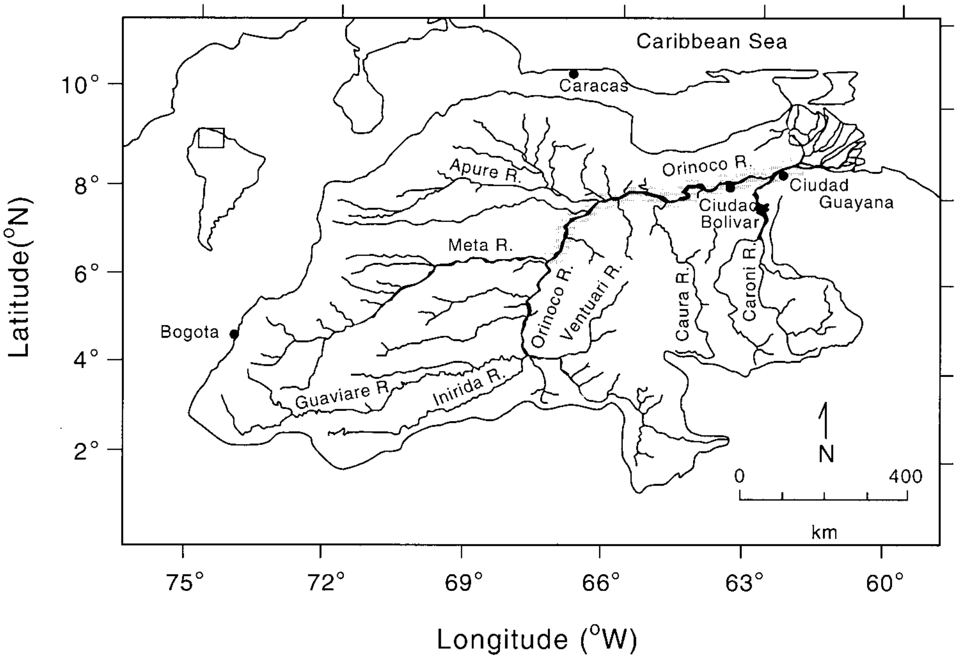

FIGURE 1. The Orinoco basin, Venezuela, showing the fringing floodplain (shaded).

cation of growth rate for consumers. Such methods have been applied to streams (Benke 1993), but not to floodplains.

Information on production of consumers is not sufficient for comprehensive foodweb analysis, which also requires information on C sources for primary consumers and on the trophic positions of the major consumer groups. Quantification of C sources for primary consumers is infeasible by direct observation in a system so biotically complex as a floodplain. Under some circumstances, however, analysis of C isotopic ratios can demonstrate the relative amounts of production supported by various C sources (e.g., Hamilton et al. 1992, Forsberg et al. 1993, Thorp et al. 1998). Trophic position of consumers also can be difficult to diagnose, especially for taxa that occupy >1 trophic level, but isotopic shifts between trophic levels, especially for N, offer new possibilities for assigning consumers to trophic positions, and thus may facilitate comprehensive foodweb analysis (Vander Zanden and Rasmussen 1999).

Data on production, C sources as shown by δ^{13}C data, and trophic levels as shown by δ^{15}N data are used here in support of a foodweb analysis for the Orinoco River floodplain, Venezuela. The analysis draws on data collected through numerous studies spanning ~15 y (Lewis et al. 2000).

Study Site: the Orinoco Fringing Floodplain

The fringing floodplain of the Orinoco River accounts for 7000 km^2 of water surface outside the river channel at maximum inundation (Hamilton and Lewis 1990a, Fig. 1); it is similar in many respects to the Amazon várzea (Lewis et al. 1995, Junk 1997). The floodplain has 3 major aquatic habitat types: flooded forest, macrophyte mats, and open water. The uncanopied regions, which contain open water and macrophyte mats, can be called floodplain lakes. The seasons of the floodplain include inundation, when the floodplain is in contact with the river, and isolation, when it is not. The inundation season in turn can be divided into phases of filling, throughflow, and drainage (Fig. 2).

At the height of inundation, 80% of the inundated area consists of flooded forest (Fig. 2), but the full extent of inundation is brief. Following drainage, the water surface area on the floodplain is mainly accounted for by uncanopied zones. Decline of water surface area continues during isolation, but at a reduced rate (Hamilton and Lewis 1987).

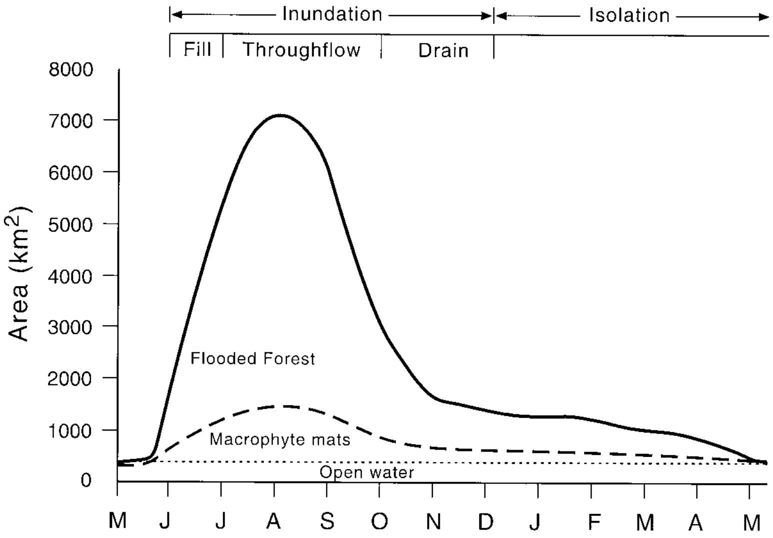

FIGURE 2. The hydrologic cycle on the Orinoco floodplain, showing the contributions of flooded forest, macrophyte mats, and open water to total area of water.

During early inundation, floodplain waters are so turbid that phytoplankton cannot grow well (Hamilton and Lewis 1990b). As inundation progresses, the water column deepens, the sediment load settles, and the water becomes transparent. Phytoplankton abundance remains low, however, because phytoplankton biomass is removed by invertebrate consumers during transit through macrophyte mats (Hamilton et al. 1990). As downgradient movement of water on the floodplain ceases, phytoplankton biomass accumulates rapidly, but ultimately may be suppressed by resuspension of fine sediment when the water is very shallow (Hamilton and Lewis 1990b).

The dominant macrophyte (~90% of macrophyte biomass) on the floodplain is *Paspalum,* a C4 grass, but C3 plants such as *Eichhornia* also are present. *Paspalum* and most other macrophytes are emergent and have extensive root growth in the water column. As water levels decline, macrophyte mats are stranded on the exposed floodplain sediments, where the desiccated biomass remains during the dry season. Inundation the following year provides the necessary moisture for decomposition of the previous year's growth, and for rapid new growth that ultimately covers ⅔ of the uncanopied zone.

Macrophytes support periphyton, which grows on roots and stems. Macrophyte mats also support a diverse community of rhizofaunal invertebrates (Lasi 1993). The rhizofauna is favored by inundation; it survives the isolation season only in limited quantities because of reduction in the area of macrophyte mats. Invertebrates are far more common in macrophyte mats than in the open-water benthic zone (Lasi 1993). Fishes of the Orinoco floodplain consist mainly of characids and siluriforms, but the neotropical knife fishes and a few taxa of other groups also are abundant (Rodríguez and Lewis 1990).

Methods

Carbon sources for consumers

Aquatic primary consumers in the Orinoco floodplain have access to 5 C sources: 1) phytoplankton, 2) periphyton, 3) macrophytes, 4) litterfall, and 5) organic matter carried to the flooplain by the river. Estimates of the magnitude of each of these sources were used in the foodweb analysis.

Net production for phytoplankton over the inundation season was estimated from concentrations of chlorophyll *a* and the thickness of the euphotic zone for a group of locations on the floodplain (Hamilton and Lewis 1990b). Measurements of chlorophyll *a* were not possible during the isolation season because of high concentrations of fine inorganic particulate material. Particulate C, which was accounted for mainly by phytoplankton during isolation, was used in estimating chlorophyll *a* (the ratio of particulate C to chlorophyll *a* is 130 mg/mg, Erikson et al. 1998). Because Orinoco floodplain lakes seldom stratify, the entire water column, the mean depth of which changes monthly, was treated as the mixing depth for purposes of estimating respiration during both the inundation and isolation seasons.

Periphyton production has not been studied on the Orinoco floodplain, but the conditions for periphyton growth on the Orinoco floodplain are very similar to those on the Amazon floodplain, for which an estimate is available (0.76 g C d^{-1} mean net production per m^2 of macrophyte mat; Putz and Junk 1997, Melack and Forsberg 2000). This estimate and information on the seasonal change in extent of macrophyte mats on the Orinoco floodplain were the basis for our estimate of total periphyton production on the Orinoco floodplain.

Paspalum repens reached a peak standing crop of 4000 g C/m^2 (Hamilton and Lewis 1987), and was adjusted upward by a factor of 2 for loss of net production to excretion, grazing, and senescence (approximate only; cf. Junk and Piedade 1993).

Colonnello (1991) estimated litterfall on the fringing floodplain of the Orinoco as 4.9 t ha^{-1} y^{-1}, which corresponds to ~250 g C m^{-2} y^{-1}. Bayley (1989) used a number twice this high for the Amazon várzea, but the várzea probably produces more litter because it has a less rigorous dry season. For present purposes, we used the Colonnello (1991) estimate for nonwoody litter, and added an equal amount for woody litter (Worbes 1997), for a total of 500 g C m^{-2} y^{-1} entering the aquatic environment from floodplain forest.

During inundation, the total organic C content of water on the Orinoco mainstem was 7 mg/L (5 mg/L dissolved, 2 mg/L suspended; Lewis and Saunders 1989). When combined with hydrologic data for an intensively studied segment of floodplain (Hamilton and Lewis 1987), these concentrations correspond to 30 g C m^{-2} y^{-1} of organic matter entering the floodplain from the river.

Use of the P/B ratio to estimate production of consumers

Banse and Mosher (1980) showed that the ratio of annual production (P_a) to mean annual biomass ($\bar{B}$) for a species population is closely related to the mass at maturity (M_s) for individuals in the population: $P_a/\bar{B} = aM_s^b$, where a and b are derived empirically from data on P_a, $\bar{B}$, and M_s. The relationship does not appear to differ systematically between temperate and tropical populations (Talling and Lemoalle 1998), except through temperature, which affects some taxa (Morin and Bourassa 1992, Benke 1993). The equation for $P_a/\bar{B}$ was used in estimating production on the Orinoco floodplain for both invertebrates and fishes.

The aquatic invertebrates of the Orinoco floodplain include rhizofauna, benthos, and zooplankton. The rhizofauna was studied by Lasi (1993), who showed that the total number of invertebrates per unit mass of roots was nearly constant at 1200 individuals/100 g of wet root and submerged stem. Dry mass (16% of wet mass) of roots and submerged stems varied from 1000 g/m^2 in the latter part of inundation to as little as 300 g/m^2 during isolation (Lasi 1993); monthly values from Lasi (1993) were used in estimating the abundance of rhizofauna. Data for M_s of rhizofauna taxa (Lasi 1993, M. A. Lasi, unpublished data) were used to estimate $P_a/\bar{B}$ from the equations of Banse and Mosher (1980), except for chironomids for which we used the more extensively documented equation of Benke (1993). Lasi (1993) showed that the benthos had a size distribution similar to that of the rhizofauna, but the number of individuals per unit area was only 10% of that found within the rhizofauna, so the production of benthos per unit area was estimated as 10% of the rhizofaunal production. Data reported by Twombly and Lewis (1987) for Lake Orsinera, which had a typical zooplankton composition for the Orinoco floodplain (Hamilton et al. 1990), was the basis for estimates of zooplankton production.

An estimate of fish production was based on intensive fish community studies (Rodríguez and Lewis 1994, 1997) involving repeated electroshocking at 20 locations along a 400-km reach of the fringing floodplain. Data on gonadal development were used to estimate M_s for 85 of the most abundant fish taxa. Data for these taxa then were used in developing an equation relating M_s to maximum size of individuals in samples and a categorical variable coding for taxonomic order ($R^2 = 0.85$). This relationship was used in estimating M_s for 31 taxa whose M_s

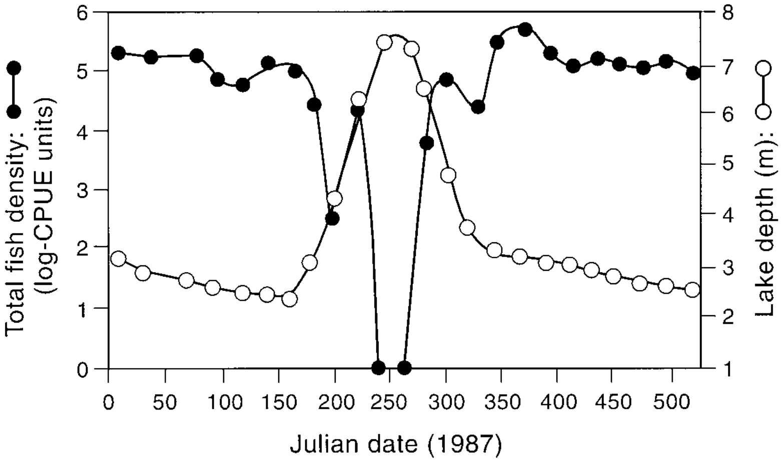

FIGURE 3. Seasonal changes, as indicated by water depth, in catch per unit area (CPUE) by electroshocking in an uncanopied area on the Orinoco floodplain (Lake Terecaya) (M. A. Rodríguez, unpublished data).

could not be estimated from gonadal development.

An equation relating M_s and $P_a/\bar{B}$ for fishes (Banse and Mosher 1980) was used to estimate $P_a/\bar{B}$ from M_s for each fish species at each sampling location. The relative biomass per unit area then was calculated for each species at each sampling location from the electroshocking data. The electroshocking data could not, however, be used in estimating absolute biomass, which instead was taken from a summary by Welcomme (1985) and a study of the Amazon várzea by Bayley (1989). Welcomme (1985) showed fish biomass to be 800 to 1000 kg/ha fresh mass in South American floodplain lakes; Bayley (1989) showed 1200 kg/ha for the Amazon várzea. We used 1000 kg/ha fresh mass, along with relative abundances of species and $P_a/\bar{B}$ for species, in estimating total fish production per unit area per year as an average across all sampling locations.

The fishes pass through a dispersal phase at maximum flood during which they are virtually absent from the Orinoco uncanopied areas (Fig. 3); this dispersal stage was excluded from fish sampling data that were used in estimating production. Otherwise, the fish were concentrated in the uncanopied areas. Fish showed a strong algal C isotope signature (Hamilton et al. 1992), indicating that the uncanopied area was the main trophic support area for them. Also, retraction of the floodplain waters did not result in an increase in number of fish captured per unit area by electroshocking, as would be expected if fish from a large area were being rapidly concentrated into uncanopied zones (Rodríguez and Lewis 1994). For these reasons, we multiplied the estimate of fish biomass per unit area × mean water surface of the uncanopied area (790 km^2) rather than assuming that it extended over the entire floodplain (7000 km^2).

Trophic shift of $\delta^{15}N$

Trophic position for consumers can be estimated from a shift in isotope ratios between trophic levels (e.g., Vander Zanden and Rasmussen 1999). Nitrogen is the most useful element for this type of analysis because it shows a large shift between levels (~3‰ cf. C at 0–1‰).

McCutchan et al. (2001) showed shifts in δ^{15}N of 3.0 ± 0.3‰ for consumers with protein-rich diets (e.g., algae or animals), but ½ this amount for consumers with protein-poor diets (e.g., vascular plant detritus). The value of δ^{15}N for algae (periphyton and phytoplankton) on the Orinoco floodplain averaged 3.5‰ (±0.4; Hamilton and Lewis 1992). Herbivorous invertebrates in the macrophyte mats or open water showed dependence on algae, as indicated by δ^{13}C, and had $\delta^{15}N = 6.0 \pm 0.4$‰, indicating a shift of 2.5‰ from the algal source (Hamilton and Lewis 1992).

Data on δ^{15}N for fish (21 species; Hamilton and Lewis 1992) were the basis for estimates of their trophic position. As indicated by the δ^{13}C

TABLE 1. Information on lakes of the Orinoco fringing floodplain relevant to estimates of phytoplankton production ($n = 15$ for inundation; $n = 11$ for isolation). Numbers in parentheses = 1 SE; data are from Hamilton and Lewis (1990b), except as indicated. Chl = chlorophyll. *Inundation* is that portion of the year when the floodplain is in contact with the river; during *isolation,* the river and floodplain are disconnected.

Variable	Inundation	Isolation	Annual
Mean depth (m)	3.4 (0.6)	1.1 (0.2)	2.3
Euphotic zone (m)[a]	2.5 (0.2)	0.4 (0.1)	1.5
Chl *a* (µg/L)	11.0 (2.0)	65.0 (15.0)	38.0
Chl *a* (mg/m²)	28.0 (6.0)	23.0 (8.0)	25.0
Gross production (g C m^{-2} d^{-1})[b]	1.8 (0.4)	1.5 (0.5)	1.6
Respiration (g C m^{-2} d^{-1})	0.7 (0.3)	0.8 (0.2)	0.8
Net production (g C m^{-2} d^{-1})	1.1 (0.2)	0.6 (0.3)	0.9

[a] Estimated as 2.8 × secchi depth (S. K. Hamilton, unpublished data)

[b] Production as g C m^{-2} d^{-1} estimated as 0.064 × mg chl *a*/m²; respiration estimated as 0.56 mg C mg chl a^{-1} h^{-1} (for tropical lakes with chl a <100 mg/m², Erickson 1998)

analysis, fish were sustained by a protein-rich diet (algae or animals). Therefore, their trophic position was estimated as:

$$T_i = 2 + (\delta^{15}N_I - 3.5–2.5)/3.0$$

where T_i is the trophic position of species i, $\delta^{15}N_i$ is the N isotope signature of species i (average of all available individual values for the species), 3.5 is the mean $\delta^{15}N$ for the original source of organic matter (algae), 2.5 is the mean shift for primary consumers of algae, and 3.0 is the expected shift in $\delta^{15}N$ for each trophic transfer involving carnivores.

Results

Carbon sources and production

Orinoco floodplain lakes ranged greatly in depth and transparency over the annual cycle, as did the amount of chlorophyll *a* per unit volume (Table 1). In contrast, the amount of chlorophyll *a* per unit area, which is the main variable of interest for predicting primary production, was similar between inundation and isolation because of an inverse relationship between mean depth of the water column and abundance of phytoplankton per unit volume (Table 1). Slightly >½ of gross production was accounted for by respiration. Net production, the basis for support of consumers that use phytoplankton, was 0.9 g C m^{-2} d^{-1} as an annual average.

Table 2 lists phytoplankton along with all other sources of C that were available to primary consumers on the floodplain. Among the C sources, phytoplankton and periphyton were of similar magnitude, and were moderately high when expressed per unit of habitat but small when expressed per unit of floodplain. Net production by macrophytes was extremely high when expressed per unit of habitat and ~30× higher than phytoplankton and periphyton production combined when expressed per unit of floodplain. Floodplain forest produced about as much C (in the form of litter) per unit habitat as phytoplankton and periphyton combined, but much less than macrophytes. Because of the

TABLE 2. Summary of C sources for primary consumers of the Orinoco floodplain. – = not applicable.

		Per unit habitat		Per unit floodplain[b]	
Carbon source	Area (km²)	Mass (g C/m²)	Net production (g C m^{-2} y^{-1})	Mass (g C/m²)	Net production (g C m^{-2} y^{-1})
Phytoplankton[a]	480	2.5	330	0.17	23
Periphyton[a]	311	1.9	250	0.08	11
Macrophytes[a]	311	4000	8000	556	1112
Forest	6209	–	500	–	443
River supply	7000	–	30	–	30
Total	–	–	–	–	1619

[a] Mean across all months; mats grow to maximum coverage of 970 km²

[b] At maximum inundation, i.e., 7000 km²

TABLE 3. Annual mean abundance and production of rhizofauna per unit area of macrophyte mat ranked by % contribution to production (groups contributing <0.3% were omitted). P_a = annual production (mg C m^{-2} y^{-1}), $\bar{B}$ = mean annual biomass (mg/m²), M_s = mass at maturity. Values of $P_a/\bar{B}$ were computed from field data on M_s and equation 3 of Banse and Mosher (1980), except for Diptera (equation from Benke 1993). – = not applicable.

Taxon	Abundance (indiv./m²)	M_s (µg/indiv.)	$P_s/\bar{B}$ ratio	Dry mass (mg/m²)	Production (mg C m^{-2} y^{-1})
Ostracoda	33,900	16.1	21	545	5800
Diptera	11,600	300	67	500	16,800
Copepoda	15,000	2.3	43	35	750
Cladocera	10,500	3.2	38	34	650
Hydracarina	2500	8.5	27	21	290
Nematoda	5000	2.4	43	12	250
Annelida	740	9.0	26	7	90
Rhizopoda[a]	80,000	0.0047	429	0.4	80
Total	160,000		–	1160	24,800

[a] Includes other taxa of similar size

great areal extent of forest, however, the contribution per unit of floodplain was much higher than that of phytoplankton and periphyton, although still less than for macrophytes. River supply (total organic transport) was only a small source of organic C (Table 2).

Rhizofaunal invertebrates were abundant numerically, but their total dry mass was modest because most organisms were small (Table 3). Although the estimated $P_a/\bar{B}$ ratios for these small organisms were quite high, production was not as high as might be expected because of low biomass. Predaceous invertebrates (Hydracarina, some copepods) accounted for only ~2% of production, which indicated that 1st-level invertebrate production passed to fish rather than to 2nd-level invertebrate consumers.

TABLE 4. Annual mean biomass and production of invertebrates and fish on the Orinoco floodplain. – = not applicable.

		Per unit habitat		Per unit floodplain	
	Area (km²)	Mass (g C/m²)	Production (g C m^{-2} yr^{-1})	Mass (g C/m²)	Production (g C m^{-2} yr^{-1})
Invertebrates					
Rhizofauna	311	0.58	24.7	0.026	1.10
Benthos	791	0.06	2.44	0.006	0.28
Zooplankton	480	0.12	5.0	0.008	0.34
Total	–	–	–	0.040	1.72
Fish	791	12.00	11.0	1.360	1.24

Among invertebrate consumers, the rhizofauna showed highest total production per unit of habitat and per unit of floodplain (Table 4). Contributions of zooplankton to production were almost equal among the copepods, cladocerans, and rotifers (Twombly and Lewis 1987). Abundance of zooplankton per unit volume was high, but biomass and production per unit area were low (Table 4) because the water was relatively shallow. Zooplankton production was only ~20% of rhizofaunal production per unit of habitat and ~33% of rhizofaunal production per unit of floodplain (Table 4).

Table 5 shows $P_a/\bar{B}$ for the 18 fish species accounting cumulatively for 50% of production across all lakes. To account for 95% of production required data on 76 species because of the high diversity of fishes (Fig. 4). The mean value of $P_a/\bar{B}$ among sites was close to 1.0, indicating the demise of most individuals by the end of the isolation season each year. Biomass of fish was high relative to that of invertebrates; fish production was about ~⅔ of invertebrate production (Table 4).

The mean of T_i for fish was 2.8 (Fig. 5), i.e., below the primary carnivore level (3.0). The distribution showed about the same number of species between trophic levels 2 and 3, in close trophic proximity to the algal food source, as between levels 3 and 4. A weighting of individ-

TABLE 5. Fish taxa accounting for 50% of production on the Orinoco floodplain. P_a = annual production (g C m^{-2} y^{-1}), $\overline{B}$ = mean annual biomass (g/m^2), M_s = mass at maturity (g/individual).

Species	Family	M_s	$P_a/\overline{B}$ ratio	Fraction of production
Cichla ocellaris	Cichlidae	134	0.73	0.062
Metynnis luna	Characidae	7	1.56	0.050
Plagioscion squamosissimus	Sciaenidae	20	1.20	0.038
Cichla temensis	Cichlidae	151	0.71	0.036
Pygocentrus notatus	Characidae	24	1.14	0.035
Semaprochilodus kneri	Prochilodontidae	45	0.97	0.028
Hydrolycus scomberoides	Characidae	90	0.81	0.027
Metynnis lippincottiae	Characidae	31	1.07	0.026
Prochilodus mariae	Prochilodontidae	60	0.90	0.026
Glyptopterichthys gibbiceps	Loricariidae	493	0.52	0.024
Metynnis hypsauchen	Characidae	15	1.30	0.024
Glyptopterichthys punctatus	Loricariidae	299	0.59	0.022
Pseudoplatystoma fasciatum	Pimelodidae	90	0.81	0.020
Loricariichthys brunneus	Loricariidae	11	1.41	0.018
Hypostomus pleocostoma	Loricariidae	148	0.71	0.016
Rhamphichthys marmoratus	Rhamphichthydae	90	0.81	0.016
Acestrorhynchus microlepis	Characidae	18	1.23	0.016
Psectrogaster ciliata	Curimatidae	37	1.03	0.015
Mean		97	0.92	0.027
SE		29	0.076	0.003

ual taxa according to their contribution to production would be ideal, but the number of taxa represented in the database for $\delta^{15}N$ was too small to support this calculation.

Combination of foodweb components

Production and consumption within the Orinoco food web were concentrated in the area of

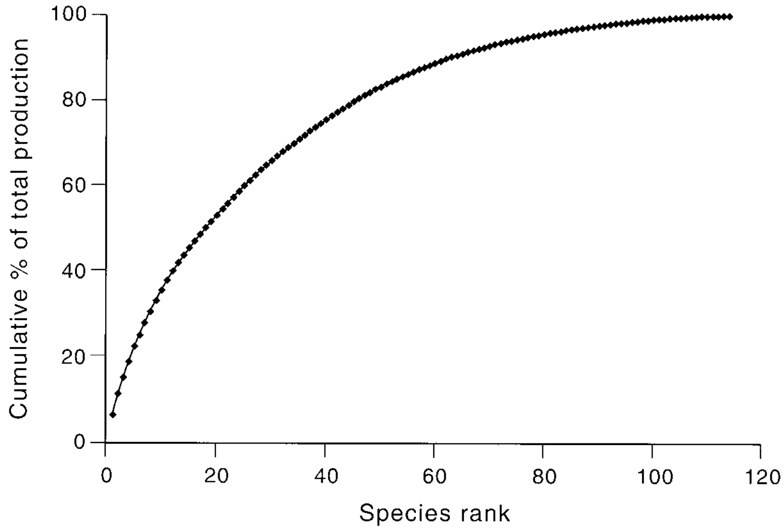

FIGURE 4. Cumulative contributions of fish species to total annual fish production on the Orinoco fringing floodplain.

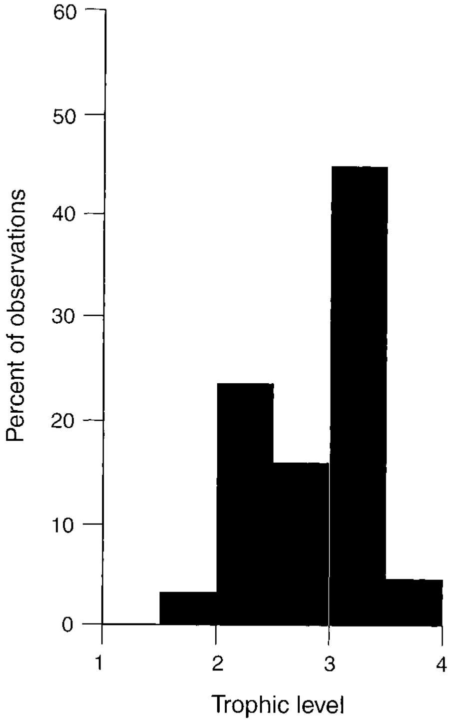

FIGURE 5. Frequency distribution of trophic level distance of individual fish species from the primary C source on the Orinoco floodplain, as indicated by shift in $\delta^{15}N$.

open water and macrophyte mats, which was used as the final basis for expressing production for all groups (Table 6). Invertebrates were treated as primary consumers of algal C, as indicated by $\delta^{13}C$ analysis and the small contribution of predaceous taxa to total production. Fish production was partitioned between direct use of algal C and indirect use of algal C through primary consumers. Data on $\delta^{15}N$ showed that algal C supported ~20% of fish production ($0.20 \times 11 = 2.2$ g C m^{-2} y^{-1}, Table 6). Corresponding consumption of algae by fish was estimated by assuming that all net production of algae is consumed, and that herbivore and fish consumers have similar growth efficiencies for algae (5.4%; see invertebrates, Table 6). Thus, the estimated consumption of algae by fish was $2.2/0.054 = 41$ g C m^{-2} y^{-1}. The low values of average T_i for fish (2.8, Fig. 5) showed that the residual portion (80%) of fish production must be explained mainly by consumption of herbivorous invertebrates, as indicated in Table 6.

TABLE 6. Summary of production by trophic level and trophic transfer efficiencies for the Orinoco fringing floodplain. Production amount is for the mean area of macrophyte mats plus open water (790 km^2). Consumer efficiency = production/consumption.

Category	Amount
Production (g C m^{-2} y^{-1})	
Primary C source (algae)	299
Invertebrates	14
Fish	11
Primary consumption (g C m^{-2} y^{-1})	
Invertebrates	258
Fish	41
Secondary consumption (g C m^{-2} y^{-1})	
Fish	14
Consumer efficiency (%)	
Invertebrates	5.4
Fish	20.0

Discussion

Error in the results

The importance of error to the foodweb analysis varies among types of data. Error in estimating the production of vascular plants (floodplain forest or macrophytes) is unimportant to the final conclusions because the stable isotope data for C showed that the food web is driven by algal production rather than by vascular plant production. In contrast, algal production must be estimated within ~25% of the true value, given that the food web runs on algal C. The likelihood of major error in these estimates is low because the underlying data were extensive and because the final estimates agreed well with independent studies of algal production on the Amazon, which has very similar conditions.

The data on $\delta^{13}C$ for C sources and for consumers are important to the analysis because they indicate ultimate C sources supporting a given species or group. This extensive data set shows low variation of $\delta^{13}C$ for a given C source (Hamilton and Lewis 1992). Data on $\delta^{13}C$ for consumers sometimes are difficult to interpret because of poor resolution of $\delta^{13}C$ for the potential C sources, but the present analysis benefits from strong isotopic separation of C sources, and from consumer C signatures that are very strongly aligned with one particular C source (algae). Therefore, the probability of serious error related to $\delta^{13}C$ is low.

Information on trophic shift for $\delta^{15}N$ is important to the analysis. The information for the Orinoco floodplain includes very broad coverage of taxa, as required for generalization (Hamilton et al. 1992). Temporal and spatial variation can, however, compromise trophic level analysis based on $\delta^{15}N$ (reviewed by Vander Zanden and Rasmussen 1999). Sampling for the Orinoco analysis was spread over the growing season, and showed strong clustering of primary consumers and primary C sources. Thus, errors in this portion of the analysis that would be large enough to affect the qualitative nature of the final conclusions seem unlikely.

Estimates for production of invertebrates depend on estimates of abundance, M_s, and the relationship between $P_a/\bar{B}$ and M_s. The estimates of $\bar{B}$ meet common standards for ecological studies of populations, i.e., they involve the analysis of multiple samples at numerous times representing the full range of annual conditions. Mass at maturity also was estimated from field samples. The relationship between $P_a/\bar{B}$ and M_s probably is the greatest source of error, but errors of ~25% would not change the conclusions qualitatively.

Estimates of fish production are subject to the same errors as those for invertebrate production, plus an additional component of error associated with the development of absolute abundance estimates from studies by others on South American floodplains. Only a gross overestimate or underestimate (25–50%) would cause problems for the analysis.

Sources of C

The Orinoco floodplain has abundant C sources for primary consumers. Sources are mainly autochthonous; transport of organic C by the river is so small (Table 2) that it was not a consideration (cf. Bayley 1989). Macrophyte production dominated, but litterfall also made a large contribution. Macrophytes and litter together accounted for ~98% of the total available C (Fig. 6). If all of this C passed to invertebrate consumers, either directly or indirectly through microbes, consumer production on the floodplain would be many times higher than was estimated.

Gross production was low because phytoplankton biomass was modest by comparison with that of many tropical lakes (Talling and Lemoalle 1998), but the estimated respiration also was low. Net production was substantial by temperate-zone standards, but within the lower half of the range observed for tropical lakes. Estimates of net production were consistent with those from the Amazon várzea, where phytoplankton grow under very similar circumstances (Schmidt 1973a, 1973b: 1 g C m^{-2} d^{-1}; Rodrigues 1994: 0.5–0.7 g C m^{-2} d^{-1}).

Stable isotope data strongly suggest that consumer production (invertebrates and fish) on the Orinoco floodplain was supported by algal C (Fig. 6). Therefore, the nutritional base for consumers on the floodplain was much smaller than it might appear. About 98% of C from organic sources appears to pass into a microbial dead end that does not support aquatic consumers to any great extent; the stable isotope data for C indicated no significant microbial loop or detrital-food-chain component bringing C from microbes living on vascular plants to invertebrates through intermediary consumers such as protozoans. Riemann and Christoffersen (1993) concluded that contributions of the microbial loop to energy flow through large organisms are likely to be minor because of the progressive loss of energy across the linkages to large organisms. On the Orinoco floodplain, however, even low efficiency of transfer could bring significant additional energy to invertebrates and fish, but no such transfer was evident.

Production of invertebrates on the floodplain was high, but not exceptionally so; it fell within the upper quartile of values reported for temperate streams by Benke (1993). Production of invertebrates was explained primarily by small taxa that have high $P_a/\bar{B}$ ratios but do not maintain a large amount of biomass. Enclosure experiments suggested that intensive predation (i.e., top-down control) may be the explanation for the small size and low standing stock of invertebrates (Lasi 1993).

Trophic efficiencies

The trophic efficiency for invertebrates (5%, Table 6) is reasonable for small invertebrates feeding on algae in tropical environments. For example, Lewis (1979) estimated the 1st-level consumer conversion efficiency of a tropical zooplankton community to be 4.4%.

As indicated by the $\delta^{15}N$ data, fish were supported by invertebrate production (14 g C

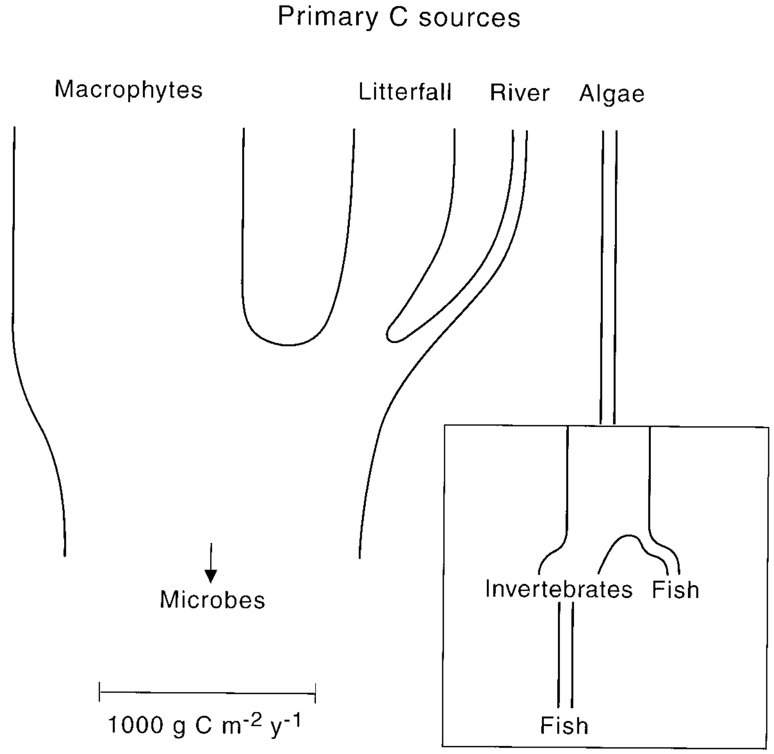

FIGURE 6. Major C and energy flows on the Orinoco fringing floodplain, expressed per unit area of maximum inundation. The box is magnified 10×.

m^{-2}y^{-1}) plus a share of algal production that was estimated from the apportionment of algal production between invertebrates and fish (Table 6: 40 g C m^{-2} y^{-1}). Thus the total of invertebrate and algal production consumed by fish was ~54 g C m^{-2} y^{-1}. Given a fish production estimate of 11 g C m^{-2} y^{-1} (Table 6), fish showed a composite efficiency of 20%. It is likely that efficiency for the carnivorous component of the total consumption was higher and efficiency for the herbivorous component was lower than the composite (Peters 1983).

One important test for completion of foodweb analysis lies in trophic efficiencies that are implied by the data on production, C sources, and trophic levels for consumers. Tropic efficiencies for the Orinoco floodplain derived from the data fell within the range of expected values, i.e., they are neither so high as to be physiologically infeasible nor so low as to be unlikely (Peters 1983). Most importantly, the support of fish is accounted for by production of food sources that are, according to isotope analysis, being used by fish.

The information in Table 6 has implications for yield of the Orinoco fishery and possibly for the yield of other tropical floodplains. Our estimate of total fish production on the Orinoco floodplain is 79,000 t/y fresh mass, which is 5× current yield (16,000 t of fish mass or 0.23 g C m^{-2} y^{-1} over the entire floodplain), or 1.8× the potential yield estimated by Novoa (1990). The data suggest that the current fish harvest accounts for 20% of fish production rather than the much lower amount (2%) cited by Bayley (1989) for the ecologically similar Amazon várzea. In this sense, Table 6 supports Novoa's (1990) estimate of 45,000 t/y, which would be just >½ of total fish production, as a reasonable upper limit for sustainable yield from the Orinoco floodplain fishery.

Explanations of energy flow

Food webs carry energy to higher trophic levels most extensively when progressively larger consumers focus their energy intake on progressively higher trophic levels. In this sense, food webs that show a high proportion of large consumers supported by the lowest trophic levels could be considered compressed, i.e., showing little energy flow at the highest trophic levels. According to Table 6, the Orinoco floodplain shows this type of compression. Fish production was derived mostly from the 1st and 2nd trophic levels rather than at and above the 2nd trophic level, as might be expected for fish in general (e.g., Vander Zanden et al. 1997). Compression of the food web is important functionally in that it explains how fish production can be high even when the primary C supply for the food web is narrowly based on algae. The same size distribution of fish, if reliant on trophic levels 2 and 3 rather than 1 and 2 could, because of losses inherent in trophic transfers, sustain only ~$\frac{1}{10}$ of the estimated production, which would be less than the current fish harvest.

The Orinoco foodweb analysis raises 2 major questions that require further work: 1) Why are the consumers so narrowly focused on algal C, given the great abundance of vascular plant C on the floodplain? 2) Why do the largest consumers (fish) rely on trophic levels 1 and 2, rather than on trophic levels 2 and 3? A partial answer to the 1st question lies in the nutritional value of algal cells, which is generally higher than that of vascular plant detritus (Minshall 1978). The nutritional value of algal cells is not a sufficient explanation in itself, however, in that one might expect the evolution of a large cluster of specialists exploiting the large source of vascular plant C. Another part of the explanation may lie in the relatively low biomass and low average size of the aquatic invertebrates, and the low abundance of benthic organisms (Tables 3, 4). These observations indicate strong predation pressure on invertebrates, as verified by enclosure experiments (Lasi 1993). Strong predation pressure may hold invertebrate populations to such low abundance that the algal food source, which is nutritionally superior to vascular plant detritus, is sufficient, i.e., there is no evolutionary incentive for exploitation of inferior food sources by invertebrates. Similarly, high predation pressure on invertebrates leads to selection for rapid growth, and thus to adaptations that focus on use of the most nutritious foods. At least some temperate floodplains may show similar properties (e.g., Thorp et al. 1998).

A compressed food web, in which fish rely on trophic levels 1 and 2, may also be a byproduct of intensive top-down control. Given that primary consumers do not exploit 98% of the available C supply (macrophytes, litter), secondary production originating from primary consumers is relatively small in relation to its potential as judged by total available C. Under these circumstances, secondary consumers, such as fish, may be forced to focus not only on primary consumers, but also to develop adaptations allowing them to make direct use of the most nutritious primary C sources.

Floodplains are traditionally viewed as highly productive of animal biomass because of their richness in primary C sources. For the Orinoco, primary C sources are indeed abundant, but productivity of consumers is not explained by efficient use of these abundant primary C supplies. Instead, high production of large consumers (fish) is maintained despite the narrow focus of primary consumers on the most nutritious C supply (algae), through adaptations leading most large consumers to feed at low trophic levels of the food web.

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