Primary production, food web structure, and fish yields in constructed and natural wetlands in the floodplain of an African river

Andrew T. Jackson, Alphonse Adite, Katherine A. Roach, and Kirk O. Winemiller

Abstract: In the Ouémé River, Africa, whedo (artificial pond) aquaculture on the floodplain is an important method of fishery production. We surveyed fishes in whedos and adjacent main-channel and floodplain habitats during the receding-water period (December 2010 – January 2011) and analyzed carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope ratios of fish and primary producer tissue samples to investigate food web structure. We also measured instream respiration, net primary production, algal biomass (chlorophyll *a*), and nutrient concentrations in the habitats. Floodplain habitats were more nutrient-rich than the river channel, and whedos were net heterotrophic (net primary production < 0). Phytomicrobenthos and C_3 macrophytes accounted for a large fraction of fish biomass in whedos and the natural floodplain depression, while the river channel was mainly supported by seston and C_3 macrophytes. Whedo food webs were dominated by piscivorous fishes and had fewer trophic transfers compared with the food web of the river channel. Our results suggest that control of aquatic macrophyte growth in whedos may yield greater algal production and consumer biomass, including harvestable fish stocks.

Résumé : L'aquaculture en whedos (étangs artificiels) dans la plaine inondable du fleuve Ouémé, en Afrique, constitue une importante méthode de production halieutique. Nous avons recensé des poissons dans des whedos et dans des habitats attenants du chenal principal et de la plaine inondable en période de décrue (de décembre 2010 à janvier 2011) et analysé les rapports d'isotopes stables de carbone (δ^{13}C) et d'azote (δ^{15}N) d'échantillons de tissus de poissons et de producteurs primaires afin d'étudier la structure du réseau trophique. Nous avons également mesuré la respiration dans le cours d'eau, la production primaire nette, la biomasse algale (chlorophylle *a*) et les concentrations de nutriments dans les différents habitats. Les habitats de plaine inondable étaient plus riches en nutriments que ceux du chenal du fleuve, et les whedos étaient caractérisés par une hétérotrophie nette (la production primaire nette < 0). Le phytomicrobenthos et les macrophytes C_3 expliquaient la présence d'une grande partie de la biomasse de poissons dans les whedos et les dépressions naturelles de la plaine inondable alors que, dans le chenal principal du fleuve, la biomasse de poissons était principalement supportée par le seston et les macrophytes C_3. Les réseaux trophiques des whedos étaient dominés par des poissons piscivores et présentaient moins de transferts trophiques que le réseau trophique du chenal du fleuve. Nos résultats portent à croire qu'un contrôle de la croissance des macrophytes aquatiques dans les whedos pourrait permettre d'accroître la production algale et de biomasse de consommateurs, y compris des stocks de poissons exploitables. [Traduit par la Rédaction]

Introduction

Tropical lowland rivers with intact floodplains and seasonal precipitation patterns are the most productive river systems in the world (Welcomme 1979). The importance of the seasonal flood pulse to secondary consumer biomass in lowland rivers was recognized by Junk et al. (1989), who proposed the flood pulse concept, which states that aquatic consumers are largely supported by macrophyte and invertebrate production (allochthonous food resources) on floodplains that becomes available during flood pulses. Fisheries production of tropical floodplain rivers provides a reliable source of protein to millions of low-income people, mostly in rural communities of developing countries (Laurenti 2002; Kura et al. 2004; Allan et al. 2005). If tropical floodplain fisheries are to be sustainably managed in the face of changing hydrology (climate change and anthropogenic influences), it is necessary to gain a better understanding of the functional dynamics that contribute to the productivity of these systems.

Many studies involving stable isotope analysis have stressed the importance of algal production sources to floodplain river food webs (e.g., Hamilton et al. 1992; Forsberg et al. 1993; Thorp and

Delong 1998; Benedito-Cecilio et al. 2000; Leite et al. 2002; Bunn et al. 2003; Herwig et al. 2004; Jepsen and Winemiller 2007). In the revised riverine productivity model, Thorp and Delong (2002) reviewed stable isotope data from tropical, temperate, and Arctic rivers, revealing this phenomenon to be true even in heterotrophic floodplain river habitats (production/respiration < 1). They hypothesized that, because the direct nutritional value of algae for metazoan consumers is greater than that of most terrestrial plants, carbon and nitrogen from algae should be the most important production source for food chains in rivers. They observed that algae-derived organic material tends to be important even when rivers are net heterotrophic, because, whereas both allochthonous (terrestrial) and autochthonous (algal) carbon fuel the microbial loop, the algae-grazer pathway usually supports secondary consumers. Thorp and Delong (1994) also recognized that locally produced organic matter from riparian zones might support consumers in some rivers. Most research using stable isotope analysis indicates that C_4 grasses are not an important production source supporting invertebrates and fishes in streams and rivers, presumably because of their low nutritional value (Thorp and Delong 1998; Clapcott and Bunn 2003; Herwig et al.

2004; Jepsen and Winemiller 2007; Zeug and Winemiller 2008). However, in some rivers, C_3 plants originating from riparian zones can become important in supporting consumers in the upper food web (e.g., Huryn et al. 2001; Winemiller 1996; Hoeinghaus et al. 2007; Zeug and Winemiller 2008). Light limitation seems to be a key process responsible for C_3 plants assuming greater importance than algae in supporting secondary consumer biomass in lotic ecosystems. For example, in heavily shaded heterotrophic streams, consumer biomass is frequently derived from terrestrial-based production sources such as leaf litter (Wallace et al. 1999; Hall et al. 2000). A recent review revealed that, in rivers carrying high loads of suspended sediment, aquatic consumers assimilate large fractions of material derived from C_3 plants, presumably because turbidity limits rates of instream primary production during periods of high flow (Roach 2013).

In addition to variance in the quality and availability of basal production sources, vertical trophic structure (food-chain length) influences fisheries production. Food-chain length denotes the number of energy transfers from the basal production source to the apex predator in an ecosystem and is thought to be a function of available energy (Elton 1927; Hutchinson 1959), ecosystem size (Schoener 1989; Post et al. 2000), and ecosystem type (Vander Zanden and Fetzer 2007). In the Upper Paraná River Basin in Brazil, Hoeinghaus et al. (2008) found that food-chain length differed significantly among aquatic ecosystem types (i.e., high-gradient rivers, low-gradient rivers, reservoirs, and reaches below reservoirs). They suggest this is a result of size-based interactions within food webs with different basal production sources and with different environmental regimes. For example, phytoplankton-based food chains in reservoirs were longer because their primary consumers (zooplankton) had smaller body sizes, and owing to size-dependent foraging, more trophic transfers were involved for energy to reach large apex predators (Hoeinghaus et al. 2008). In contrast, detritus-based systems may experience fewer energy transfers to reach apex predators because detritivores can be relatively large invertebrates and fishes, and large predators can therefore be supported by short food chains (Layman et al. 2005).

Here, we investigated relationships among in situ nutrient concentrations, algal primary production, and food web structure in natural and modified floodplain habitats of the Ouémé River, a lowland river in Benin, Africa, to infer how anthropogenic manipulations to floodplain habitat might influence fishery production. During the annual flood pulse, the Ouémé River breaches its banks, and aquatic habitats of the floodplain are colonized by fishes from the river channel. Artificial ponds constructed in the Ouémé River floodplain (whedos) enhance floodplain fisheries for rural communities. When floodwaters recede, fishes become isolated in whedos and remain there until harvested by people near the end of the dry season. We estimated vertical trophic structure and basal production sources supporting fish assemblages in aquatic floodplain habitats (i.e., whedos and a natural floodplain depression) and a river channel habitat at the beginning of the dry season when aquatic floodplain habitats first become isolated from the main channel.

We hypothesized that fishes from the natural floodplain depression and river channel would mainly assimilate material derived from algae. Although algae may be less abundant in floodplains than detritus derived from terrestrial plants, algae are more nutritious, have higher energy densities, and contain more labile organic molecules than terrestrial primary producers, and therefore they should be disproportionately assimilated into consumer biomass (Thorp and Delong 2002). However, we hypothesized that fishes in whedos would mainly assimilate material derived from C_3 macrophytes. Early in the dry season, whedos become densely covered by aquatic macrophytes that limit algal growth through shading. Furthermore, concentrations of inorganic nutrients are very low in many tropical rivers owing to

strongly leached soils and high levels of precipitation (e.g., Cotner et al. 2006). We predicted that the combination of low light and low concentrations of inorganic nutrients in whedos might limit rates of water-column and benthic primary production. However, we also recognized the possibility that algae might support whedo consumers, particularly in whedos with less vegetation cover. Aquatic floodplain habitats of West Africa are similar to the billabongs of Australia studied by Bunn and Boon (1993) in that they are shallow isolated water bodies with abundant macrophyte growth. Although stable isotope analysis was unable to identify the specific basal production source supporting consumer biomass in billabongs, the depleted ^{13}C signatures of secondary consumers indicated that macrophyte contributions were small. Because some of the direct consumers of algae and detritus in floodplain habitats are large-bodied grazing fishes, it is likely that much of the primary production reaches apex predators in a few trophic transfers and that whedo food webs may be shorter than the food web in the river channel (Hoeinghaus et al. 2008).

To test these hypotheses, stable isotope ratios ($^{13}C/^{12}C$, $^{15}N/^{14}N$) of tissue samples were analyzed to estimate basal production sources assimilated by consumer taxa and to estimate their trophic positions. As a plant grows, it assimilates carbon in a characteristic ratio of $^{13}C/^{12}C$ and nitrogen in a characteristic ratio of $^{15}N/^{14}N$ depending on the photosynthetic pathway it uses and its environmental conditions. As carbon pools are assimilated into consumer tissue, their isotopic ratios undergo little change and thus can be used to estimate the relative proportions of alternative pools contributing to the tissue mass. Nitrogen isotopic ratios are not as conserved. As N is assimilated into tissues of consumers during transformation between trophic levels, the ratio of $^{15}N/^{14}N$ becomes slightly more enriched with ^{15}N (the process of trophic fractionation), and thus the N isotopic ratio is useful for estimating the trophic position of consumers (Post 2002). A meta-analysis of stable isotope studies in aquatic systems revealed that trophic fractionation of $^{15}N/^{14}N$ averages 2.5‰ per trophic level, but there is variation among tissues, species, and trophic levels (Vander Zanden and Rasmussen 2001; Caut et al. 2009). By accounting for fractionation, $^{15}N/^{14}N$ ratios can also be used in conjunction with isotope ratios of carbon and other elements to estimate basal production sources supporting consumers at various trophic levels. Basal production sources can be estimated if production sources are sufficiently and consistently divergent in their $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios. If this is the case, a stable isotope mixing model can be used to estimate probabilities of production sources assimilated by consumers. We also measured instream respiration (R), net primary production (NPP), algal biomass (chlorophyll a), and nutrient concentrations in each of the habitats to understand factors that might reduce algal biomass, causing a food web to be supported by terrestrial C_3 macrophytes.

Methods

Study area

The Ouémé River, located in Benin, West Africa, flows from the Atacora Mountains to Lake Nokoue, an estuary emptying into the Gulf of Guinea (Fig. 1). The hydrologic regime is seasonal, with a mean daily discharge of 170 m³·s⁻¹. A total of 116 fish species have been documented in the Ouémé Basin (Lévêque et al. 1990, 1992). At our study site near the city of Adjohoun, small-scale farming and whedo aquaculture are practiced on the floodplain. Whedos are long, narrow ponds an average of 1 m deep, 5.5 m wide, and from 40 to 1000 m long. During the major wet season, from March to July, and minor wet season, from September to mid-November, floodwaters inundate the floodplain, and the whedos are colonized by fishes migrating from the river channel. Little rainfall occurs during other months (Adite et al. 2005). As the floodwaters recede, fishes are trapped in the whedos, where they are har-

Fig. 1. Map of study site in Ouémé River Basin, Benin, Africa. Benin is located in western Africa and is bordered by Togo in the west, Burkina Faso and Niger in the north, and Nigeria in the east.
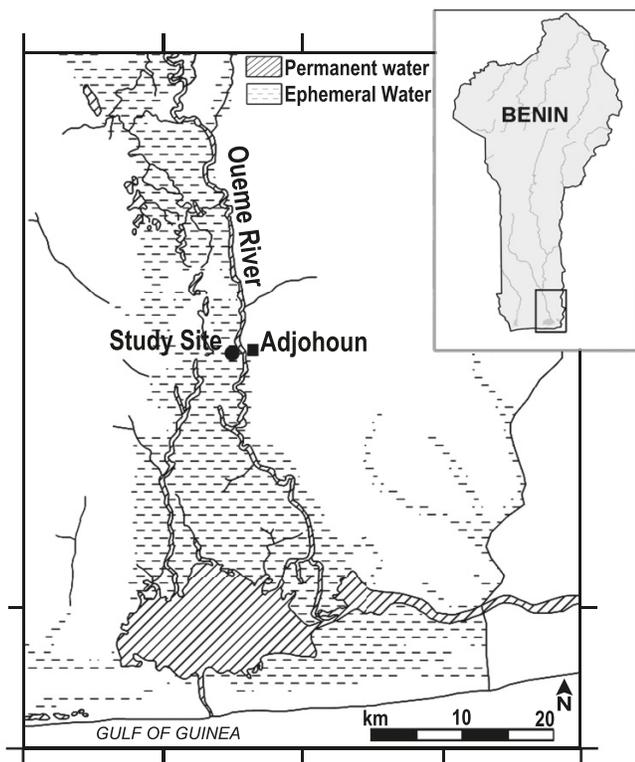
vested biannually, at the end of the two dry seasons. During the dry season, most whedos are >90% covered by aquatic vegetation. The dominant aquatic macrophyte species include *Leersia hexandra*, *Polygonum salicifolium*, *Ipomea aquatica*, and *Aeschynomene afraspera*. Natural floodplain habitats also contain floating and emergent macrophytes, but vegetation cover is not as dense as that of the whedos. The invasive macrophyte *Impomea aquatica* is also present in slackwater habitats of the Ouémé River main channel. An additional type of aquaculture, akadjavi, is practiced in the main channel. Once floodwaters recede, rectangular plots are fenced along the banks with sticks or palm fronds lodged in the sediment. Terrestrial vegetation is placed inside the plots to attract and provide habitat for fishes. Akadjavis are harvested before the onset of the wet season.

Sample collections for stable isotope analysis

Samples of fishes and primary producers were collected from 11 whedos plus one natural floodplain depression and one site in the Ouémé River main channel during the receding-water period from December 2010 to January 2011. Fish collections in the whedos were carried out by first isolating a 20 m reach with a 2 cm mesh barrier net, removing the aquatic vegetation from within that section, and seining (net 2 m × 6 m, 0.5 cm mesh) five times before surrounding the area with the barrier net in a purse-seine manner to capture the remaining fishes. We also collected aquatic macroinvertebrates (e.g., adult water beetles, decapod crustaceans) that were captured in the seine net. A section (21 m × 29 m × 1 m) of a natural floodplain depression was surveyed using a seine (2 m × 6 m, 0.5 cm mesh). To collect fish species present in structurally complex habitats along the shoreline of the river channel, an akadjavi (10 m × 6 m × 1 m) was encircled with a net (2 cm mesh), all sticks and vegetation were removed from within the net, and the net was pulled from the water in a purse-seine fashion. To collect fish species present in open-water areas of the

main channel, a 2 m cast net (1 cm mesh) was cast 58 times in water approximately 1 m deep. Catch per unit effort (CPUE) was calculated for floodplain habitats based on transect length, width, and thalweg depth. River channel CPUE was calculated based on the area and water depth of the akadjavi and the volume sampled by the cast net (diameter × depth summed for all throws). Although sampling effort was the same among whedos and the natural floodplain depression, gear bias could have contributed to differences in CPUE between floodplain habitats and the river channel. Captured fishes were anesthetized using tricaine methanesulfonate (MS-222) following Texas A&M Animal Use Protocol 2005-117 and preserved in formalin after removal of a tissue sample for isotopic analysis. Samples of muscle tissue from the dorso-lateral region of fishes and whole bodies of macroinvertebrates were preserved in salt for subsequent stable isotope analysis, a technique that has negligible influence on stable isotope signatures (Arrington and Winemiller 2002). Fishes were identified using taxonomic keys in Lévêque et al. (1990, 1992) and counted. Voucher specimens were cataloged in the Texas Cooperative Wildlife Collection at Texas A&M University.

Production sources were collected by hand from each habitat, including C$_3$ macrophytes, C$_4$ grasses, seston, and phytomicrobenthos. Macrophyte leaf and grass samples were collected from the dominant species of plants from the riparian zone. Phytomicrobenthos samples from whedos were scraped with a spatula from the surfaces of leaves and roots of submerged aquatic macrophytes. Phytomicrobenthos samples from the natural floodplain depression and river channel were scraped from the surfaces of macrophytes and rocks near the water surface. This sampling technique was unlikely to produce a pure sample of benthic algae, and thus phytomicrobenthos samples were likely composed of a combination of periphyton, fine particulate organic matter, and associated microorganisms. Seston samples from all sites were collected by filtering water through a pre-combusted Whatman GF/F filter. Seston samples were likely composed of a combination of phytoplankton, suspended organic matter, and bacteria. All primary producer samples were preserved in salt for stable isotope analysis.

Nutrient concentrations and algal primary production

Nutrient concentrations (mg·L^{-1}) were measured in the field by filtering water through a pre-combusted Whatman GF/F filter and measuring soluble reactive phosphorus (SRP), NH$_4^+$, NO$_2^-$, and NO$_3^-$ in the filtrate using colorimetric kits and a Hach DR 2800 spectrophotometer. We report values for dissolved inorganic nitrogen (DIN), the sum of NH$_4^+$, NO$_2^-$, and NO$_3^-$.

Chlorophyll *a* of the water column and benthos was measured at each site by taking triplicate samples of approximately 500 mL of water in polyethylene bottles for the water column and approximately 13 cm^3 of sediment in a Petri dish for the benthos. The water was filtered through a Whatman GF/C filter, and the filter and sediment were immediately placed into individual dark vials for 24 h extraction using 90% ethanol. Chlorophyll *a* was then measured using a Hach DR 2800 spectrophotometer (666 and 750 nm) and corrected for phaeophytin by subtracting absorbances after addition of 0.1 mol·L^{-1} HCl (Wetzel and Likens 1991).

Light and dark chambers were used to estimate *R*, NPP, and gross primary production (GPP) of the water column and benthos. Water-column measurements followed Wetzel and Likens (1991), and benthic measurements followed Cotner et al. (2006). We performed 10 water-column incubations (5 light and 5 dark bottles) and 2 benthic incubations (1 light and 1 dark chamber) at each site near midday. For water-column metabolism, 300 mL biological oxygen demand (BOD) bottles were filled with water and incubated at approximately 0.5 m depth. Changes in DO concentrations were then measured using a YSI model 85 DO probe. For benthic measurements, two circular Plexiglass benthic chambers were pressed into the sediment to enclose the substrate and ap-

proximately 8 L of water. DO concentrations were measured every 10 min with an internally logging Hydrolab MiniSonde. Light chamber measurements were taken for 3 h, and dark chamber measurements were taken for 1.5 h so that DO concentrations did not decrease below ambient levels. A respiratory quotient of 0.8 and a photosynthetic quotient of 1.2 were used when converting data from O_2 to C. The methods in Dollar et al. (1991) were used to calculate benthic flux measurements. Water-column fluxes in DO were subtracted from the total benthic chamber flux, resulting in sediment-only fluxes. Water-column and benthic R, NPP, and GPP were estimated by multiplying by 24 (R) or 12 (NPP and GPP).

Stable isotope analysis

In the laboratory at Texas A&M University, samples of primary producers, fishes, and macroinvertebrates were rinsed and then soaked in distilled water for 4 h, then rinsed again to remove salt. All samples were then dried for 48 h at 60 °C and ground to a fine powder using a mortar and pestle. Subsamples (1.5–3.0 mg) were weighed into Ultra-Pure tin capsules (Costech Analytical, Valencia, California, USA) and sent to the University of Georgia's Analytical Chemistry Laboratory for analysis of carbon and nitrogen stable isotope ratios using a Delta V isotope ratio mass spectrometer coupled to an NA1500 CHN Carlo Erba combustion analyzer via a Thermo Conflo III Interface. Isotopic ratios are reported in δ notation, and standards were Pee Dee Belemnite limestone and atmospheric nitrogen for $\delta^{13}C$ and $\delta^{15}N$, respectively. For fish muscle tissues having a C/N ratio > 3.5, $\delta^{13}C$ values were corrected for the effect of lipids using the equation $\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99$ (C:N) (Post et al. 2007).

The MixSIR model was used to estimate contributions of basal production sources to fish biomass in each whedo, the natural floodplain depression, and the main channel (Moore and Semmens 2008; Jackson et al. 2009; Semmens et al. 2009). This Bayesian model uses stable isotope data to estimate feasible ranges of source contributions, taking into account variation in consumer and primary producer stable isotope signatures and trophic fractionation (TF) of isotopic ratios. We used the equation TF = 2.5‰ × (mean trophic position – 1) and a standard deviation of 2.5 from a meta-analysis (Vander Zanden and Rasmussen 2001) as model input for trophic fractionation. Here, mean trophic position was calculated using the equation discussed below, where $\delta^{15}N_{reference}$ was the mean $\delta^{15}N$ of all potential basal production sources for a site. In the whedos, potential basal production sources included C_3 macrophytes, C_4 grasses, phytomicrobenthos, and seston. We did not include samples of seston as a source in whedos where water-column net primary production values were low (<0.05 mg C·m⁻³·day⁻¹). Means and standard deviations of $\delta^{13}C$ and $\delta^{15}N$ from in situ samples of C_3 macrophytes, C_4 grasses, phytomicrobenthos, and seston were used as MixSIR inputs for whedos. For a few whedos in which C_3 macrophyte and C_4 grass ($n = 3$), phytomicrobenthos ($n = 2$), or seston ($n = 2$) samples were not obtained, we used the grand means and standard deviations of all whedo C_3 macrophytes, C_4 grasses, phytomicrobenthos, or seston as MixSir model inputs. In the natural floodplain depression and main channel, potential basal production sources included C_3 macrophytes, C_4 grasses, phytomicrobenthos, and seston. For these sites, in situ means and standard deviations of potential basal production sources were used as inputs for the MixSIR model.

Trophic position estimates were based on fractionation of $\delta^{15}N$ between fishes and basal production sources. Trophic position of each individual was calculated using the equation Trophic position = $[(\delta^{15}N_{consumer} - \delta^{15}N_{reference})/2.54] + 1$ from Zeug and Winemiller (2008), where $\delta^{15}N_{reference}$ was the mean of the two primary producer $\delta^{15}N$ means that the MixSIR model indicated were most important to a consumer species in its respective site, and 2.54‰ was the mean trophic fractionation value from a meta-analysis (Vanderklift and Ponsard 2003). Again, for

the few whedos where C_3 macrophyte or phytomicrobenthos samples were not taken, we used the grand means of all whedo C_3 macrophytes or phytomicrobenthos as the $\delta^{15}N$ means for calculation of $\delta^{15}N_{reference}$ for those sites.

For each of the habitat assemblages, we created frequency histograms of 5% and 95% confidence percentiles of each basal production source to consumer biomass, as well as frequency histograms of the mean trophic position of each species. Patterns in basal production source and trophic position were similar among all the whedos. MixSIR results indicated that in whedos, mean 5% confidence percentiles for fish assemblages ranged from 2 to 17 for C_3 macrophytes, from 6 to 25 for C_4 grasses, and from 2 to 36 for phytomicrobenthos, and 2 for seston in whedos where it was included as a potential basal production source. Mean 95% confidence percentiles for fish assemblages ranged from 37 to 77 for C_3 macrophytes, from 20 to 32 for C_4 grasses, from 50 to 83 for phytomicrobenthos, and from 40 to 47 for seston. In the whedos, minimum trophic position of fish species ranged from 1.0 to 2.7, and maximum trophic position ranged from 2.4 to 3.9. Thus, we pooled whedo data when creating the frequency histograms.

Results

Nutrients and algal biomass and production

In the whedos, DIN ranged from 0.3 to 1.0 mg·L⁻¹, and SRP ranged from 0.3 to 4.0 mg·L⁻¹. Mean DIN was higher in whedos (mean = 0.5 mg·L⁻¹) compared with concentrations measured in the natural floodplain depression (0.2 mg·L⁻¹) and main channel (0.3 mg·L⁻¹). Concentrations of SRP were higher in the natural floodplain depression (1.7 mg·L⁻¹) than the mean value for whedos (1.4 mg·L⁻¹) and concentrations measured in the main channel (0.5 mg·L⁻¹).

In the whedos, water-column chlorophyll a ranged from 0.9 to 54.3 mg·m⁻³, and benthic chlorophyll a ranged from 0.4 to 8.2 mg·m⁻². Water-column and benthic chlorophyll a concentrations were higher in the natural floodplain depression (water column = 25.8 mg·m⁻³, benthic = 5.4 mg·m⁻²) compared with the mean value for whedos (water column = 16.6 mg·m⁻³, benthic = 3.4 mg·m⁻²) and concentrations measured in the river channel (water column = 11.6 mg·m⁻³, benthic = 3.3 mg·m⁻²). Benthic chlorophyll a concentrations were consistently lower compared with water-column chlorophyll a concentrations (Fig. 2).

Water-column respiration (R) was similar among habitats (whedo mean = 63 mg C·m⁻³·day⁻¹, natural floodplain depression value = 45 mg C·m⁻³·day⁻¹, river channel value = 71 mg C·m⁻³·day⁻¹; Fig. 3). Benthic R was greater in magnitude than water-column R and differed among habitats (whedo mean = 211 mg C·m⁻²·day⁻¹, natural floodplain depression value = 164 mg C·m⁻³·day⁻¹, river channel value = 344 mg C·m⁻²·day⁻¹). Water-column and benthic NPP did not reveal a pattern of between-habitat variation similar to that of chlorophyll a. Water-column NPP was more variable than water-column R among the habitats, with highest in situ production occurring in the river channel and the lowest values occurring in whedos (river channel value = 73 mg C·m⁻³·day⁻¹, natural floodplain depression value = 8 mg C·m⁻³·day⁻¹, whedo mean = –27 mg C·m⁻³·day⁻¹). Benthic NPP was highest in the natural floodplain depression (746 mg C·m⁻²·day⁻¹). Benthic NPP was negligible in the river channel (–2 mg C·m⁻²·day⁻¹), probably because of the coarse inorganic sediments and low abundance of benthic algae. Benthic NPP was negative in the whedos (mean = –120 C·m⁻²·day⁻¹). Negative total NPP (water column + benthic) in the whedos indicated that these habitats were strongly heterotrophic.

Fish abundance

Nine families and 15 species were collected from whedos; samples contained between 61 and 353 (mean = 166) individuals and between 6 and 9 (mean = 7.6) species (see online supplementary

Fig. 2. Water-column and benthic chlorophyll *a* collected from whedo (+1 standard deviation), natural floodplain depression (floodplain), and river channel habitats.

Fig. 3. Respiration (*R*) and net primary production (NPP) of the water column (upper panel) and benthos (lower panel) in whedo (+1 standard deviation), natural floodplain depression (floodplain), and main channel habitats.

Table 1. Abundance of fishes captured in habitats of the Ouémé River and floodplain (i.e., natural floodplain depression).

Habitat	Abundance	
	No. of individuals·m^{-3}	Biomass (g·m^{-3})
Whedo 1	1.0	18.0
Whedo 2	1.2	19.5
Whedo 3	5.4	73.1
Whedo 4	0.7	47.3
Whedo 5	2.3	172.0
Whedo 6	0.8	29.2
Whedo 7	1.5	34.6
Whedo 8	4.1	65.9
Whedo 9	6.1	50.5
Whedo 10	6.1	125.8
Whedo 11	1.4	43.3
Floodplain	0.1	1.1
Main channel	1.8	27.6

and *Clarias agboyiensis*, and most whedos contained *Brienomyrus niger* (91%), *Clarias gariepinus* (64%), and *Erpetoichthys calibaricus* (55%). CPUE for whedos ranged from 0.7 to 6.1 individuals·m^{-3}; CPUE was 0.1 individuals·m^{-3} in the natural floodplain depression and 1.8 individuals·m^{-3} in the river channel (Table 1). Total biomass per unit volume ranged from 18 to 172 g·m^{-3} in the whedos, and was 1.1 g·m^{-3} in the natural floodplain depression and 27.6 g·m^{-3} in the river channel.

Stable isotope analysis of fishes

A total of 398 consumer (whedos = 296, floodplain = 33, main channel = 69) and 138 autotroph (whedos = 98, floodplain = 25, main channel = 15) samples were analyzed for stable isotope ratios. Consumer specimens representing 15 common fish species and 5 macroinvertebrate taxa from whedos were retained for stable isotope analysis, 13 fish species and 4 macroinvertebrate taxa were retained from the natural floodplain depression, and 33 fish species and 1 macroinvertebrate species were retained from the river channel. Consumer δ^{13}C ranged from −14.7‰ to −30.1‰ in whedos, from −21.0‰ to −30.1‰ in the natural floodplain depression, and from −19.8‰ to −30.8‰ in the river channel. Consumer δ^{15}N ranged from 2.4‰ to 12.5‰ in the whedos, from 3.7‰ to 11.7‰ in the natural floodplain depression, and from 6.8‰ to 12.8‰ in the river channel. Producer δ^{13}C ranged from −10.3‰ to −30.1‰ in the whedos, from −11.7‰ to −31.7‰ in the natural floodplain depression, and from −13.4‰ to −32.4‰ in the river channel. Producer δ^{15}N ranged from 0.7‰ to 12.2‰ in the whedos, from −1.0‰ to 9.5‰ in the natural floodplain depression, and from −3.2‰ to 7.4‰ in the river channel.

Basal production sources supporting consumer biomass

Qualitative interpretation of stable isotope ratio biplots showed that consumer δ^{13}C signatures generally lie between those of phytomicrobenthos, C$_3$ macrophytes, and C$_4$ grasses in most floodplain habitats, indicating that all these basal production sources could contribute to consumer biomass (Fig. 4). Most consumer δ^{15}N values were consistently higher than those of basal production sources, but there were some exceptions. C$_3$ macrophytes were variable in their δ^{15}N ratios and were more enriched than consumers in some cases. Aquatic beetles (Coleoptera) had a more depleted δ^{15}N signature than the producers in floodplain habitats, indicating that one or more primary production sources assimilated might not have been sampled. In general, the plots revealed a consistent pattern for the 11 whedos in which consumer signa-

Appendix S1[1]). From the natural floodplain depression, 11 families and 13 species were collected, and 33 species from 18 families were collected from the river channel. All whedos contained the species *Ctenopoma petherici*, *Parachanna obscura*, *Polypterus senegalus*,

---

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2012-0403.

Fig. 4. Carbon and nitrogen isotope ratio biplots of the mean values of primary producers (triangles) and consumers (circles) taken from two representative whedos, a natural floodplain depression (Floodplain), and the Ouémé River channel. Common species of consumer are labeled as follows: Br-nig, *Brienomyrus niger*; Cl-agb, *Clarias agboyiensis;* Cl-gar, *Clarias gariepinus*; Col, Coleopteran beetle; Ct-pet, *Ctenopoma petherici*; Er-cal, *Erpetoichthys calabaricus*; Hem, Hemipteran insect; He-odo, *Hepsetus odoe*; Or-nil, *Oreochromis niloticus*; Pa-obs, *Parachana obscura*; Po-sen, *Polypterus senegalus*; and Xe-nig, *Xenomystus nigri*. Production source types from each site are labeled as follows: C3, C$_3$ macrophyte; C4, C$_4$ grass; Pmb, phytomicrobenthos. Horizontal and vertical bars represent 1 standard deviation.
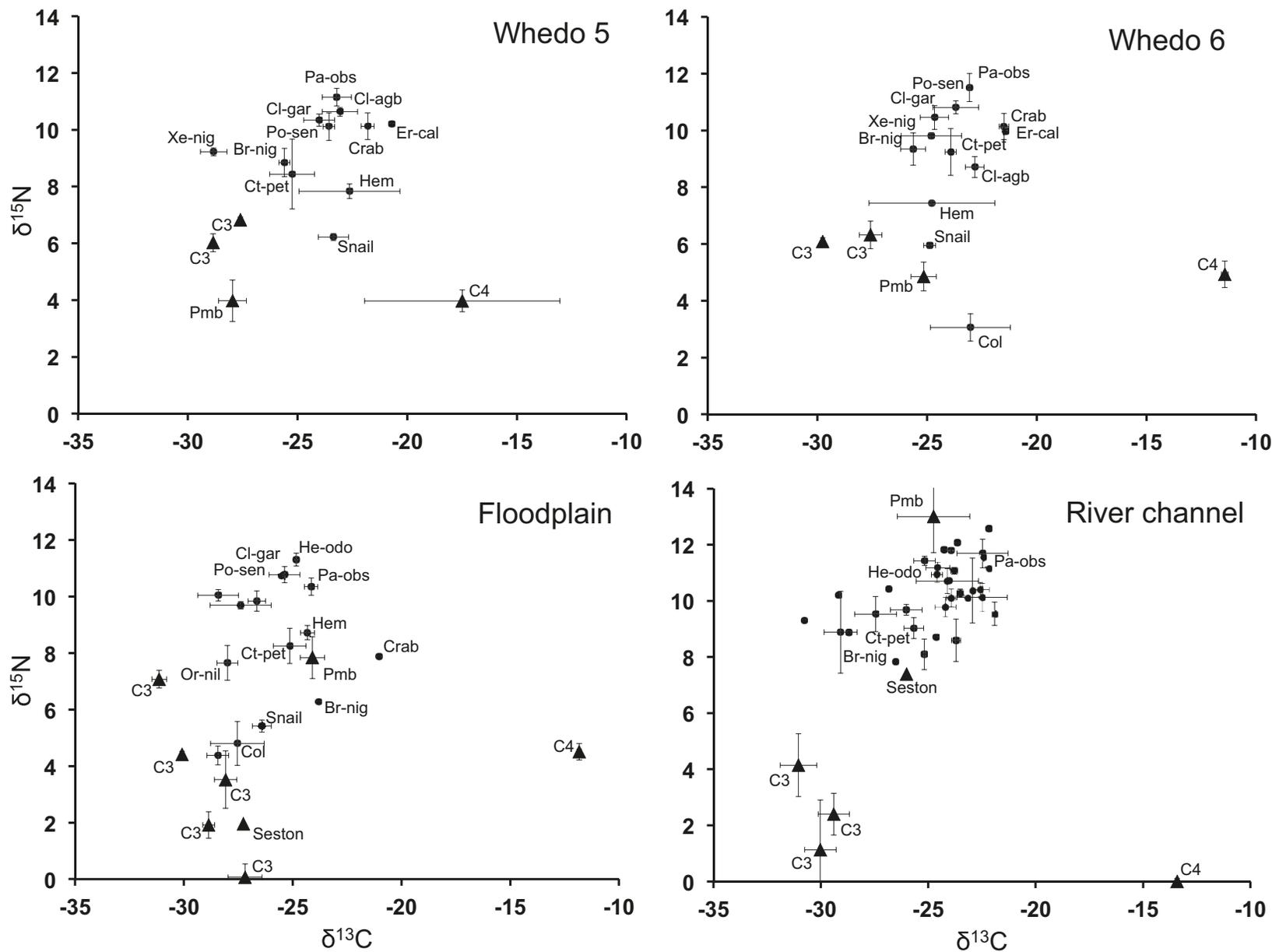
Fig. 5. Frequency histograms of 5% and 95% confidence percentiles of basal production source contributions to fish biomass for whedo, natural floodplain depression (floodplain), and river channel habitats.
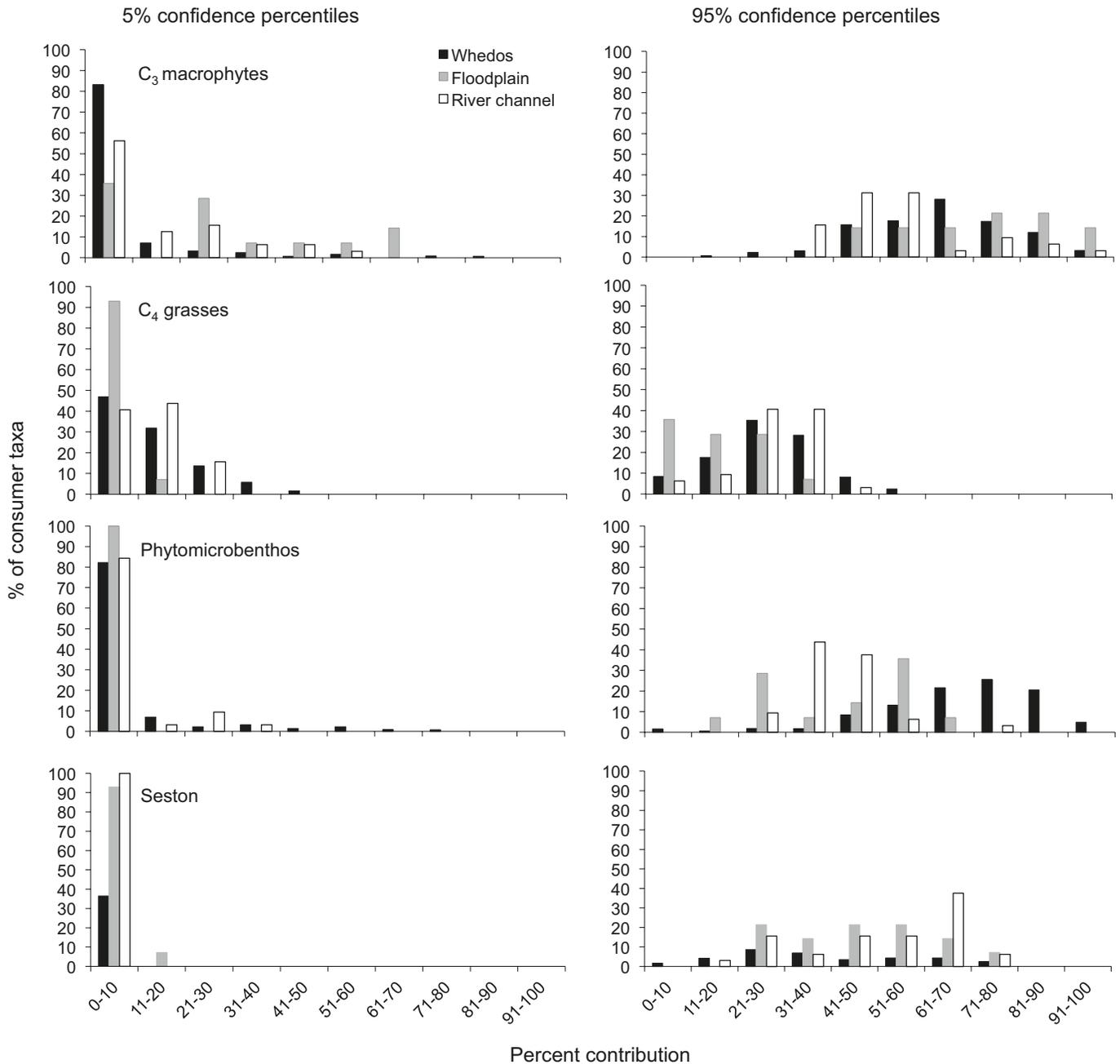
tures were tightly clumped and positioned above phytomicrobenthos and C₃ macrophytes.

MixSIR model estimates indicated that both C_3 macrophytes and phytomicrobenthos accounted for a large fraction of consumer biomass in whedos. Both of these production sources had high 95% confidence percentiles (Fig. 4). For C_3 macrophytes, 53% of species from whedos had 95% confidence percentiles ≥65. For phytomicrobenthos, 65% of whedo species had 95% confidence percentiles ≥65. Species from whedos assimilated smaller fractions of material derived from C_4 grasses, but many species had fairly high 5% confidence percentiles (Fig. 5). In whedos, C_4 grasses had 5% confidence percentiles ≥25 for 10% of consumer species, indicating its importance in supporting the biomass of at least some species. In the natural floodplain depression, C_3 macrophytes seemed to be important contributors to consumer bio-

mass, with 71% of species having 95% confidence percentiles ≥65 for these sources. Phytomicrobenthos and seston also seemed to contribute to consumer biomass, with 43% and 50% of consumers having a 95% confidence percentile ≥50 for these sources, respectively. Most fish species of the natural floodplain depression had 95% confidence percentiles <5% for C_4 grasses (70% of species), indicating that this source probably contributed little to fish biomass. Consumers from the river channel apparently had assimilated material from a mixture of sources, with only 32% of consumer taxa having a 95% confidence percentile ≥50 for any basal production source. Seston and C_3 macrophytes seemed to contribute the largest fractions to consumer biomass, with 59% of species having a 95% confidence percentile >50 for these sources. Phytomicrobenthos had 95% confidence percentiles ≥50 for only 9% of species, and all species had a 95% confidence percentile ≤50

Fig. 6. Mean trophic position (+1 standard deviation) of three fish species collected from whedo, natural floodplain depression (floodplain), and river channel habitats.
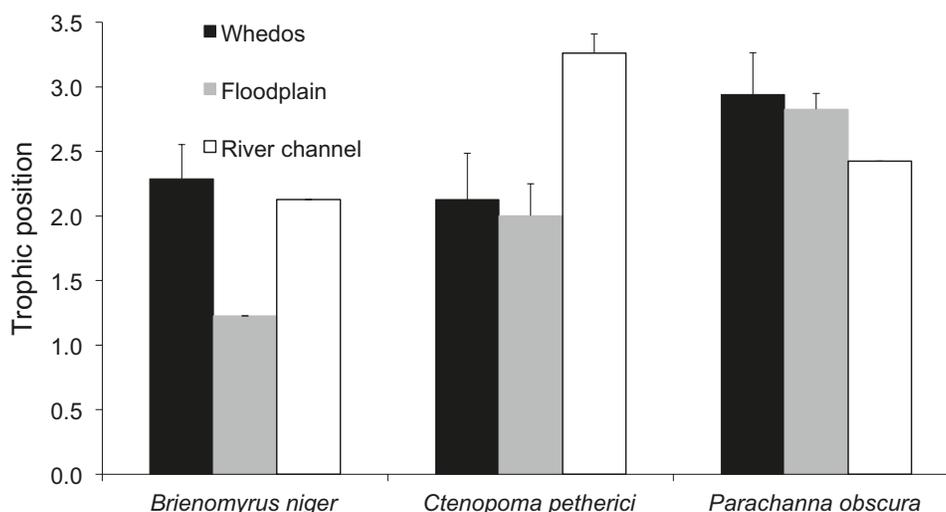
for terrestrial C_4 grasses, indicating minor contributions to consumers.

Trophic position estimates

Qualitative interpretation of stable isotope signature biplots indicated relatively consistent trophic structure among the whedos, with conspecifics from different sites occupying the same locations within isotope space. Mean trophic position of consumer taxa ranged from 0.03 (adult water beetle) to 3.9 (*Clarias agboyiensis*, *Erpetoichthys calabaricus*, *Parachanna obscura*) in the whedos, from 0.7 (adult water beetle) to 3.2 (*Hepsetus odoe*) in the natural floodplain depression, and from 2.1 (*Brienomyrus niger*) to 4.0 (*Mormyrops anguilloides*) in the river channel. Mean trophic position of conspecific *Brienomyrus niger* was similar in whedos and the river channel and lower in the natural floodplain depression (Fig. 6). For *Ctenopoma petherici*, mean trophic position was similar in whedos and in the natural floodplain habitat and higher in the river channel. Mean trophic position of *Parachanna obscura* was similar in all habitats, but was lowest in the river channel (Fig. 6). Trophic position distributions of fish assemblages were similar among habitats. The distribution of trophic positions in the river channel had a higher mean and seemed to be more left skewed compared with distributions for floodplain habitats (river channel mean = 3.1, whedo mean = 2.7, natural floodplain depression mean = 2.5; Fig. 7). Although fish assemblage trophic position means were similar between the whedo and natural floodplain depression habitats, trophic position distributions of the whedo habitats were slightly more left skewed compared with distributions for the natural floodplain depression. These findings indicate that fish assemblages of the whedos had a higher relative abundance of piscivores than the natural floodplain depression.

Discussion

The main objectives of the present study were to investigate relationships among in situ nutrient concentrations, algal primary production, and food web structure in natural and modified floodplain habitats of the Ouémé River to infer how anthropogenic manipulations to floodplain habitat might influence fishery production. We originally predicted that fishes from the natural floodplain depression and river channel would mainly assimilate material derived from algae. We hypothesized that fishes in whedos would mainly assimilate material derived from C_3 macrophytes because of limitation of algal growth through shading by aquatic macrophytes, but we also recognized the possibility that algae might support whedo consumers, particularly in whedos

with less vegetative cover. Results indicated that biomass from a combination of basal production sources was assimilated by fishes inhabiting whedo, natural floodplain depression, and river channel habitats. Algae contained in seston and phytomicrobenthos appeared to be the most important basal production source supporting invertebrates and fishes in habitats of the Ouémé River channel and natural floodplain depression. Assimilation estimates of consumers for seston were higher in these habitats compared to the whedos. At the time of our sampling, whedos were covered by dense layers of aquatic macrophytes (mean coverage 94%) that hindered algal production by shading. Though NPP in whedos was negative, indicating heterotrophy, periphyton (phytomicrobenthos) was collected from macrophyte leaves and roots near the water surface. Mixing model estimates indicated that C_3 macrophytes were an important primary production source for whedo food webs. Despite the high abundance of C_4 grasses within or fringing all habitats surveyed, these grasses apparently are not an important production source supporting fishes in the Ouémé River floodplain ecosystem.

These results agree with other stable isotope studies that have investigated food web structure of floodplain habitats and basal production sources contributing to consumer biomass (e.g., Hamilton et al. 1992; Thorp and Delong 1998; Bunn et al. 2003; Herwig et al. 2004). For example, Bunn et al. (2003) found that within turbid pools in the Cooper Creek floodplain of Australia, phytomicrobenthos, despite being limited to shallow nearshore areas, was the most important production source supporting consumers. In aquatic floodplain habitats of the Orinoco River, Hamilton et al. (1992) found that, although aquatic macrophytes were more abundant, algal production provided the foundation for the majority of fish biomass. Several studies have documented the importance of C_3 macrophytes to floodplain fish assemblages. Although C_4 grasses are frequently available in high abundance as a potential food source, river studies have revealed little or no metazoan assimilation of material from C_4 grasses, probably owing to its refractory nature (e.g., Thorp and Delong 1998; Herwig et al. 2004; Clapcott and Bunn 2003; Jepsen and Winemiller 2007; Zeug and Winemiller 2008). Apparently, the bulk of organic matter from C_4 grasses is processed by microbes and subsequently buried in sediments or exported to the atmosphere as CO_2, though a small fraction may enter the upper food web when consumers eat detritus that has been processed through the microbial loop (Cole et al. 2011). Jepsen and Winemiller (2007) found only 2 of 60 fish species sampled from four floodplain rivers in Venezuela that had high $\delta^{13}C$ values indicative of assimilation of

Fig. 7. Frequency histograms of trophic positions of fishes constituting species assemblages in whedo, natural floodplain depression (floodplain), and river channel habitats.

Trophic position
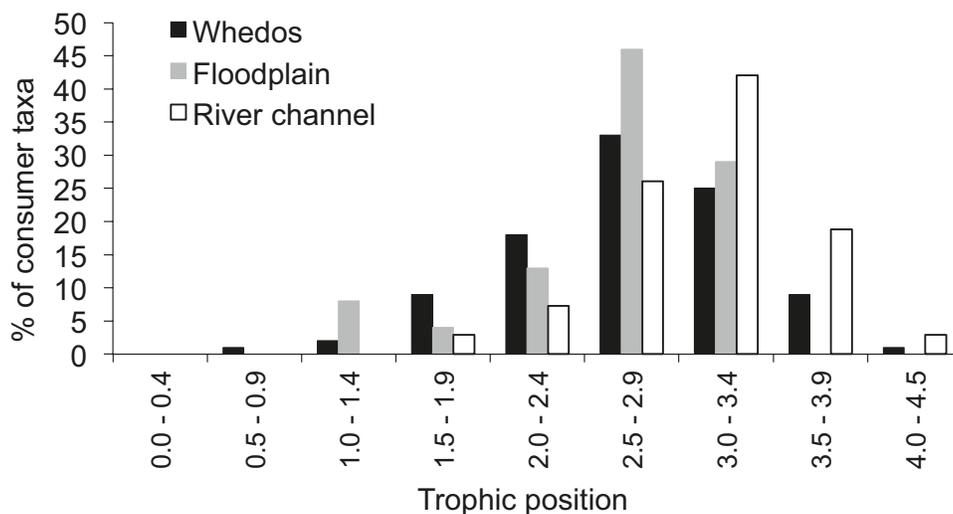
material from C_4 grasses — a macrophyte grazer, *Schizodon isognathus*, and a predator inhabiting shallow littoral habitats, *Hoplerythrinus unitaeniatus*.

Although mean DIN in whedos was higher than concentrations measured in the natural floodplain depression and river channel, and SRP in the natural floodplain depression and river channel habitats was within the range of concentrations measured in whedos, our results indicate that whedos were strongly heterotrophic ($P/R < 1$). In contrast, the natural floodplain depression and river channel were net autotrophic ($P/R > 1$). Although whedos were net heterotrophic, mean chlorophyll *a* values in the whedos were in between values measured for the natural floodplain depression and the river channel, indicating that terrestrial vegetative cover was not dense enough to completely limit growth of benthic algae. Overall, ecosystem metabolism in whedos appears to be dominated by microbial decomposers that consume dead plant material, and this trophic pathway was dominant over those originating from autochthonous aquatic primary production and linking to invertebrates and fishes.

Trophic position estimates for a few invertebrates placed them at the level of primary producer, which obviously is inaccurate. This error could have occurred for several reasons. For example, the fractionation constant 2.54‰ may not have been applicable to some species, or the reference values for the presumed basal production sources may not have been correct in some cases. Another potential source of error would be if one or more important production sources supporting the food web were not included in the analysis. Despite these potential sources of error, overall trends of basal production source contributions and trophic position estimates were fairly consistent. An additional source of bias in interhabitat comparisons could have been lack of replication in sampling river channel and natural floodplain depression habitats. Because of logistical, time, and resource constraints, only one site within the river channel and one natural floodplain depression were sampled. Because we collected multiple samples of the principal basal sources and the most common consumer taxa within structurally complex habitats as well as adjacent open-water areas in both the channel and natural floodplain depression, our descriptions of food web ecology based on stable isotope analysis should be representative for the region. Given the high degree of consistency observed for food web structure and estimates of production sources among whedos, isolated habitats having large potential for divergent species assemblage structure,

it seems unlikely that our interpretations for the other two habitat types were strongly biased by lack of spatial replication.

Comparison of frequency histograms of fish trophic positions according to habitat indicated that mean trophic position was higher in the river channel than natural and artificial floodplain habitats. This finding is consistent with studies that have documented longer food chains in aquatic ecosystems supported largely by seston (phytoplankton) compared with those supported mostly by phytomicrobenthos (periphyton) and macrophytes (detritus) (e.g., Layman et al. 2005; Hoeinghaus et al. 2008). Mean trophic position of whedo fishes was also lower compared with that of fishes from the natural floodplain depression, and 87% of fishes captured in whedos are clearly identified as piscivores. Whedo fish assemblages had highly consistent composition (Jackson et al. 2013), likely because hypoxic conditions resulting from aquatic macrophytes covering the surface of shrinking aquatic habitats select for fishes that possess adaptations for aerial respiration, and the period of habitat isolation results in strong influence of predation on assemblage structure. For example, the predatory African lungfish, *Protopterus annectens*, is an obligatory air breather. In addition, the species *Clarias abgoyiensis*, *C. gariepinus*, *Erpetoichthys calabaricus*, *Parachanna obscura*, *Parachanna africana*, and *Polypterus senegalus* are all predatory species that have accessory organs used for aerial respiration (e.g., Hyrtl 1854; Purser 1926; Munshi 1962). After the onset of hypoxia, these apex predators dominated fish species assemblages of whedos (Jackson et al. 2013).

Findings from whedos are consistent with studies that have documented high percentages of predatory fishes in isolated floodplain habitats in the tropics (e.g., Lowe-McConnell 1964; Winemiller 1990). In studies of small floodplain systems in Venezuela and Costa Rica, relative abundance of piscivores increased as aquatic habitat shrank during the dry season, and local populations of herbivorous and invertivorous fishes were reduced by predation (Winemiller 1990, 1996). The flood pulse concept predicts that, during floods, fishes colonize productive aquatic habitats of floodplains, consume food resources derived from terrestrial plant production, and eventually return to the main channel. This floodplain biomass could be viewed as a spatial food web subsidy supporting the river channel (Winemiller and Jepsen 2004). The flood pulse concept was partially supported by the present study. Floodplain fish assemblages of the Ouémé River floodplain appeared to be partially supported by C_3 macrophytes.

However, fishes that become isolated in floodplain habitats are either consumed by predators in situ or are harvested and therefore do not subsidize the river channel food web. Furthermore, fish assemblages in autotrophic natural floodplain and river channel habitats, as well as heterotrophic whedos, were largely supported by autochthonous production sources (algae). This finding supports the riverine productivity model (Thorp and Delong 2002). Microbial respiration in these habitats is probably based almost entirely on decomposition of macrophyte biomass, with little material from this pathway entering the upper food web (Jackson and Eldridge 1992; Gaedke et al. 1996; Thorp and Delong 2002).

Elucidation of the trophic structure in habitats of the floodplain and main channel of the Ouémé River has important implications for management of fisheries resources. Fish biomass in whedos appears to be supported, at least in part, by algae. Two main factors associated with aquatic macrophyte biomass likely limit fishery production in whedos: restriction of algal production by shading and hypoxia caused by decomposition of and respiration by aquatic macrophytes that only allows fish species having adaptations for aerial respiration to persist (Jackson et al. 2013). Macrophytes have been documented to enhance fisheries production by providing a refuge from predation (e.g., Gilinsky 1984). In our study system, because piscivorous fishes already dominate whedo fish assemblages shortly after whedos become hydrologically disconnected from the river channel during the falling-water period (Jackson et al. 2013), it is unlikely that macrophyte biomass enhances fishery production via this mechanism. Because nutrient concentrations are relatively high in whedo habitats, control of aquatic macrophyte growth in whedos could result in greater algal production and consumer biomass that includes harvestable fish stocks. However, some aquatic macrophyte biomass may be important as a structural matrix for periphyton growth. A manipulative experimental approach would allow for a better understanding of the factors limiting fishery biomass in whedos. Given the interest that already exists in whedo aquaculture as a means to increase fishery production and food security for local people in developing countries (Denny et al. 2006; Hauber et al. 2011), additional research, including manipulative experiments, is needed in this system to improve our understanding of ecological dynamics and how they are influenced by biological diversity.

Acknowledgements

References

Adite, A., Winemiller, K.O., and Fiogbe, E.D. 2005. Ontogenetic, seasonal, and spatial variation in the diet of *Heterotis niloticus* (Osteoglossiformes: Osteoglossidae) in the Sô River and Lake Hlan, Benin, West Africa. Environ. Biol. Fishes, **73**: 367–378.

Allan, J.D., Abell, R., Hogan, Z., Revenga, C., Taylor, B.W., Welcomme, R.L., and Winemiller, K.O. 2005. Overfishing of inland waters. BioScience, **55**: 1041–1051. doi:10.1641/0006-3568(2005)055[1041:OOIW]2.0.CO;2.

Arrington, D.A., and Winemiller, K.O. 2002. Use of preserved biological specimens for stable isotope analysis. Trans. Am. Fish. Soc. **131**: 337–342. doi:10.1577/1548-8659(2002)131<0337:PEOSIA>2.0.CO;2.

Benedito-Cecilio, E., Araujo-Lima, A.A.R.M., Forsberg, B.R., Bittencourt, M.M., and Martinelli, L.C. 2000. Carbon sources of Amazonian fisheries. Fish. Manage. Ecol. **7**(4): 305–315. doi:10.1046/j.1365-2400.2000.007004305.x.

Bunn, S.E., and Boon, P.I. 1993. What sources of organic carbon drive food webs in billabongs? A study based on stable isotope analysis. Oecologia, **96**: 85–94.

Bunn, S.E., Davies, P.M., and Winning, M. 2003. Sources of organic carbon supporting the food web of an arid zone floodplain river. Freshw. Biol. **48**: 619–635. doi:10.1046/j.1365-2427.2003.01031.x.

Caut, S., Angulo, E., and Courchamp, F. 2009. Variation in discrimination factors (Δ15N and Δ13C): the effect of diet isotopic values and applications for diet reconstruction. J. Appl. Ecol. **46**: 443–453. doi:10.1111/j.1365-2664.2009.01620.x.

Clapcott, J.E., and Bunn, S.E. 2003. Can C4 plants contribute to aquatic food webs of subtropical streams? Freshw. Biol. **48**: 1105–1116. doi:10.1046/j.1365-2427.2003.01077.x.

Cole, J.J., Carpenter, S.R., Kitchell, J., Pace, M.L., Solomon, C.T., and Weidel, B. 2011. Strong evidence for terrestrial support of zooplankton in small lakes based on stable isotopes of carbon, nitrogen, and hydrogen. Proc. Natl. Acad. Sci. **108**: 1975–1980. doi:10.1073/pnas.1012807108. PMID:21245299.

Cotner, J.B., Montoya, J.V., Roelke, D.L., and Winemiller, K.O. 2006. Seasonally variable riverine production in the Venezuelan llanos. J. N. Am. Benthol. Soc. **25**: 171–184. doi:10.1899/0887-3593(2006)25[171:SVRPIT]2.0.CO;2.

Denny, P., Kipkemboi, J., Kaggwa, R., and Lamtane, H. 2006. The potential of fingerpond systems to increase food production from wetlands in Africa. Int. J. Ecol. Environ. Sci. **32**: 41–47.

Dollar, S.J., Smith, S.V., Vink, S.M., Obrebski, S., and Hollibaugh, J.T. 1991. Annual cycle of benthic nutrient fluxes in Tomales Bay, California, and contribution of the benthos to total ecosystem metabolism. Mar. Ecol. Progr. Ser. **79**: 115–125. doi:10.3354/meps079115.

Elton, C.S. 1927. Animal ecology. Macmillan Company, New York.

Forsberg, B.R., Aruajo-Lima, C.A.R.M., Martinelli, L.A., Victoria, R.L., and Bonassi, J.A. 1993. Autotrophic carbon sources for fish of the Central Amazon. Ecology, **74**(3): 643–652. doi:10.2307/1940793.

Gaedke, U., Straile, D., and Pahl-Wostl, C. 1996. Trophic structure and carbon flow dynamics in the pelagic community of a large lake. *In* Food webs: integration of patterns and dynamics. *Edited by* G.A. Polis and K.O. Winemiller. Chapman and Hall, New York.

Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology, **65**: 455–468. doi:10.2307/1941408.

Hall, R., Wallace, O.J.B., and Eggert, S.L. 2000. Organic matter flow in stream food webs with reduced detrital resource base. Ecology, **81**: 3445–3463. doi:10.1890/0012-9658(2000)081[3445:OMFISF]2.0.CO;2.

Hamilton, S.K., Lewis, W.M., Jr., and Sippel, S.J. 1992. Energy sources for aquatic animals in the Orinoco River Floodplain: evidence from stable isotopes. Oecologia, **89**: 324–330.

Hauber, M.E., Bierbach, D., and Linsenmair, K.E. 2011. The traditional whedo aquaculture system in Northern Benin. J. Appl. Aquacult. **23**: 67–84. doi:10.1080/10454438.2011.549792.

Herwig, B.R., Soluk, D.A., Dettmers, J.M., and Wahl, D.H. 2004. Trophic structure and energy flow in backwater lakes of two large floodplain rivers assessed using stable isotopes. Can. J. Fish. Aquat. Sci. **61**(1): 12–22. doi:10.1139/f03-139.

Hoeinghaus, D.J., Winemiller, K.O., and Birnbaum, J.S. 2007. Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups. J. Biogeogr. **34**: 324–338.

Hoeinghaus, D.J., Winemiller, K.O., and Agostinho, A.A. 2008. Hydrogeomorphology and river impoundment affect food-chain length of diverse Neotropical food webs. Oikos, **117**: 984–995. doi:10.1111/j.0030-1299.2008.16459.x.

Huryn, A.D., Riley, R.H., Young, R.G., Arbuckle, C.J., Peacock, K., and Lyon, G. 2001. Temporal shift in contribution of terrestrial organic matter to consumer production in a grassland river. Freshw. Biol. **46**: 213–226. doi:10.1046/j.1365-2427.2001.00648.x.

Hutchinson, G.E. 1959. Homage to Santa Rosalia, or Why are there so many kinds of animals? Am. Nat. **93**: 145–159. doi:10.1086/282070.

Hyrtl, J. 1854. Zur Anatomie von *Heterotis ehrenbergii* C. V. Denkschriften der Akademie der Wissenschaften in Wien, **8**: 73–88.

Jackson, A.L., Inger, R., Bearhop, S., and Parnell, A. 2009. Erroneous behaviour of MixSIR, a recently published Bayesian mixing model: a discussion of Moore & Semmens. Ecol. Lett. **12**: E1–E5. doi:10.1111/j.1461-0248.2008.01233.x. PMID:18691222.

Jackson, A.T., Adite, A., Roach, K.A., and Winemiller, K.O. 2013. Fish assemblages of an African river floodplain: a test of alternative methods of community structure. Ecol. Freshw. Fish, [In press.] doi:10.1111/eff.12026.

Jackson, G.A., and Eldridge, P.M. 1992. Food web analysis of a planktonic system off Southern California. Progr. Oceanogr. **30**: 223–251. doi:10.1016/0079-6611(92)90014-Q.

Jepsen, D.B., and Winemiller, K.O. 2007. Basin geochemistry and isotopic ratios of fishes and basal production sources in four neotropical rivers. Ecol. Freshw. Fish, **16**: 267–281.

Junk, W.J., Bayley, P.B., and Sparks, R.E. 1989. The flood pulse concept in river–floodplain systems. *In* Proceedings of the International Large Rivers Symposium. *Edited by* D.P. Dodge. Can. Spec. Publ. Fish. Aquat. Sci. **106**: 110–127.

Kura, Y., Revenga, C., Hoshino, E., and Mock, G. 2004. Fishing for answers: making sense of the global fish crisis. World Resource Institute, Washington, D.C.

Laurenti, G. 2002. Fish and fishery products: world apparent consumption statistics based on food balance sheets. FAO Fisheries Circular No. 821, rev. 6. FAO Fisheries Department, Rome.

Layman, C.A., Winemiller, K.O., Arrington, D.A., and Jepsen, D.B. 2005. Body size and trophic position in a diverse tropical food web. Ecology, **86**: 2530–2535. doi:10.1890/04-1098.

Leite, R.G., Araujo-Lima, C.A.R.M., Victoria, R.L., and Martinelli, L.A. 2002. Stable isotope analysis of energy sources for larvae of eight fish species from the Amazon floodplain. Ecol. Freshw. Fish, **11**: 56–63.

Lévêque, C., Paugy, D., and Teugels, G. G. 1990. The fresh and brackish water fishes of West Africa. Vol. 1. Musée Royale de l'Afrique Centrale. Editions de l'ORSTOM, Tervuren, Belgique.

Lévêque, C., Paugy, D., and Teugels, G.G. 1992. The fresh and brackish water fishes of West Africa. Vol. 2. Musée Royale de l'Afrique Centrale. Editions de l'ORSTOM, Tervuren, Belgique.

Lowe-McConnell, R.H. 1964. The fishes of the Rupununi savannah district of British Guiana, South America. Part I. Ecological groupings of fish species and effects of the seasonal cycle on the fish. J. Linn. Soc. Lond. Zool. **45**: 103–144. doi:10.1111/j.1096-3642.1964.tb00490.x.

Moore, J.W., and Semmens, B.X. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecol. Lett. **11**: 470–480. doi:10.1111/j.1461-0248.2008.01163.x. PMID:18294213.

Munshi, J.S.D. 1962. On the accessory respiratory organs of *Ophiocephalus punctatus* (Bloch). Proc. R. Soc. Edinb. **8**: 128–146.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology, **83**: 703–718. doi:10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2.

Post, D.M., Pace, M.L., Hairston, N.G., Jr. 2000. Ecosystem size determines food-chain length in lakes. Nature, **405**: 1047–1049. doi:10.1038/35016565. PMID:10890443.

Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., and Montaña, C.G. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia, **152**: 179–189. doi:10.1007/s00442-006-0630-x. PMID:17225157.

Purser, G.L. 1926. *Clamoichthys calabaricus* (J. A. Smith). Part 1. The alimentary and respiratory systems. Trans. R. Soc. Edinb. **54**: 767–784.

Roach, K.A. 2013. Environmental factors affecting incorporation of terrestrial material into large river food webs. Freshw. Sci. **32**(1): 283–298. doi:10.1899/12-063.1.

Schoener, T.W. 1989. Food webs from the small to the large. Ecology, **70**: 1559–1589. doi:10.2307/1938088.

Semmens, B.X., Moore, J.W., and Ward, E.J. 2009. Improving Bayesian isotope mixing models: a response to Jackson et al. (2009). Ecol. Lett. **12**: 6–8.

Thorp, J.H., and Delong, M.D. 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. Oikos, **70**: 97–104.

Thorp, J.H., and Delong, M.D. 1998. Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. Oecologia, **117**: 551–563. doi:10.1007/s004420050692.

Thorp, J.H., and Delong, M.D. 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. Oikos, **96**: 543–550. doi:10.1034/j.1600-0706.2002.960315.x.

Vander Zanden, M.J., and Fetzer, W.W. 2007. Global patterns of aquatic food chain length. Oikos, **116**: 1378–1388. doi:10.1111/j.0030-1299.2007.16036.x.

Vander Zanden, M.J., and Rasmussen, J.B. 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: implications for aquatic food web studies. Limnol. Oceanogr. **46**: 2061–2066. doi:10.4319/lo.2001.46.8.2061.

Vanderklift, M.A., and Ponsard, S. 2003. Sources of variation in consumer diet $\delta^{15}N$ enrichment: a meta-analysis. Oecologia, **136**: 169–182. doi:10.1007/s00442-003-1270-z. PMID:12802678.

Wallace, J.B., Eggert, S.L., Meyer, J.L., and Webster, J.R. 1999. Effects of resource limitation on a detrital-based ecosystem. Ecol. Monogr. **69**: 409–442. doi:10.1890/0012-9615(1999)069[0409:EORLOA]2.0.CO;2.

Welcomme, R.L. 1979. Fisheries ecology of flood plain rivers. Longman, London.

Wetzel, R.G., and Likens, G.E. 1991. Limnological analysis. 2nd ed. Springer, New York.

Winemiller, K.O. 1990. Spatial and temporal variation in tropical fish trophic networks. Ecol. Monogr. **60**: 331–367. doi:10.2307/1943061.

Winemiller, K.O. 1996. Factors driving temporal and spatial variation in aquatic floodplain food webs. *In* Food webs: integration of patterns and dynamics. *Edited by* G.A. Polis and K.O. Winemiller. Chapman and Hall, New York.

Winemiller, K.O., and Jepsen, D.B. 2004. Migratory neotropical fish subsidize food webs of oligotrophic blackwater rivers. *In* Food webs at the landscape level. *Edited by* G.E. Polis, M.E. Power, and G.R. Huxel. University of Chicago Press, Chicago, Illinois.

Zeug, S.C., and Winemiller, K.O. 2008. Evidence supporting the importance of terrestrial carbon in a large-river food web. Ecology, **89**: 1733–1743. doi:10.1890/07-1064.1. PMID:18589537.