FISH ASSEMBLAGE AND FOOD WEB STRUCTURE IN WHEDOS (SHALLOW FLOODPLAIN HABITATS) OF THE OUEME RIVER, WEST AFRICA

A Thesis

by

ANDREW THOMAS JACKSON

Submitted to the Office of Graduate Studies of
Texas A&M University
In partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2012

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	Kirk O. Winemiller
Committee Members,	Kevin Conway
	Jason West
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ABSTRACT

Fish Assemblage and Food Web Structure in Whedos (Shallow Floodplain Habitats) of
the Oueme River, West Africa.
August, 2012
Andrew Thomas Jackson, B.S.; M.S., Texas A&M University
Chair of Advisory Committee: Dr. Kirk O. Winemiller

In the Oueme River, a lowland river in Benin, Africa, artificial ponds constructed in the floodplain (whedos) are colonized during the high-water period by a presumably random sample of fishes from the river channel. As water slowly recedes from the floodplain, fishes are isolated in whedos until they are harvested near the end of the dry season. I surveyed fishes in whedos and adjacent main-channel and floodplain habitats during two low-water (2008 and 2009) and one falling-water (2010-2011) periods, and measured a suite of physicochemical variables including dissolved oxygen, temperature, specific conductivity, and percent cover of aquatic vegetation in the falling-water period to investigate if fish assemblage structure of whedos resulted from stochastic or deterministic processes. I also investigated food web structure of whedos by analyzing carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios of fish and primary producer tissue samples, and samples of net primary production, soluble reactive phosphorus (SRP), NH_4^+, NO_2^-, and NO_3^- collected during the falling-water period. Whedos were covered with dense growth of aquatic vegetation, and dissolved oxygen concentrations were lower in whedos compared to a natural floodplain depression and the main channel.

Multivariate analyses revealed that habitat types were distinct with regard to fish assemblage structure and abiotic conditions. Assemblages in whedos and natural floodplain depressions were differentiated from those of the river channel, with the floodplain habitats being dominated by piscivorous fishes that tolerate aquatic hypoxia. These results indicate that fish assemblage structure of whedos was influenced by deterministic processes during the falling- and low-water periods when these water bodies were isolated. Floodplain habitats were more nutrient-rich than the river channel, and whedos were net heterotrophic. Microphytobenthos and C_3 macrophytes accounted for a large fraction of fish biomass in whedos, compared with the river channel, which was mainly supported by seston. Whedo food webs had fewer trophic transfers compared to the food web of the river channel.

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CHAPTER I

INTRODUCTION TO THE RESEARCH PROBLEM

BACKGROUND

Inland fisheries currently provide 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). Production of harvestable fish biomass in large rivers is dependent on floodplain habitats due to their structural complexity and abundant energy resources (Welcomme 1979). Tropical lowland rivers with intact floodplains and seasonal precipitation patterns are the most productive river systems in the world, with many fishes colonizing and reproducing on floodplains following seasonal overbank flooding (Junk et al. 1989, Winemiller 1991, 1996a). Seasonal patterns of hydrology and habitat heterogeneity of tropical floodplain rivers contribute to high species diversity of fishes (Winemiller 1991, 2004).

Population growth and the resulting increase in anthropogenic manipulation of fluvial habitats threaten to disrupt the processes that sustain biodiversity and ecosystem services through altered hydrology (e.g. climate change and anthropogenic diversions), changing floodplain landscapes (e.g. deforestation and conversion for agriculture), and overfishing. If inland fisheries are to be sustainably managed, it is necessary to gain a better understanding of the processes that give rise to the productivity of these systems.

This thesis follows the style and format of Ecology.

This study contributes to that understanding by adding a description of the factors influencing inland fisheries of the lower Oueme River floodplain in West Africa.

Whedos ("fish pond" in the local Fon language of Southern Benin) are a traditional method of harvesting fish biomass from the floodplains of several large rivers around the world (Welcomme 1979) and have recently been adopted by people living along the Niger River in northern Benin to supplement decreasing fisheries yields (Hauber et al. 2011a, 2011b). Though whedos provide an important source of protein and livelihoods for low-income communities, it is currently unclear whether the expansion of this aquaculture practice has the potential to harm the recruitment of fish stocks that it exploits. Whedo harvests would pose little threat to inland fisheries if they mostly eliminate those exploits fishes that would have died naturally in harsh floodplain habitats during the dry season (Welcomme 1976). More recently, it has been suggested that the increasing prevalence of whedos may cause unforeseen negative effects on fish abundance and diversity (Hauber et al. 2011b). Because whedos have already been adopted by many rural communities in West Africa and have been shown to be highly productive (> 1 ton of fish/hectare, Welcomme 1976, Balarin 1988), it might be better to increase the productivity of existing whedos instead of increasing densities of whedos on floodplains.

The objectives of this thesis were: 1) to investigate fish species assemblages of whedos on the Oueme River floodplain at the beginning of the dry season when they first become isolated, and at the end of the dry season when they are harvested; 2) to elucidate whether species assemblages in whedo and natural floodplain habitats result from stochastic colonization during annual floods (the null hypothesis), or whether they result from biotic interactions (e.g. predation and competition) and/or abiotic environmental filtering (e.g. aquatic hypoxia selecting for fishes that possess adaptations for aerial respiration); 3) to estimate vertical trophic structure and the basal production sources supporting fish assemblages in whedos, a natural floodplain depression, and river channel habitats at the beginning of the dry season; and 4) to use the results obtained from this study to formulate suggestion as to how to potentially increase fisheries yield of existing whedos on the Oueme River floodplain.

STUDY AREA

The Oueme River flows from its headwaters in the Atakora Mountains in Benin (West Africa) approximately 500 km to Lake Nokoue, a large brackish estuary that empties into the Gulf of Guinea near the city of Cotonou. The Oueme's average discharge is 170 m^3/s. The Oueme Basin supports approximately 116 fish species (Lévêque et al. 1990, 1992). The study area was located near the town of Adjohon in the south-central region of Benin (Fig. 1.1). The region experiences a major wet season from March to July and a minor wet season from September to mid-November, with other months receiving little or no rainfall (Adite et al. 2005). On the floodplain (Figure 1.2) near Adjohon, the dominant land uses are small-scale farming and aquaculture in ponds called whedos (Figure 1.3). Whedos are long, narrow ponds constructed in the floodplain that hold fishes that colonize from the river during the annual flood pulse (Welcomme et al. 2006, Hauber et al. 2011a, 2011b). Whedos in the study area are, on average, 1-m deep by 5.5-m wide, and range from 40 to 1000 m in length. During the dry season, whedos are unmanaged and become covered with aquatic macrophytes that create conditions of low dissolved oxygen (DO) due to tissue senescence, decomposition, microbial respiration, and inhibition of gas exchange at the water surface. Whedos are harvested at the end of the dry season by first isolating a section of the whedo with nets, then removing all of the aquatic vegetation in that section (Figure 1.4). Fishes are then harvested by hand in the cleared section before the barrier net is used to encircle the remaining fish and vegetation in a purse seine fashion. This process is then repeated sequentially in sections along the entire length of the whedo.

Akadjavi is another form of aquaculture practiced in the region. Akadjavis are built along the bank of the Oueme River at the onset of the dry season after the floodwaters have receded (Figure 1.5). Terrestrial vegetation is arranged in rectangular plots that are surrounded and held in place with sticks or palm fronds lodged in the sediment. Akadjavis are constructed to attract and provide habitat for fishes. After several weeks to a month or more, each akadjavi is surrounded by a net, the vegetation is removed from within, and the entrapped fishes are harvested by pulling the net onto land in a purse seine fashion.

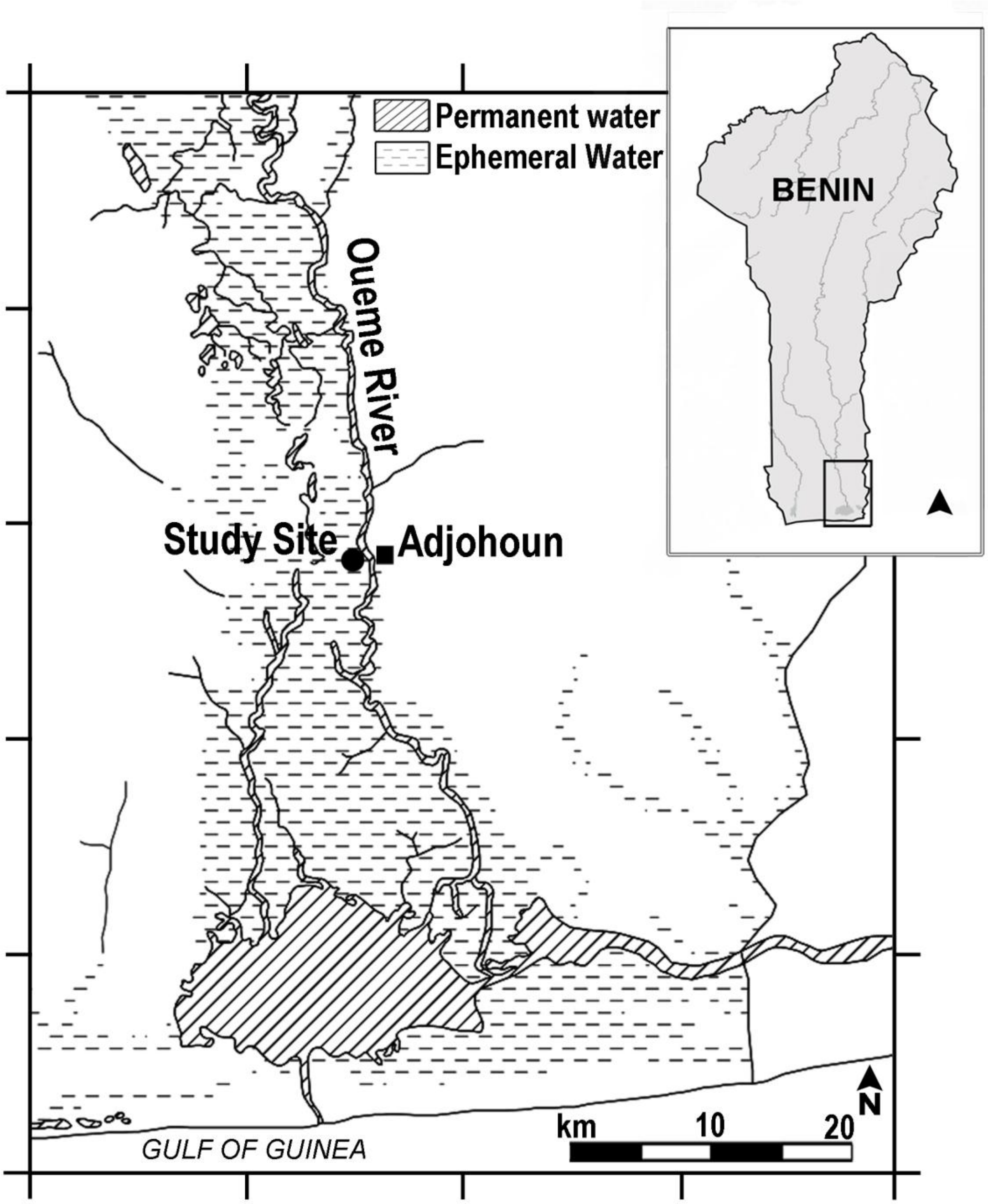


Figure 1.1. Map of study site in Oueme River basin Benin Africa.

Figure 1.2. Floodplain and an inundated natural depression.

Figure 1.3. A network of whedos on the Oueme River floodplain (Welcomme et al. 2006).

Figure 1.4. Whedo before, during, and after removal of aquatic vegetation.

Figure 1.5. Oueme River and akadjavis.

CHAPTER II

FISH ASSEMBLAGE STRUCTURE OF WHEDOS ON THE OUEME RIVER FLOODPLAIN, WEST AFRICA

INTRODUCTION

Early models of community structure and dynamics mainly focused on species interactions such as competition and predation that limit the growth of populations. More recent metacommunity models add to this a consideration of how spatiotemporal environmental variation and movement affect community dynamics (Leibold et al. 2004, Holyoak et al. 2005). The patch dynamics model hypothesizes that local community composition derives from a trade-off between competitive ability and dispersal ability (Hutchinson 1953, Townsend 1989). Environmental disturbance provides opportunity for competitively inferior species to colonize habitat patches and persist until they are displaced by competitively superior species or impacted by a subsequent disturbance. Even if disturbance and colonization dynamics are essentially stochastic, the model assumes non-random sequences of local community transition resulting from differential colonization and competitive abilities. In contrast, the species-sorting metacommunity model predicts that community structure is a result of environmental heterogeneity and the habitat selection and environmental filtering that result from it (Whittaker 1962, Holt 1985). The mass effect metacommunity model proposes that community structure is a function of spatial dynamics whereby dispersal following source-sink population dynamics allows for competitively inferior species to persist in local patches by immigration of individuals from communities where abiotic and biotic conditions are more favourable (Shmida & Wilson 1985, Pulliam 1988, Leibold et al. 2004). Finally, the neutral model of metacommunity dynamics (Hubbell 2001) serves as a sort of null model to which predictions from other models can be compared. According to the neutral model, species are equivalent in their dispersal and competitive abilities so that community structure largely results from stochastic processes. In a recent conceptual synthesis of community ecology, Vellend (2010) proposed that community structure is a product of selection, drift, speciation and dispersal, with some of these processes assuming greater importance at certain times and places.

Since their advent, the differing metacommunity models have been used to explain fish community structure in lotic and floodplain habitats. For example, several studies have invoked the species-sorting concept to explain fish community structure (e.g., oxbow lakes, Winemiller et al. [2000]; floodplain river, Arrington and Winemiller [2006]; stream, Hoeinghaus et al. [2007]). In a study of ephemeral freshwater pond communities, Urban (2004) advocated the necessity of integrating the species-sorting and mass effect models if metacommunity theories are to be successfully applied. The patch dynamics model frequently has been used to explain community structure in streams and rivers (Pringle et al. 1988, Townsend 1989, Winemiller et al. 2010). Walker and Cyr (2007) used the neutral model to described fish and zooplankton communities from a broad range of lakes worldwide, but the model was unable to predict phytoplankton community structure.

In the Oueme River, a lowland river in Benin, Africa, artificial ponds constructed in the floodplain (whedos) enhance floodplain fisheries of rural communities, but they also provide an excellent model system for examining metacommunity dynamics. When the river breaches its banks during the annual flood pulse, the floodplain is colonized by adult fishes from the river channel, and fishes either spawn in aquatic habitats of the floodplain or spawn in the river channel with juveniles subsequently dispersing onto the floodplain. When the waters recede, fishes become isolated in the whedos where they remain until harvested during the dry season. This study investigated fish metacommunities of the Oueme River in Benin, West Africa by examining fish species assemblages of floodplain habitats at the beginning of the dry season when they first become isolated, and at the end of the dry season when they are harvested. Of particular interest was the question of whether species assemblages in floodplain habitats result from stochastic colonization during annual floods (the null hypothesis), or whether they were a function of biotic interactions and/or environmental filtering.

Following the patch dynamics model, I hypothesize that fish assemblages in whedos will have high species diversity during the beginning of the dry season. This is because juveniles of most species in the river disperse into floodplain habitats that are productive (resource rich) with good water quality. As water levels gradually fall, dense growth of floating aquatic macrophytes causes dissolved oxygen in whedos to decline and whedos should be dominated by species that possess adaptations for aerial respiration (Junk et al. 1989, Winemiller 1996b). As the dry season progresses young fishes grow and coexist in whedos at ever increasing densities, whedo assemblages may become dominated by predatory fishes with accessory respiratory adaptations, and species richness declines. Predatory fishes having adaptations for aerial respiration such as walking catfishes (*Clarias agboyiensis*, *C. gariepinus)*, the bichir *Polypterus senegalus,* the snakehead *Parachanna obscura*, and the lungfish *Protopterus annectens* are common in lowland rivers of West Africa. At the end of the dry season, whedo fish assemblages also may be influenced by competition within the top trophic level in addition to predation and environmental filtering in response to hypoxia. I hypothesize that fish assemblage dynamics in whedos are consistent with the patch dynamics metacommunity model whereby non-competitive or vulnerable species are initially common during the flood pulse but are then replaced gradually by superior competitors and predators during the period of patch isolation. There is at the same time a significant component of the species sorting model, because the onset of aquatic hypoxia during whedo isolation selectively eliminates intolerant fish species. I hypothesize that the mass effect model will not describe this system because once whedos become isolated, there essentially is no dispersal and there is little interannual survival of residents because fishermen remove nearly all fishes at the end of the dry season.

METHODS

Sample collections - low water periods

Fishes were surveyed in nine whedos, one natural floodplain depression, and one site in the Oueme River from May to July (late dry season) 2008, and in 11 whedos, one natural floodplain depression, and one site in the Oueme River from February to March 2009 (low-water period). First, a 20-m reach at one end of the whedo was blocked with a 2-cm mesh barrier net, aquatic vegetation was removed, and the area was seined (2x6 m, 0.5-cm mesh) five times before encircling the area with the barrier net to capture any remaining fishes. A 2x6-m seine with 0.5-cm mesh was used to survey natural depressions in the floodplain. To survey fishes from structurally complex habitat along the shoreline of the river channel, we collected akadjavis. The area was encircled with a net (2-cm mesh), all sticks and vegetation were checked for fishes before being removed, and the net was pulled from the water to capture the remaining fish. A 2-m cast net (1-cm mesh) also was used to sample adjacent open-water areas in the main channel. Captured fishes were euthanized using tricaine methanesulfonate (MS-222) following Texas A&M Animal Use Protocol 2005-117, and then preserved in formalin. Specimens were identified using taxonomic keys in Lévêque et al. (1990, 1992). Voucher specimens were cataloged into the Texas Cooperative Wildlife Collection at Texas A&M University.

Sample collections - falling water period

During the falling water period of December 2010 and January 2011, fishes were surveyed using the same methods from 11 whedos plus one natural floodplain depression and one site in the Oueme River channel during the falling-water period. To allow for estimates of abundance in terms of catch-per-unit effort (CPUE), dimensions of each sampled habitat were measured, including the transect length, transect width, and thalweg depth. The area and water depth of the akadjavi was measured. For the river channel, CPUE was calculated based on the volume of the akadjavi and also based on the volume sampled by the cast net (diameter x depth summed for all throws). Additionally, the wet weights of site collections were recorded for later estimation of total biomass of fishes per unit volume.

Physicochemical variables – falling water period

Physicochemical variables were not measured at the survey sites during low-water periods in 2008 and 2009. DO (mg/L), conductivity (microsiemens/cm), pH, and temperature (ºC) were measured during December 2010 and January 2011 in each habitat with a Hach minisonde. Measurements were taken every ten minutes for approximately two hours. Replicate conductivity, pH, and temperature measurements were averaged, but the maximum DO recording was used to characterize DO in the habitats. For each habitat, percent surface area coverage and height of aquatic macrophytes were estimated visually.

Analysis of fish assemblage structure

Variation in fish assemblage structure among habitats was examined using non-metric multidimensional scaling (NMDS) ordination with 2 dimensions (k=2) based on Bray-Curtis similarity matrices computed from species presence/absence data. Significant differences in assemblage structure were identified using one-way analysis of similarity (ANOSIM). We tested for significant differences in assemblage structure among whedo, natural floodplain depression, and main channel habitats sampled in 2008, 2009, and 2010-2011. Because this ordination strongly differentiated between whedos versus the main channel and natural floodplain depression sites, the analysis was repeated with only data from whedos sampled in 2008, 2009, and 2010-2011 to evaluate assemblage structure of these habitats during different phases of the hydrological cycle. NMDS ordination also was performed on whedo data from the low-water period (2008 and 2009 samples) and the falling-water period (2010-2011) samples. For the 2010-2011 data, associations between habitat, physicochemical, and fish CPUE data were explored using canonical correspondence analysis (CCA). Significant associations at $p < 0.05$ were identified using Bartlett's test. All statistical analyses were performed using the software programs PRIMER-E version 5 and PCORD.

RESULTS

Physicochemical variables – falling water period

Dimensions of areas sampled in whedos ranged from 39 to >1000 m (average = 595 m) in length, 4 to 6.3 m (average = 5 m) in width, and 0.39 to 1.3 m (average = 0.78 m) in maximum depth (Table 2.1). Most (73%) of the whedo samples were ≥ 95% covered in aquatic vegetation that was on average 90.7 cm in height above the water surface (Table 2.2). Dominant aquatic macrophytes were *Leersia hexandra, Polygonum salicifolium, Ipomea aquatica,* and *Aeschynomene afraspera*.

Dissolved oxygen concentrations were much lower in the whedos (range ≤ 0.2 to 0.8 mg/L) compared to either the natural floodplain depression (maximum 3.0 mg/L) or main channel (maximum 6.0 mg/L, Table 2.2). Specific conductivity was higher in whedos (mean = 212.7 µS/cm) compared to the natural floodplain depression (specific conductivity = 135 µS/cm) and main channel habitats (105 µS/cm). pH averaged 6.2 in the whedos, 6.4 in the natural floodplain depression, and 6.9 in the main channel. Temperature ranged from 23-27°C in whedos and the natural floodplain depression, and temperature in the main channel was 30°C.

Table 2.1. GPS coordinates and dimensions of all habitats measured in 2010-2011. Natural floodplain depression = floodplain.

Habitat	**GPS coordinates**	**Approximate Length (m)**	**Width (m)**	**Maximum depth (m)**
Whedo 1	N 6° 41.853', E 02° 28.212'	1000	5.0	1.3
Whedo 2	N 6° 41.701', E 02° 28.185'	100	5.8	1.2
Whedo 3	N 6° 41.620', E 02° 28.319'	1000	5.4	0.4
Whedo 4	N 6° 41.600', E 02° 28.264'	500	4.6	0.9
Whedo 5	N 6° 41.577', E 02° 28.267'	450	4.0	0.6
Whedo 6	N 6° 41.544', E 02° 28.235'	450	6.3	1.0
Whedo 7	N 6° 41.674', E 02° 28.272'	500	5.5	0.7
Whedo 8	N 6° 41.591', E 02° 28.271'	1000	4.1	0.8
Whedo 9	N 6° 41.549', E 02° 28.321'	500	4.8	0.6
Whedo 10	N 6° 41.458', E 02° 28.308'	1000	4.8	0.4
Whedo 11	N 6° 41.431', E 02° 28.223'	39	4.7	0.8
Floodplain	N 6° 41.422', E 02° 28.204'	N/A	N/A	1.3
Main channel	N 6° 42.104', E 02° 28.537'	N/A	125	2.4

Table 2.2. Physicochemical variables measured in each of the habitats in January 2010. Dissolved oxygen = DO, specific conductivity = cond, temperature = temp, percent surface area coverage of aquatic macrophytes = veg % surface area, and natural floodplain depression = floodplain. Dissolved oxygen concentrations shown were the maximum DO concentration measured in each habitat.

Habitat	**DO (mg/L)**	**Cond (µS/cm)**	**pH**	**Temp (°C)**	**Veg % surface cover**
Whedo 1	0.8	180	6.3	26	75
Whedo 2	0.5	180	6.3	26	95
Whedo 3	0.7	200	6.3	26	90
Whedo 4	0.4	175	6.3	26	95
Whedo 5	0.6	185	6.2	26	100
Whedo 6	0.4	250	6.1	27	90
Whedo 7	0.6	350	6.3	26	100
Whedo 8	0.6	230	6.1	25	100
Whedo 9	0.4	280	6.1	26	100
Whedo 10	0.6	270	6.3	23	98
Whedo 11	0.2	225	6.1	25	95
Floodplain	3.0	135	6.4	26	50
Main channel	6.0	105	6.9	30	0

Fish assemblage structure

In 2008 during the low-water period, a total of 13 fish species representing nine families and 11 genera was collected in floodplain habitats. Whedos contained between seven to ten species with high species overlap (Table 2.3). Seven species representing five families were captured in the natural floodplain depression, 86% of which were also found in whedos. In contrast, 18 fish species representing 11 families were collected in the river channel of which only five (26%) were found in whedos. All whedos contained *Ctenopoma petherici*, *Parachanna obscura*, *Polypterus senegalus* and *Clarias agboyiensis*, and most whedos had *Erpetoichthys calibaricus* (89%), *Clarias gariepinus* (89%), *Brienomyrus niger* (67%) and *Parachanna africana* (67%), all of which possess adaptations for aerial respiration.

In 2009, 14 fish species representing 11 families and 12 genera were collected, with whedos yielding between seven to 12 species. Nine fish species representing seven families were captured in the natural floodplain depression, 89% of which were also found in whedos. In contrast, 17 fish species representing 11 families were collected in the river channel, of which only five (28%) were collected in whedos. All whedos contained the species *Ctenopoma petherici*, *Parachanna obscura*, *Polypterus senegalus*, *Clarias agboyiensis* and *Clarias geriepinus,* and most whedos contained *Heterotis niloticus* (64%), *Brienomyrus niger* (64%), *Protopterus annectens* (55%)*, Xenomystus nigri* (55%), *Parachana africana* (55%) and *Erpetoichthys calabaricus* (55%)

Table 2.3. Percent occurrence of species collected from whedos during the low-water period in 2008 and 2009 and the falling-water period in 2010/2011.

			Low Water Period		**Falling Water Period**	
Order	**Family**	**Species**	**% whedos present 2008**	**% whedos present 2009**	**% whedos present 2010/2011**	**% of total abundance 2010/2011**
Lepidosireniformes	Protopteridae	*Protopterus annectens*	11	55	36	0.5
Polypteriformes	Polypteridae	*Erpetoichthys calabaricus*	89	55	55	0.6
Polypteriformes	Polypteridae	*Polypterus senegalus*	100	100	100	5.4
Osteoglossiformes	Arapaimidae	*Heterotis niloticus*	22	64	0	0
Osteoglossiformes	Mormyridae	*Brienomyrus niger*	67	64	91	5.5
Osteoglossiformes	Mormyridae	*Mormyrus rume*	11	0	0	0
Osteoglossiformes	Notopteridae	*Xenomystus nigri*	44	55	36	0.8
Characiformes	Hepsetidae	*Hepsetus odoe*	0	27	0	0
Siluriformes	Clariidae	*Clarias agboyiensis*	100	100	100	55.8
Siluriformes	Clariidae	*Clarias gariepinus*	89	100	64	4.3
Siluriformes	Clariidae	*Gymnallabes typus*	0	0	18	0.2
Siluriformes	Malapteruridae	*Malapterurus beninensis*	11	0	18	0.2
Perciformes	Anabantidae	*Ctenopoma petherici*	100	100	100	22.1
Perciformes	Channidae	*Parachana africana*	67	55	18	0.4
Perciformes	Channidae	*Parachana obscura*	100	100	100	4.1
Perciformes	Cichlidae	*Hemichromis fasciatus*	0	0	9	0.1
Perciformes	Cichlidae	*Oreochromis niloticus*	0	27	9	0.1
Perciformes	Cichlidae	*Sarotherodon galilaeus*	0	9	9	0.1

In 2010-2011 during the falling-water period, 1,831 fish specimens representing nine families, 13 genera, and 15 species were collected from whedos. Whedos contained between 61 to 353 (average = 166) individuals and between six to nine (average = 7.6) species, with high species overlap among sites. A total of 131 specimens representing 11 families and 13 species was collected from the natural floodplain depression. Seven (54%) of the species caught in the natural floodplain depression also were found in whedos (47% of the total species in whedos). In contrast, a total of 434 specimens was collected in the river channel representing 18 families and 33 species of which only four (12%) were found in the whedos. All whedos contained the species *Ctenopoma petherici*, *Parachanna obscura*, *Polypterus senegalus* and *Clarias agboyiensis*, and most whedos contained *Brienomyrus niger* (91%), *Clarias gariepinus* (64%) and *Erpetoichthys calibaricus* (55%, Figure 2.1). CPUE for whedos ranged from 0.75 to 6.1 individuals/m^3; CPUE was 0.8 individuals/m^3 in the natural floodplain depression and 1.79 individuals/m^3 in the river channel (Table 2.4). 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, 60.6 g/m^3 in the river-channel akadjavi, and 18.3 g/m^3 in the river channel open water sampled with the cast net.

Figure 2.1. The dominant species caught in the whedos in 2008, 2009, and 2010. All are predatory species with adaptations for aerial respiration.

Table 2.4. Abundance catch-per-unit-effort (CPUE) of species collected from whedo, natural floodplain depression (floodplain), and river channel habitats during the falling-water period in 2010-2011.

Order	**Family**	**Species**	**Average whedo CPUE**	**Floodplain CPUE**	**Main channel CPUE**
Lepidosireniformes	Protopteridae	*Protopterus annectens*	< 0.1	0	0
Polypteriformes	Polypteridae	*Erpetoichthys calabaricus*	< 0.1	0	0
Polypteriformes	Polypteridae	*Polypterus endlicheri*	0	0	< 0.1
Polypteriformes	Polypteridae	*Polypterus senegalus*	0.1	< 0.1	0
Osteoglossiformes	Mormyridae	*Brienomyrus niger*	0.1	< 0.1	< 0.1
Osteoglossiformes	Mormyridae	*Hyperopisus bebe*	0	0	< 0.1
Osteoglossiformes	Mormyridae	*Mormyrops anguilloides*	0	0	< 0.1
Osteoglossiformes	Mormyridae	*Mormyrus rume*	0	0	< 0.1
Osteoglossiformes	Mormyridae	*Pollimyrus isidori*	0	0	0.2
Osteoglossiformes	Notopteridae	*Xenomystus nigri*	< 0.1	0	0
Clupeiformes	Clupeidae	*Pellonula leonensis*	0	0	< 0.1
Cypriniformes	Cyprinidae	*Labeo brachypoma*	0	0	< 0.1
Characiformes	Alestidae	*Brycinus longipinnis*	0	< 0.1	< 0.1
Characiformes	Alestidae	*Brycinus macrolepidotus*	0	0	0.2
Characiformes	Alestidae	*Brycinus nurse*	0	0	< 0.1
Characiformes	Alestidae	*Hydrocynus vittatus*	0	0	< 0.1
Characiformes	Distichodontidae	*Distichodus rostratus*	0	0	< 0.1
Characiformes	Distichodontidae	*Neolebias unifasciatus*	0	< 0.1	0
Characiformes	Hepsetidae	*Hepsetus odoe*	0	< 0.1	< 0.1
Siluriformes	Bagridae	*Bagrus docmak*	0	0	< 0.1
Siluriformes	Clariidae	*Clarias agboyiensis*	1.2	< 0.1	0
Siluriformes	Clariidae	*Clarias gariepinus*	0.1	< 0.1	0
Siluriformes	Clariidae	*Gymnallabes typus*	< 0.1	0	0

Table 2.4 continued.

Order	**Family**	**Species**	**Average whedo CPUE**	**Floodplain CPUE**	**Main channel CPUE**
Siluriformes	Clariidae	*Heterobranchus longifilis*	0	0	< 0.1
Siluriformes	Claroteidae	*Chrysichthys aluuensis*	0	0	< 0.1
Siluriformes	Claroteidae	*Chrysichthys ogooensis*	0	0	< 0.1
Siluriformes	Malapteruridae	*Malapterurus beninensis*	< 0.1	0	0
Siluriformes	Mochokidae	*Synodontis schall*	0	0	0.6
Siluriformes	Mochokidae	*Synodontis velifer*	0	0	< 0.1
Siluriformes	Schilbeidae	*Schilbe intermedius*	0	0	0.1
Cyprinodontiformes	Nothobranchiidae	*Aphyosemion bitaeniatum*	0	0.1	0
Cyprinodontiformes	Poeciliidae	*Gambusia sp.*	0	< 0.1	0
Synbranchiformes	Mastacembelidae	*Mastacembelus praensis*	0	0	< 0.1
Perciformes	Cichlidae	*Tilapia guineensis*	0	0	0.1
Perciformes	Cichlidae	*Tilapia mariae*	0	0	< 0.1
Perciformes	Eleotridae	*Eleotris senegalensis*	0	0	< 0.1
Perciformes	Anabantidae	*Ctenopoma petherici*	0.5	< 0.1	< 0.1
Perciformes	Channidae	*Parachana africana*	< 0.1	0	0
Perciformes	Channidae	*Parachana obscura*	0.1	< 0.1	< 0.1
Perciformes	Cichlidae	*Chromidotilapia guntheri*	0	0	0.3
Perciformes	Cichlidae	*Hemichromis fasciatus*	< 0.1	0	0.1
Perciformes	Cichlidae	*Oreochromis niloticus*	< 0.1	< 0.1	0
Perciformes	Cichlidae	*Sarotherodon galilaeus*	< 0.1	0	< 0.1
Perciformes	Cichlidae	*Sarotherodon melanotheron*	0	0	< 0.1
Perciformes	Cichlidae	*Tilapia cessiana*	0	0	< 0.1

NMDS (k=2) comparing assemblage structure among whedo, natural floodplain depression, and main channel habitats sampled in 2008, 2009, and 2010-2011 (based on species presence-absence data) yielded an ordination with a “good” stress value of 0.09 (Figure 2.2). ANOSIM indicated that whedos were significantly different from the natural floodplain depressions (R = 0.731, $p = 0.002$) and the main channel (R = 0.997, $p = 0.001$). In comparing assemblage structure among whedos sampled in 2008, 2009 and 2010-2011, NMDS (k=2) generated an ordination with a “fair” stress value of 0.16 (Figure 2.3). Whedos sampled in 2008 were not significantly different from whedos sampled in 2009 (ANOSIM, R = 0.053, $p = 0.216$) or 2010-2011 (R = 0.081, $p = 0.125$). However, whedos sampled in 2009 were significantly different from whedos sampled in 2010-2011 (R = 0.205, $p = 0.008$). When comparing assemblages from whedos sampled during the low-water period (Feb. 2008 and Mar. 2009) with whedos sampled during the falling-water period (Dec. 2010- Jan. 2011), NMDS (k=2) yielded an ordination with a fair stress value of 0.16. Assemblage structure of whedos was significantly different between low-water and the falling-water periods (ANOSIM, R = 0.173, $p = 0.015$).

Canonical correspondence analysis (CCA) of fish CPUE and six environmental variables collected in 2010-2011 in whedo, natural floodplain depression, and river channel habitats yielded three pairs of canonical axes explaining 59.4% of variation in the dataset (Figures 2.4 and 2.5). Environmental axis 1 explained 43.8% of the variance and contrasted whedos with higher % vegetation cover and specific conductivity with the natural floodplain depression and main channel habitats having higher maximum depth, temperature, pH, and DO. Environmental axis 2 explained 11.7% of the variance and contrasted whedos with higher maximum depth, temperature, and pH with whedos having higher specific conductivity. Whedos with greater depth, temperature, and pH were dominated by the species *Brienomyrus niger*, *Clarias gariepinus*, *Ctenopoma pethérici*, *Parachanna obscura*, *Polypterus senegalus*, and *Xenomystus nigri*. Whedos with greater specific conductivity tended to contain higher densities of *Clarias agboyiensis*, *Erpetoichthys calabaricus, Gymnallabes typus*, *Malapterurus beninensis*, *Parachanna africana*, and *Protopterus annectens*.

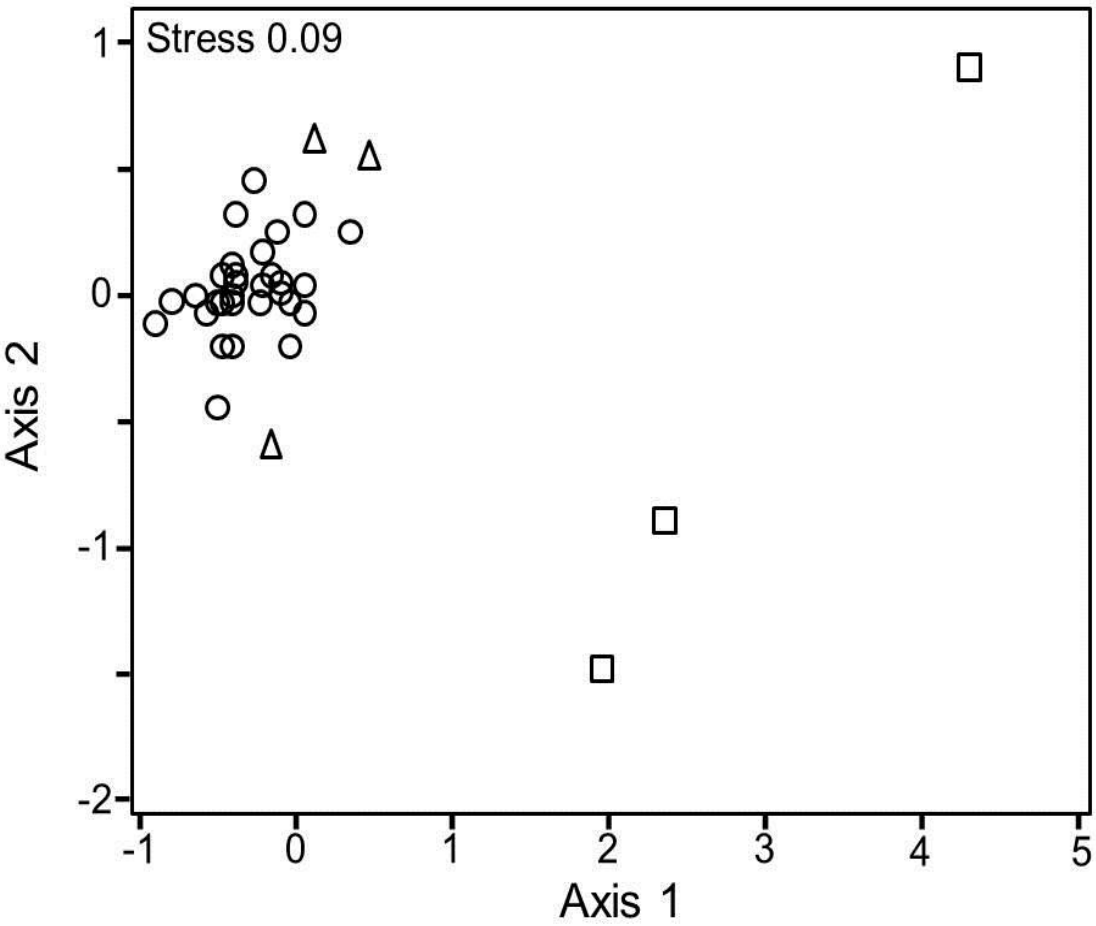


Figure 2.2. Nonmetric multidimensional scaling analysis (NMDS) comparing assemblage structure (presence-absence data) among whedo (circle), natural floodplain depression (triangle), and main channel (square) habitats sampled in 2008, 2009, and 2010-2011.

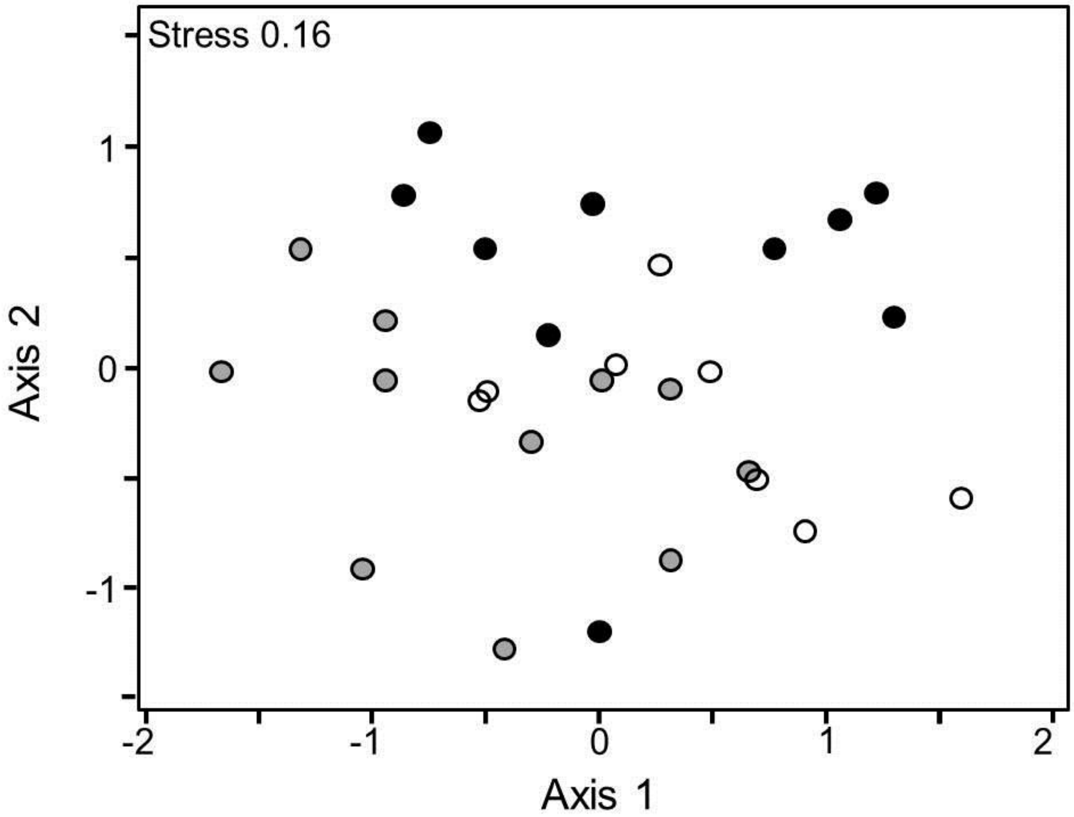


Figure 2.3. Nonmetric multidimensional scaling analysis (NMDS) comparing assemblage structure (presence-absence data) among whedo habitats sampled in 2008 (white circle), 2009 (grey circle), and 2010-2011 (black circle).

Figure 2.4. Canonical correspondence analysis (CCA) of fish CPUE in the whedo, natural floodplain depression, and main channel habitats and six physicochemical variables collected in 2010/2011. Dissolved oxygen = DO, specific conductivity = SpCond, temperature = Temp, percent surface area coverage of aquatic macrophytes = VegCover, and maximum depth = MaxDep. Ap-bit = Aphyosemion bitaeniatum, Ba-doc = *Bagrus docmak*, Br-nig = *Brienomyrus niger,* Br-bar = *Brycinus longipinnis*, Br-mac = *Brycinus macrolepidotus*, Br- nur = *Brycinus nurse*, Ch- gun = *Chromidotilapia guntheri*, Ch-alu = *Chrysichthys aluuensis*, Ch-ogo = *Chrysichthys ogooensis*, Cl-agb = *Clarias agboyiensis*, Cl-gar = *Clarias gariepinus*, Ct-pet = *Ctenopoma petherici,* Di-ros = *Distichodus rostratus*, El-sen = *Eleotris senegalensis*, Er-cal = *Erpetoichthys calabaricus*, Ga-sp. = *Gambusia sp.*, Gy-typ = *Gymnallabes typus*, He-fas = *Hemichromis fasciatus*, He-odo = *Hepsetus odoe*, Hy-vit = *Hydrocynus vittatus*, He-lon = *Heterobranchus longifilis*, Hy-be = *Hyperopisus bebe*, La-bra = *Labeo brachypoma*, Ma-ben = *Malapterurus beninensis*, Ma-pra = *Mastacembelus praensis*, Mi-elo = *Micralestes elongatus*, Mo-ang = *Mormyrops anguilloides*, Mo-rum = *Mormyrus rume*, Ne-uni = *Neolebias unifasciatus*, Or-nil = *Oreochromis niloticus*, Pa-afr = *Parachana africana*, Pa-obs = *Parachana obscura,* Pe-leo = *Pellonula leonensis*, Po-isi = *Pollimyrus isidori*, Po-end = *Polypterus endlicheri*, Po-sen = *Polypterus senegalus*, Pr-ann = *Protopterus annectens*, Sa-gal = *Sarotherodon galilaeus*, Sa-mel = *Sarotherodon melanotheron*, Sc-int = *Schilbe intermedius*, Sy-sch = *Synodontis schall*, Sy-vel = *Synodontis haugi*, Ti-ces = *Tilapia cessiana*, Ti-gui = *Tilapia guineensis*, Ti-mar = *Tilapia mariae,* and Xe-nig = *Xenomystus nigri*.

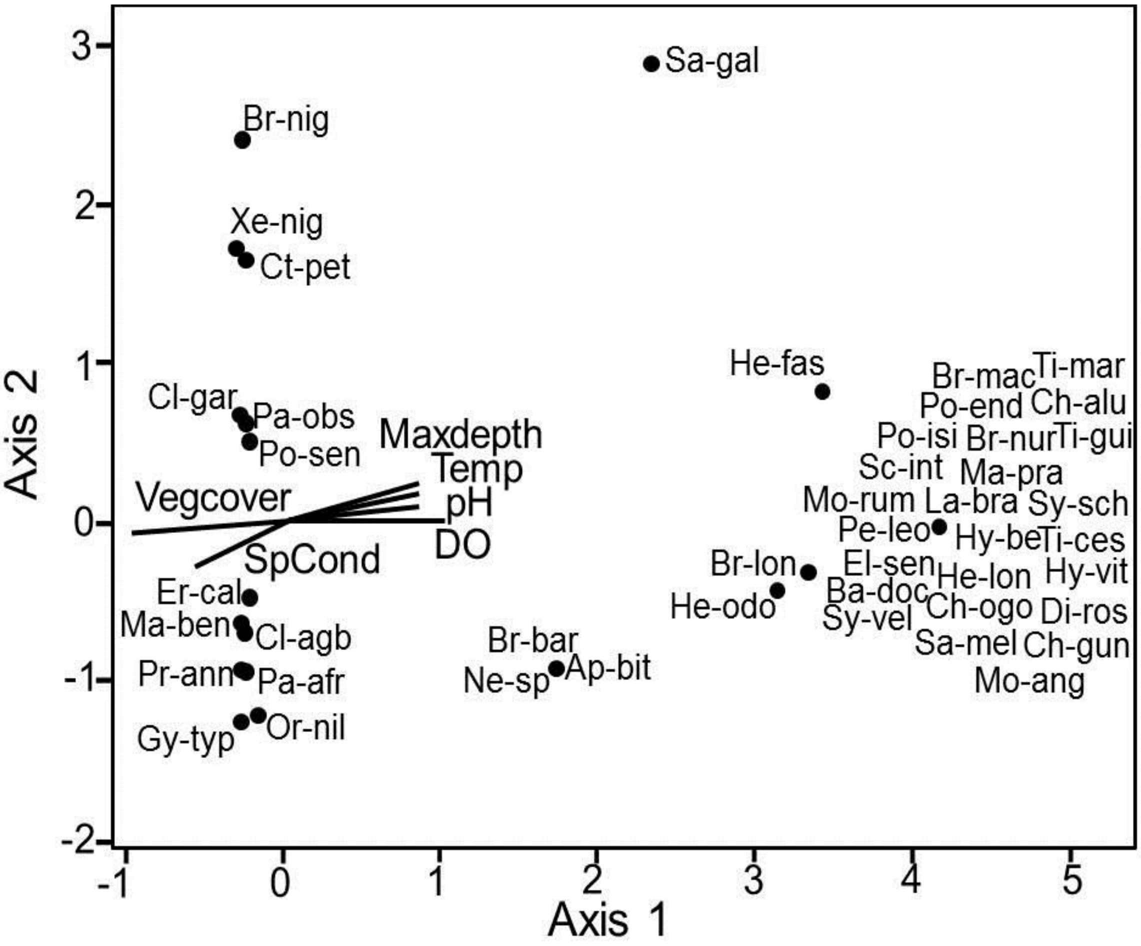


Figure 2.4 Continued.

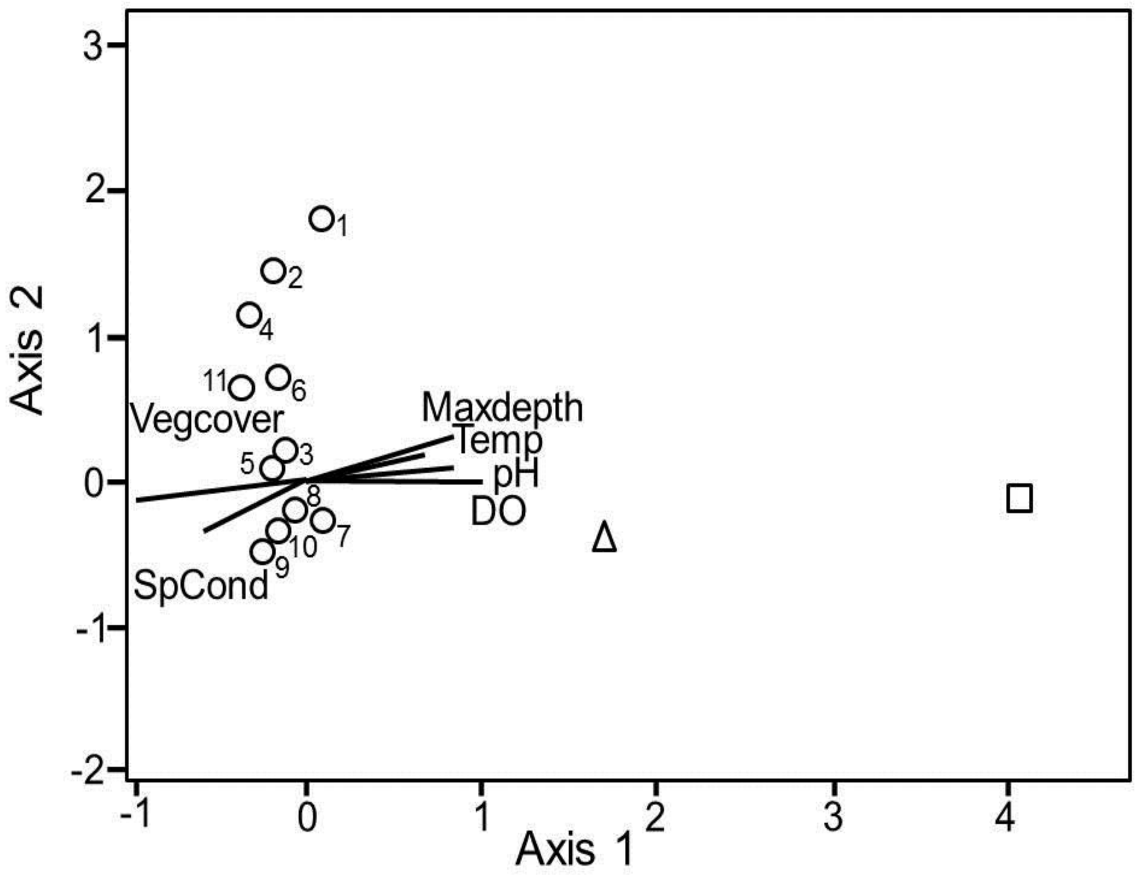


Figure 2.5. Canonical correspondence analysis (CCA) of fish CPUE in whedo (circle), natural floodplain depression (triangle), and main channel (square) habitats collected in 2010/2011 and vectors revealing axis loadings of six physicochemical variables. Codes for vectors are defined in figure 2.4.

DISCUSSION

The objective of this study was to test the applicability of metacommunity models as a way of describing fish assemblage structure of shallow floodplain habitats of the lower Oueme River. Whedos sampled in 2008, 2009, and 2010-2011 were compared to test for differences in fish assemblage structure between hydrologic periods (falling vs. low-water) and for correlations between assemblage structure, and abiotic environmental conditions within habitats. Habitat types were distinct with regard to assemblage structure and abiotic conditions. Significant correlations existed between aspects of assemblage structure and physicochemical parameters.

If assemblage structure in the floodplain habitats results only from stochastic dispersal during the flood pulse, then high overlap would be expected between the main channel and floodplain habitats in assemblage ordination plots. This was not the case. Although there was a small amount of overlap, fish assemblages in the main channel and floodplain were distinct in that 66% of the 44 species found in the main channel were not found in samples from the floodplain (i.e., both the whedos and natural floodplain depressions). Furthermore, 96% of the individuals captured from the main channel in 2010-2011 were species absent in samples from floodplain habitats. Fish assemblage structure was distinct in the natural floodplain depression and whedo habitats, with only seven (28%) of the 25 species found on the floodplain common to both. Assemblages in whedos and natural floodplain depressions were differentiated from those of the main channel by domination of fishes that can tolerate conditions of low dissolved oxygen in floodplain habitats (72% of species in whedos, 61% in natural floodplain depressions, and 23% in the main channel).

The fishes that dominated the communities of the whedos in both the falling and low-water periods possess adaptations for accessory or, in the case of the *Protopterus annectens* (the African lungfish), obligatory aerial respiration (Graham 1997). For example, the species *Ctenopoma petherici*, *Parachanna obscura*, and *Parachanna africana* possess paired suprabranchial chambers that harbor labyrinth structures covered with respiratory epithelium (Munshi 1962, Liem 1984, Pinter 1986, Liem 1987). The African lungfish is an obligatory air breather that possesses a pair of lungs that developed from an outpocketing of the gut, and can aestivate within a mucus cocoon buried in the ground for as long as four years (Parker 1892, Smith 1931, Johnels and Svensson 1954, Lomholt, J.P. 1993). The catfishes *Clarias agboyiensis* and *Clarias gariepinus* possess aborescent organs in the branchial cavity that are covered by modified vascularized epithelium (Geoffroy St. Hilaire 1802a, Munshi 1967). Although its air breathing organ has yet to be identified, aerial respiration has been observed in the mormyrid *Brienomyrus niger* (Benech and Lek 1981, Mortiz and Linsenmair 2007). The osteoglossiforms *Xenomystus nigri* and *Heterotis niloticus* can absorb oxygen from air using a gas bladder lined with highly vascularized epithelium (Hyrtl 1854, Greenwood 1963). The bichirs *Erpetoichthys calabaricus* and *Polypterus senegalus* use highly-furrowed, paired lungs for aerial respiration (Geoffery St. Hilaire 1802b, Purser 1926). In addition to having adaptations for aerial respiration, fishes of the families Clariidae, Channidae, Anabantidae, and Protopteridae are known to survive dry periods by burrowing in mud to retain moisture, and by moving over land in search of habitat (Day 1877, Smith 1931, Johnels 1957, Donnelly 1973, Pinter 1986, Pace and Gibb 2011).

Large differences in physicochemical conditions in river channel and floodplain habitats provided a foundation for species sorting based on environmental filtering. Dissolved oxygen concentrations in the whedos (range ≤ 0.2 to 0.8 mg/L) and natural floodplain depression (≤ 3.0 mg/L) were much lower than those recorded in the main channel (≤ 6.0 mg/L). Water temperatures in the whedos and floodplain were generally lower than those measured in the main channel, which makes these DO differences even more notable. These observations run counter to the physical relationship between DO saturation and temperature. Low DO in the whedos was caused by the high densities of floating aquatic macrophytes (average coverage 94%). These die and decompose, inhibit gas exchange at the surface of the water, and hinder algal photosynthesis by limiting light availability through shading. In the natural floodplain depression, aquatic macrophyte coverage was less than in the whedos, but still 50%, and high biomass of macrophytes in lentic ecosystems commonly causes low DO (Killgore and Hoover 2001, Rose and Crumpton 1996). There also were differences in pH, specific conductivity, and depth among floodplain habitats; however the dominance of fishes with adaptations for aerial respiration in whedo assemblages indicates that dissolved oxygen was the predominant environmental filter structuring communities in these habitats. Whereas little difference was observed in assemblage structure in whedos between the low and falling-water periods, there was a higher degree of divergence in fish assemblages from natural floodplain depressions during different hydroperiods. Only 44% of the species found in natural floodplain depressions were present during both hydroperiods, with a higher percentage of fishes in the low-water period (85%) being tolerant to hypoxia compared with the falling-water period (61%). In whedos 72% of species were present during both hydroperiods. In the whedos, this is likely due to the fact that dense coverage of aquatic macrophytes and low DO concentrations were already present early in the falling-water period. The patterns observed in the natural floodplain habitats may be due to decline in DO as aquatic macrophyte biomass increased, or due to evaporative loss that caused temperatures to increase as the water depth and surface area decreased with the progression of the dry season.

Findings from the Oueme River are consistent with similar studies that have documented a deterministic relationship between abiotic environmental variables and community structure in aquatic floodplain habitats (Winemiller 1989, Chapman and Liem 1995, Winemiller et al. 2000, Killgore and Hoover 2001, Petry et al. 2003a). For example, Chapman and Liem (1995) found that in the Njuguta River in Uganda, hypoxic floodplain habitats with dense coverage of aquatic macrophytes at the water surface had fewer non-air breathing fishes than habitats with large areas of open water at the surface. Winemiller et al. (2000) found that in the floodplain of the Brazos River in Texas, USA, shallow oxbow lakes with high densities of aquatic macrophytes experienced reduced levels of wind mixing, phytoplankton biomass, and DO that resulted in lower species diversity. Furthermore, studies frequently show that hypoxia is an ecological barrier in that it limits the dispersal of fishes between aquatic habitats (Roberts 1975, Kramer 1983, Suthers and Gee 1986, Kramer 1987, Saint-Paul and Soares 1987).

Biotic interactions also affect fish assemblage structure in river floodplain habitats (Lowe-McConnell 1964, Robinson and Tonn 1989, Rodriguez and Lewis 1997). For example, in the drying lagoons of the upper Paraná River floodplain in Brazil, community structure was strongly influenced by abiotic environmental variables as well as predation and competition as lagoons shrink and resources become limited (Okada et al. 2003, Petry et al. 2003b). Predator-prey interactions probably influence species assemblage structure in floodplain habitats of the Oueme River. During the falling and low-water periods, most fishes in the whedos and natural floodplain depressions sampled were piscivores. Predation has been inferred to drive community changes in floodplain habitats as the water level falls and fish densities increase (e.g. Lowe-McConnell 1964, Winemiller 1990). For example, Montaña et al. (2011) found that on the floodplains of the Cinaruco, La Guardia, and Ventuari rivers of Venezuela, as habitats shrink during the dry season, there is a shift in the trophic structure of fish assemblages from domination by herbivores and invertivores to domination by piscivores. Several studies have shown that the presence of piscivorous fish(es) affects community structure, with prey species selecting habitats that provide refuge from predation (e.g. Werner et al. 1983, Schlosser and Angermeier 1990, Harvey 1991, Gilliam and Fraser 2001, Layman and Winemiller 2004). In the isolated aquatic habitats of the Oueme River floodplain, however, it is unlikely that prey species are able to avoid predation through habitat selection. This is because low DO forces fishes that cannot breathe air to spend more time at the surface performing aquatic surface respiration that increases risk of predation (Kramer et al. 1983, Chapman and Liem 1995).

The neutral model of metacommunity dynamics can be rejected for fish assemblages in aquatic floodplain habitats of the lower Oueme River. However, each of the other three metacommunity models is consistent with aspects of these fish assemblages. The natural floodplain depressions had a more diverse fish assemblage during the falling-water period when several species lacked obvious adaptations for accessory aerial respiration. During the low-water period, most fishes in the natural and human-constructed floodplain habitats were piscivores tolerant of hypoxia. Following colonization of these habitats during the flood pulse, fishes that lack accessory respiratory adaptations and that were vulnerable to piscivores apparently were eliminated. This scenario is consistent with the patch dynamics metacommunity model. After flooding, floodplain habitats become isolated, and remain so until fishermen harvest them. Consistent with the mass effect model, fish communities of floodplain habitats can be explained in part by a source (river channel)-sink (floodplain) dynamic whereby fishes are able to persist in a hostile habitat because of immigration from more favorable habitats. In this floodplain ecosystem, harsh environmental conditions result in a subset of regional fish diversity consisting of predatory species resistant to aquatic hypoxia. This suggests that stochastic colonization of the floodplain followed by environmental filtering (species sorting model), predation (patch dynamics), or a combination of both mechanisms drive species assemblage structure at the local scale.

In a conceptual synthesis of community ecology, Vellend (2010) stated that the four metacommunity models “do not represent logically distinct classes of ecological processes.” Indeed, three of the metacommunity models could be invoked to describe the patterns of fish assemblage structure that we observed. Vellend (2010) argues that all patterns of ecological communities can be understood based on just four processes: selection, drift, speciation, and dispersal. On the floodplain of the lower Oueme River, our findings suggest that of these four processes selection (i.e. filtering of species by hypoxia and/or predation) and dispersal (i.e. colonization of the floodplain by fishes from the river channel during seasonal floods) play the most prominent roles in shaping local community structure. Our results support the idea that none of the metacommunity models fully explains community structure. The framework proposed by Vellend (2010) more closely captures the processes creating fish assemblage patterns in aquatic floodplain habitats of the Oueme River.

CHAPTER III

FOOD WEB STRUCTURE OF WHEDOS ON THE OUEME RIVER FLOODPLAIN, WEST AFRICA

INTRODUCTION

Although floodplain ecosystems are spatially and temporally complex, and may seem to be driven by stochastic processes (Hubbell 2001), a high degree of order has been observed in both abiotic and biotic processes (e.g., Winemiller 1996a, Lewis et al. 2000, Arrington and Winemiller 2006). In tropical floodplain rivers, seasonal hydrology has allowed biota to respond adaptively to habitat heterogeneity, resulting in high species diversity (Winemiller 1991, 2004). Tropical lowland rivers with intact floodplains and seasonal precipitation patterns are the most productive river systems in the world, as fish colonize floodplains to reproduce following seasonal overbank flooding (Junk et al. 1989, Winemiller 1991, 1996a). 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 and Aruajo-Lima 1993, Thorp et al. 1998, Benedito-Cecilio et al. 2000, Leite et al. 2002, Bunn et al. 2003, Herwig et al. 2004). Although algal production sources appear to support consumers most of the time, some studies indicate that during periods of high flow, terrestrial sources of primary production become important in supporting consumers in the upper food web (e.g. Winemiller 1996b, Zeug and Winemiller 2008). The Riverine Productivity Model by Thorp and Delong (1994) proposes that algal carbon is the main production source for most riverine consumers, because algae is more nutritious and labile than terrestrial carbon sources. In 2002, Thorp and Delong published a review of stable isotope data from tropical, temperate, and arctic rivers that reveals this to be true even in heterotrophic floodplain river habitats ($P/R<1$). In contrast, the Flood Pulse Concept proposes aquatic consumers are largely supported by terrestrial production from floodplains that becomes available during flood pulses (Junk et al. 1989). Recent research has supported both the Riverine Productivity Model (e.g., Hamilton et al. 1992, Bunn et al. 1999, Lewis et al. 2001, Medeiros and Arthington 2010) and the Flood Pulse Concept (e.g. Clappcott and Bunn 2003, Reid et al. 2008, Zeug and Winemiller 2008). 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 (Thorp and Delong 1998, Clapcott and Bunn 2003, Herwig et al. 2004, Zeug and Winemiller 2008).

In addition to basal production source contributions, vertical trophic structure (food-chain length) is an important feature of aquatic communities that 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 (Briand and Cohen 1987, Vander Zanden and Fetzer 2007). Hoeinghaus et al. (2008) found that food-chain length was significantly shorter in tropical rivers compared to lotic ecosystems (i.e., 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 are longer because their primary consumers (zooplankton) have smaller body sizes, and due to size-dependent foraging, more energy transfers are needed to reach large apex predators. In contrast, detritus-based systems may experience fewer energy transfers to reach apex predators because detritivores can be relatively large species of invertebrates and fishes, and large predators therefore can be supported by short food chains (Layman et al. 2005).

In the Oueme River, a lowland river in Benin, Africa, artificial ponds constructed in the floodplain (whedos) enhance floodplain fisheries of rural communities. When the Oueme breaches its banks during the annual flood pulse, aquatic habitats of the floodplain are colonized by fishes from the river channel. When floodwaters recede, fishes become isolated in aquatic floodplain habitats (i.e., whedos and natural floodplain depressions) and remain there until harvested by people near the end of the dry season. Early in the dry season, whedos become covered by dense growth of aquatic macrophytes that limit algal growth through shading. This project estimates vertical trophic structure and basal production sources supporting fish assemblages in whedos, a natural floodplain depression, and river channel habitats at the beginning of the dry season when aquatic floodplain habitats have first become isolated from the main channel.

In congruence with the Riverine Productivity Model, I hypothesized that fishes in the floodplain assimilate biomass derived mostly from algae. Although it may be less plentiful in whedo habitats, algae are more nutritious, have higher energy densities, and contain more labile organic molecules than terrestrial primary producers, and therefore should be disproportionately assimilated into consumer biomass (Thorp and Delong 2002). Because primary consumers of benthic algal- and detritus-based food webs of floodplains can be large-bodied metazoans and can therefore reach apex predators in few trophic transfers, food webs in whedos should also be shorter than those of the river channel (Hoeinghaus et al. 2008). 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 that have abundant macrophyte growth. Although stable isotope analysis was unable to identify the specific basal production source of consumer biomass in billabongs, the depleted ^{13}C signatures of secondary consumers indicated that macrophyte contributions were small. However, the Flood Pulse Concept hypothesizes that floodplain habitats also should, at least in part, be supported by C_3 macrophytes but not C_4 grasses during the beginning of the dry season, because these plants are abundant on the flooded plain, and C_3 macrophytes are more nutritious than C_4 grasses (Junk et al. 1989). Stable isotope analysis using a Bayesian mixing model should be able to elucidate basal production sources supporting fish biomass in whedos and natural habitats of the Oueme River floodplain.

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 by consumers in trophic pathways, their isotopic ratios reflect the ratios assimilated by primary producers. 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), thus the N isotopic ratio is useful for estimating the trophic position of consumer species (Post 2002). By accounting for fractionation (2.5‰ per trophic level on average), $^{15}N/^{14}N$ ratios also can be used in conjunction with isotopic ratios of C and other elements to estimate basal production sources supporting consumers at various trophic levels (Vander Zanden and Rasmussen 2001). This is possible 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.

METHODS

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 Oueme River channel during the falling-water period from December 2010 to January 2011. Fish collections were carried out in the whedos by first isolating a 20-m reach with a 1-cm mesh barrier net, removing the aquatic vegetation from within that section, and seining (2x6 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. A 2x6-m seine with 0.5-cm mesh was used to survey the natural floodplain depression. To survey fishes from structurally complex habitat along the shoreline of the river channel, I collected fishes inhabiting a single akadjavi. The akadjavi was encircled with a net (2-cm mesh), all sticks and vegetation were checked for fishes before being removed, and the net was pulled from the water to capture the remaining fish. A 2-m cast net (1-cm mesh) also was used to sample adjacent open-water areas in the main 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 were taken from the dorso-lateral region and preserved in salt for subsequent stable isotope analysis. Salt has a negligible influence on stable isotope signatures (Arrington and Winemiller 2002). Fishes were identified using taxonomic keys in Lévêque et al. (1990, 1992). Voucher specimens were cataloged into the Texas Cooperative Wildlife Collection at Texas A&M University.

Production sources including C_3 macrophytes, C_4 grasses, and microphytobenthos were collected by hand from each habitat. Macrophyte leaf and grass samples were collected from the dominant species of plants from the riparian zone. Microphytobenthos samples from whedos were scraped with a spatula from the surfaces of leaves and roots of submerged aquatic macrophytes. Microphytobenthos samples from the natural floodplain depression and river channel were scraped from surfaces of macrophytes and rocks near the water surface. This sampling technique was unlikely to produce a pure sample of benthic algae, thus microphytobenthos 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 Whatman GF/C filter. Seston samples were likely composed of a combination of phytoplankton, suspended organic matter, and bacteria. All primary producer samples were preserved in salt (NaCl) for stable isotope analysis.

Nutrient concentrations and algal primary production

Concentrations (mg/L) of soluble reactive phosphorus (SRP), NH_4^+, NO_2^-, and NO_3^- were measured in the field using colorimetric kits and a Hach DR 2800 spectrophotometer. Light and dark chambers were used to estimate respiration (R), net primary production (NPP) and gross primary production (GPP) of the water column following Wetzel and Likens (1991). Six 300-mL light and six 300-mL dark biological oxygen demand (BOD) bottles were filled with water from each site and incubated at approximately 0.5-m depth. Changes in DO concentration were measured using an YSI

Model 85 DO probe. 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 hour extraction using 90% ethanol, after which chlorophyll *a* was measured using a Hach DR 2800 spectrophotometer (666 and 750 nm) and corrected for phaeophytin by subtracting absorbances after addition of 0.1N HCl.

Stable isotope analysis

In the laboratory at Texas A&M University, samples of primary producers, fishes, and invertebrates were rinsed and then soaked in distilled water for 4 h, and 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 fishes 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 the whedos, natural floodplain depression, and main channel habitats (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. I used the equation TF= 2.5‰ x (mean trophic position - 1) and standard deviation = 2.5 from a meta-analysis as model input for trophic fractionation (Vander Zanden and Rasmussen 2001). Here, mean trophic position was calculated using the equation discussed below where $\delta^{15}N_{reference}$ was the average $\delta^{15}N$ of all potential basal production sources for a site. In the whedos, potential basal production sources included C_3 macrophytes, C_4 grasses, microphytobenthos and seston. I did not include samples of seston as a source in whedos where water-column gross primary production values were low (< 0.05 mg C/m^3/d). Means and standard deviations of $\delta^{13}C$ and $\delta^{15}N$ from *in situ* samples of C_3 macrophytes, C_4 grasses, microphytobenthos and seston were used as MixSIR inputs for whedos. For a few whedos in which C_3 macrophyte and C_4 grass (n = 3), microphytobenthos (n = 2), or seston (n = 2) samples were not obtained, I used the grand means and standard deviations of all whedo C_3 macrophytes, C_4 grasses, microphytobenthos, 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, microphytobenthos, 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 $TP = [(\delta^{15}N_{consumer} - \delta^{15}N_{reference})/2.54] + 1$ from Zeug and Winemiller (2008), where $\delta^{15}N_{reference}$ was the mean of the two primary producer $\delta^{15}N$ averages estimated to be 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 microphytobenthos samples were not taken, I used the grand means of all whedo C_3 macrophytes or microphytobenthos as the $\delta^{15}N$ averages for calculation of $\delta^{15}N_{reference}$ for those sites.

RESULTS

Nutrients and algal biomass and production

Concentrations of dissolved inorganic nitrogen (DIN) were higher in whedos (mean = 0.50 mg/L) compared to the natural floodplain depression (0.18 mg/L) and main channel habitats (0.34 mg/L, Table 3.1). Soluble reactive phosphorus (SRP) concentrations were higher in the natural floodplain depression (1.74 mg/L) than in whedos (1.4 mg/L) and the main channel (0.49 mg/L).

Water-column chlorophyll *a* differed among habitats (natural floodplain depression value = 25.8 mg/m^3, whedos average = 16.6 mg/m^3, river channel value = 11.6 mg/m^3). Benthic chlorophyll *a* concentration also was higher in the natural floodplain depression (5.4 mg/m^2) compared to concentrations measured in whedos (average = 3.4 mg/m^2) and the river channel (3.3 mg/m^2). Benthic chlorophyll *a* concentrations were consistently lower compared to water-column chlorophyll *a* concentrations (Figure 3.1).

Water-column respiration (R) was similar among habitats (whedo average = 63 mg C/m^3/d, natural floodplain depression value = 45 mg C/m^3/d, river channel value = 71 mg C/m^3/d, Figure 3.2). Benthic R was greater in magnitude than water-column R, and differed among habitats (whedo average = 211 mg C/m^2/d, natural floodplain depression value = 164 mg C/m^2/d, river channel value = 344 mg C/m^2/d). 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 lowest values occurring in whedos (river channel value = 73 C/m^3/d, natural floodplain depression value = 8 C/m^3/d, whedo average = -27 C/m^3/d). Benthic NPP was highest in the natural floodplain depression (746 C/m^2/d). Benthic NPP was negligible in the river channel (-2 C/m^2/d), probably because the course inorganic sediments and low abundance of benthic algae. Benthic NPP was negative in the whedos (average = -120 C/m^2/d). Negative total NPP (water column + benthic) in the whedos indicated that these habitats were strongly heterotrophic.

Stable isotope analysis

A total of 398 consumer (whedos = 296, floodplain = 33, main channel = 69) and 138 plant (whedos = 98, floodplain = 25, main channel = 15) samples was analyzed for stable isotope ratios. Consumer specimens representing 15 fish species and five species of macroinvertebrate were collected from whedos, 13 fish species and 4 species of macroinvertebrate were collected from the natural floodplain depression, and 33 fish species and 1 species of macroinvertebrate were collected from the river channel. All whedos contained the species *Ctenopoma petherici*, *Parachanna obscura*, *Polypterus senegalus senegalus* and *Clarias agboyiensis*, and most whedos contained *Brienomyrus niger* (91%), *Clarias gariepinus* (64%) and *Erpetoichthys calibaricus* (55%).

Table 3.1. Chlorophyll *a* and nutrient concentrations in habitats in habitats of the Oueme River and floodplain measured in January 2010. Benthic chl*a* = benthic chlorophyll a, Water column chl*a* = water column chlorophyll a, SRP = soluble reactive phosphorus, DIN = dissolved inorganic nitrogen (sum of NH_4^+, NO_2^-, and NO_3^-), and Floodplain = natural floodplain depression.

Habitat	Benthic chl*a* (mg/m^2)	Water column chl*a* (mg/m^3)	SRP (mg/L)	DIN (mg/L)
Whedo 1	3.0	28.5	0.5	0.6
Whedo 2	0.4	8.0	0.3	0.3
Whedo 3	6.3	54.3	1.9	0.3
Whedo 4	1.6	11.6	2.4	0.4
Whedo 5	1.6	20.5	0.5	0.3
Whedo 6	8.2	13.4	0.8	0.8
Whedo 7	6.8	18.7	2.7	0.7
Whedo 8	1.6	13.4	4.0	0.5
Whedo 9	2.2	0.9	1.2	0.8
Whedo 10	2.5	8.9	0.5	0.4
Whedo 11	3.5	4.5	1.4	1.0
Floodplain	5.4	25.8	1.7	0.2
Main Channel	3.3	11.6	0.5	0.3

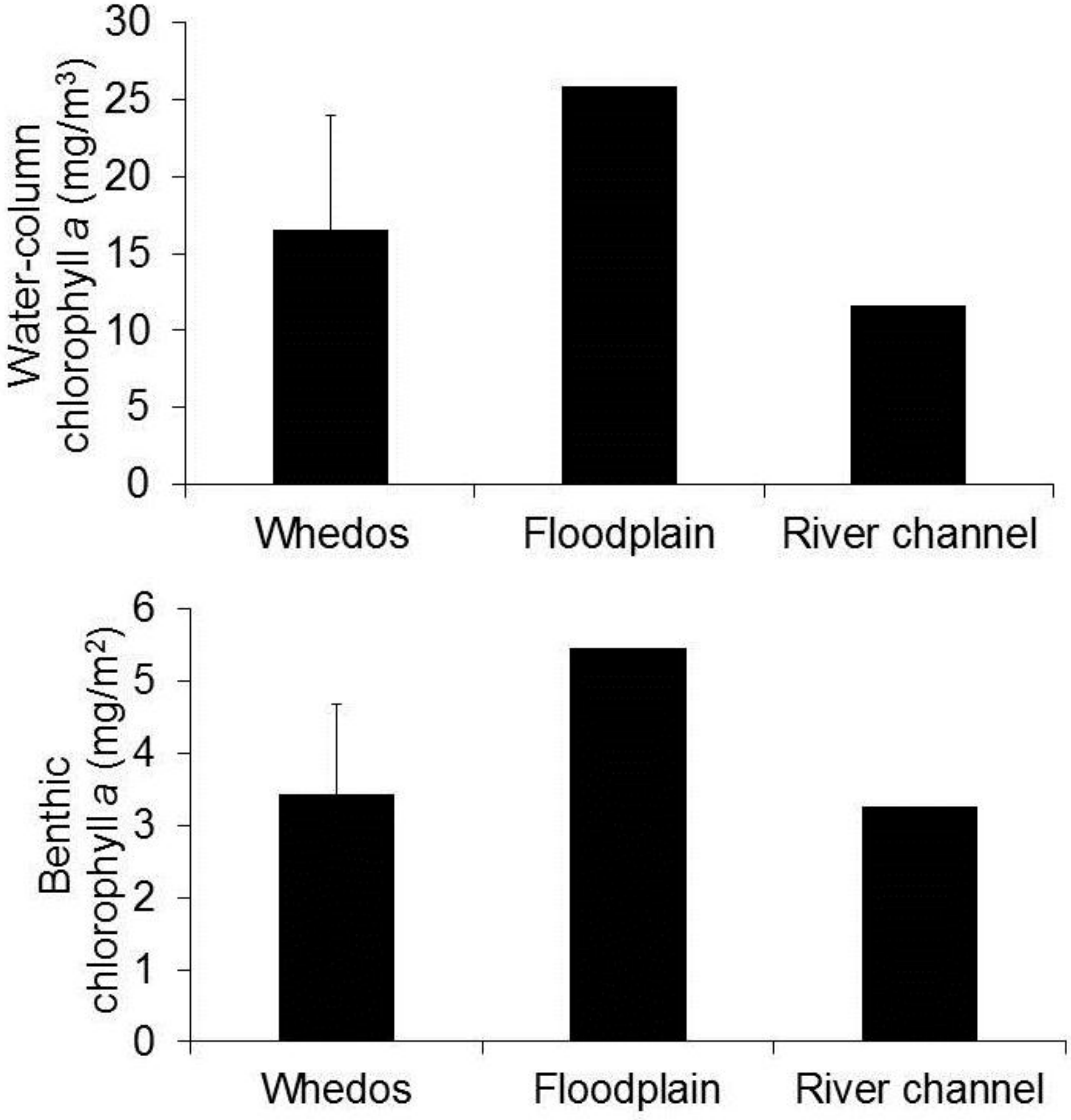
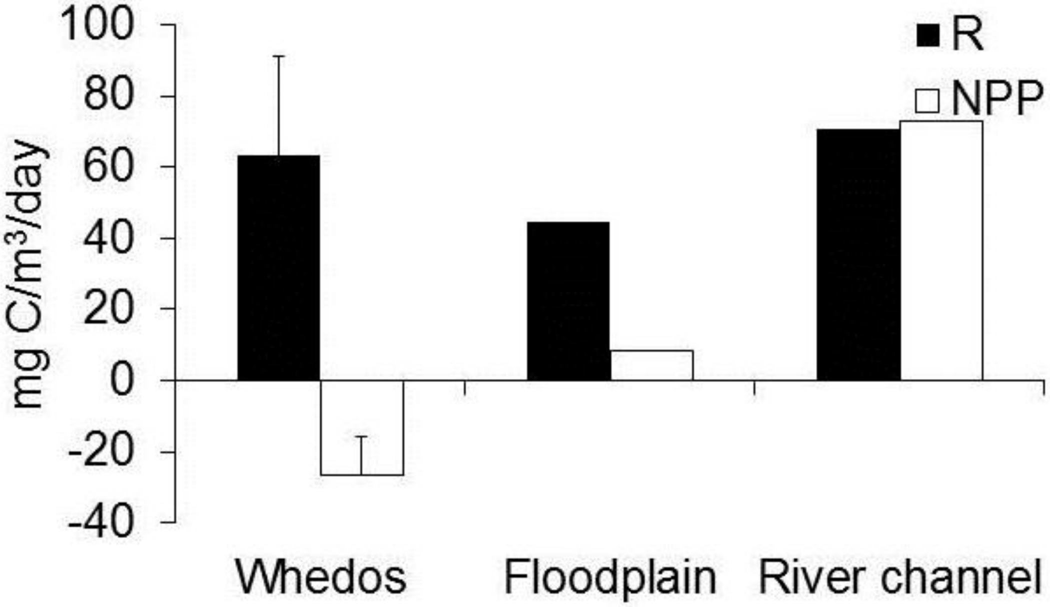


Figure 3.1. Water column and benthic chlorophyll *a* collected from whedo, natural floodplain depression (floodplain), and river channel habitats.



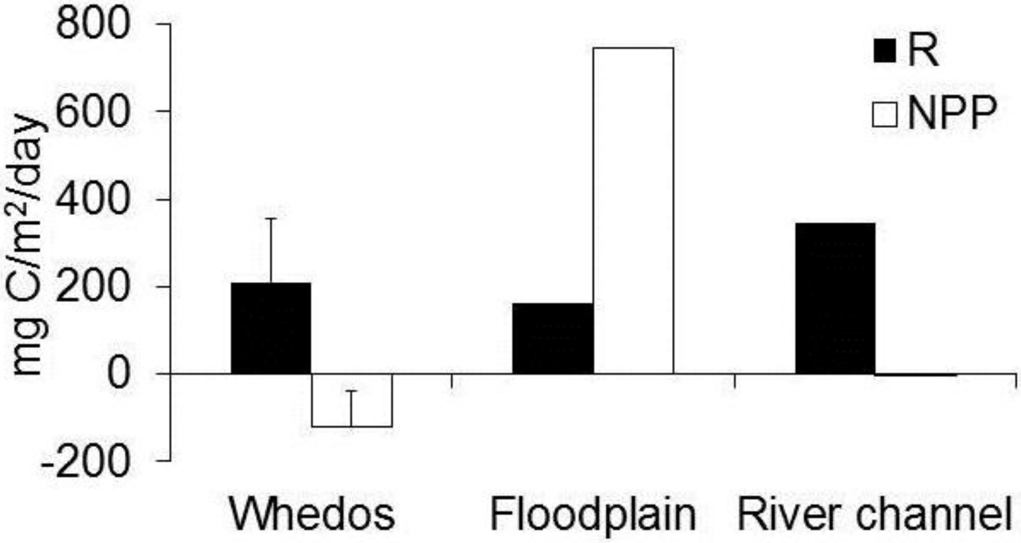


Figure 3.2. Respiration (R) and net primary production (NPP) of the water-column (top figure) and benthos (bottom figure) in whedo, natural floodplain depression (floodplain), and main channel habitats.

Macrophyte biomass on the floodplain was dominated by the species *Leersia hexandra*, *Polygonum salicifolium*, *Ipomea aquatic*, and *Aeschynomene afraspera*. 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 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 bi-plots shows that consumer δ^{13}C signatures generally lie between those of microphytobenthos, C_3 macrophytes, and C_4 grasses in most floodplain habitats, indicating that all of these basal production sources could contribute to consumer biomass (Figure 3.3). 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. Coleopteran beetles had a more depleted δ^{15}N signature than the producers in floodplain habitats, indicating that one or more primary production sources on which they feed might not have been sampled. In general, the plots revealed a consistent pattern for the 11 whedos in which consumer signatures were tightly clumped and positioned above microphytobenthos and C_3 macrophytes.

MixSIR model estimates indicated that both C_3 macrophytes and microphytobenthos accounted for a large fraction of consumer biomass in whedos (Appendix 1). Both of these production sources had high 95% confidence percentiles (Figure 3.4). For C_3 macrophytes, 53% of species from whedos had 95% confidence percentiles ≥ 65. For microphytobenthos, 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 (Figure 3.4). In whedos, C_4 grasses had 5% confidence percentiles ≥ 25 for 10% of consumer species, indicating its importance in supporting biomass of at least some species. In the natural floodplain depression, C_3 macrophytes seemed to be important contributors to

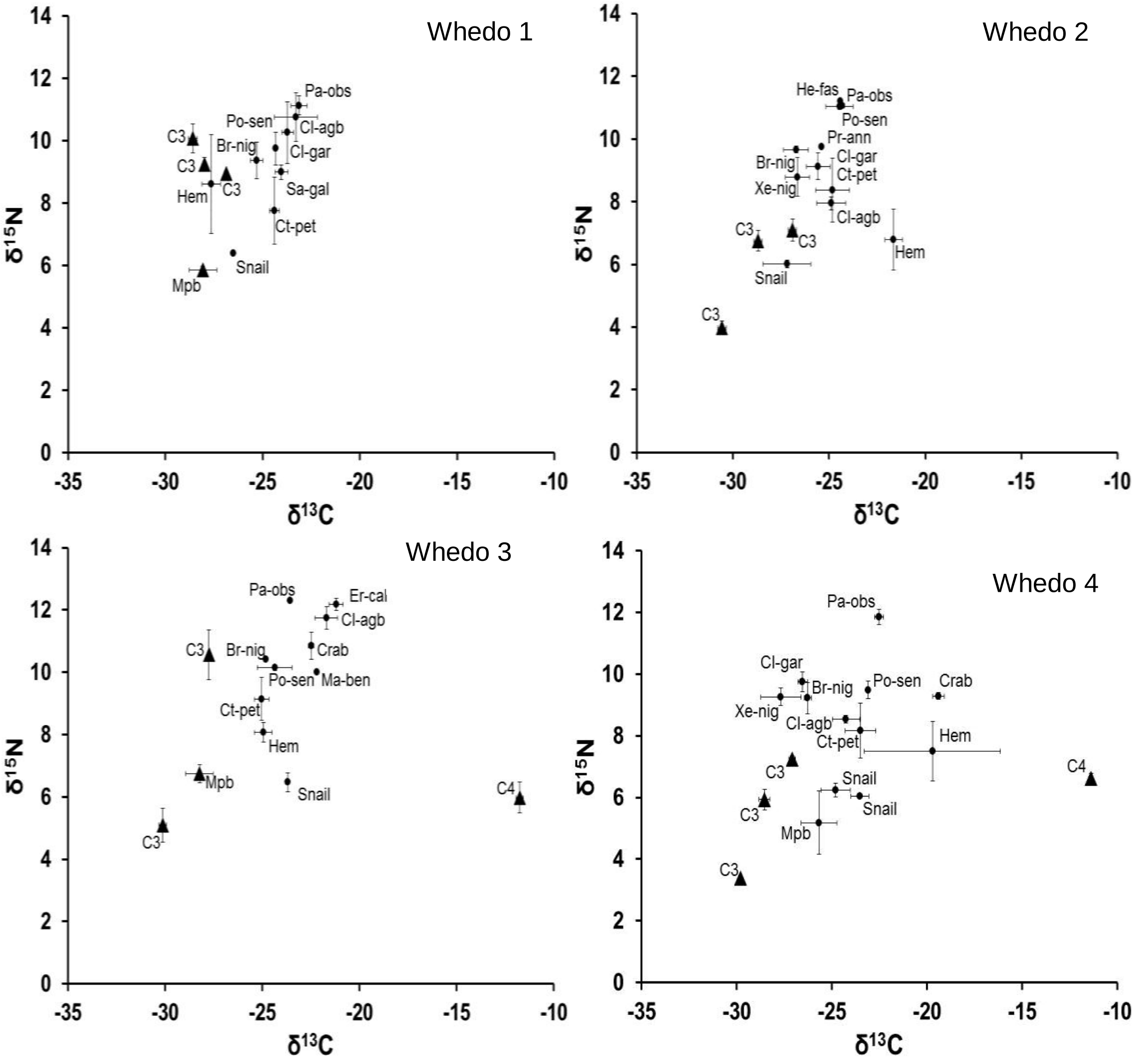


Figure 3.3. Carbon and nitrogen isotope ratio biplots of the mean values of primary producers (triangles) and consumers (circles) taken from whedos, a natural floodplain depression (Floodplain), and the Oueme River channel. Common species of consumer are labeled: Br-nig = *Brienomyrus niger,* Cl-agb = *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-afr = *Parachana africana*, Pa-obs = *Parachana obscura,* Po-sen = *Polypterus senegalus*, Pr-ann = *Protopterus annectens*, and Xe-nig = *Xenomystus nigri*. Production sources type from each site is labeled: C3= C$_3$ macrophyte, C$_4$ = C$_4$ grass, Mpb = microphytobenthos.

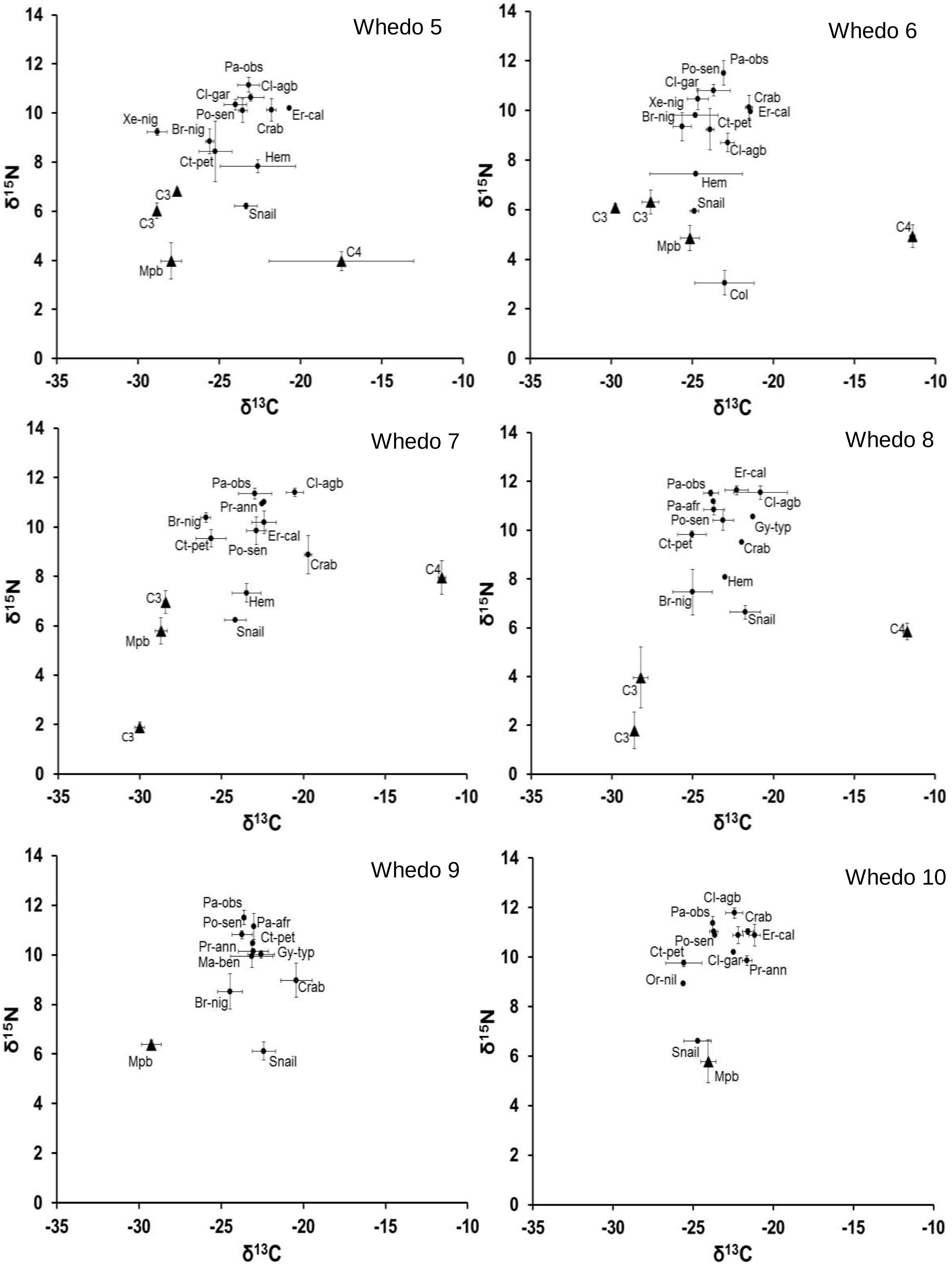


Figure 3.3. Continued.

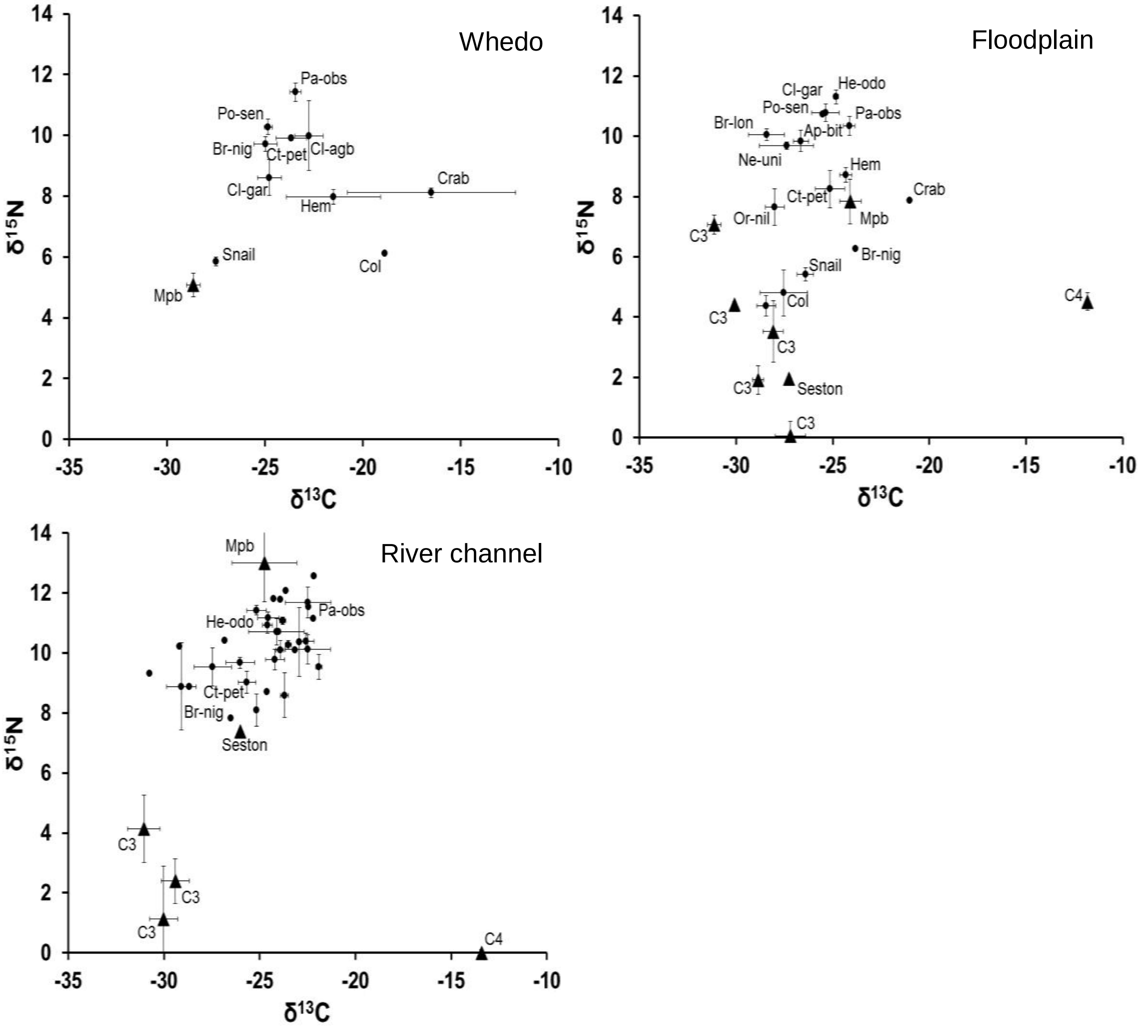


Figure 3.3. Continued.

consumer biomass, with 71% of species having 95% confidence percentiles ≥ 65 for these sources. Microphytobenthos and seston also seem 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 seem to contribute the largest fractions to consumer biomass, with 59% of species having a 95% confidence percentile > 50 for these sources, respectively. Microphytobenthos had 95% confidence percentiles ≥ 50 for only 9% of species, and all species had a 95% confidence percentiles ≤ 50 for terrestrial C_4 grasses, indicating minor contributions to consumers.

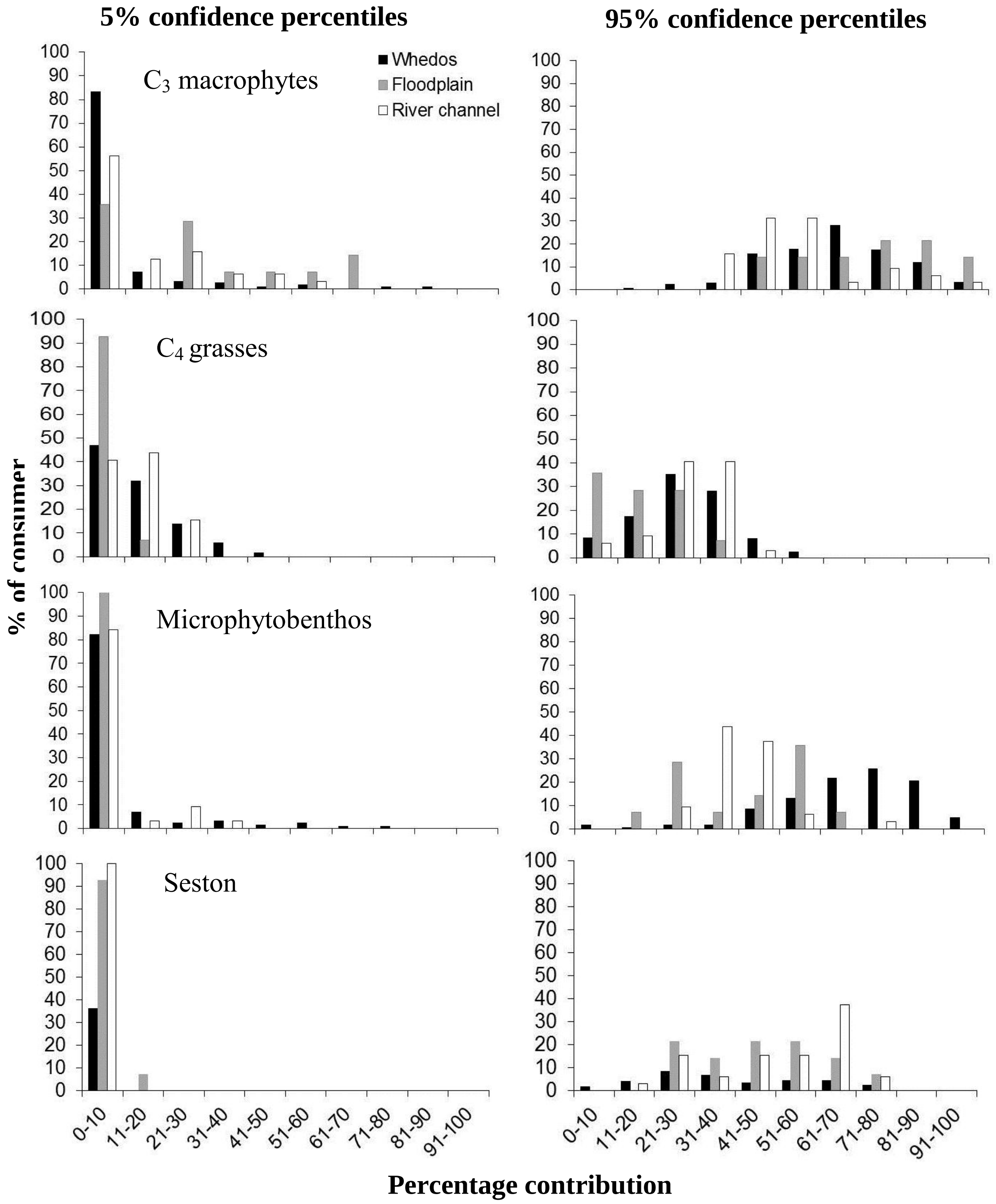


Figure 3.4. Frequency histograms of 5% and 95% confidence percentiles of basal production sources contributions to fish biomass for whedo, natural floodplain depression (floodplain), and river channel habitats.

Trophic position estimates

Qualitative interpretation of stable isotope signature bi-plots indicates relatively consistent trophic structure among the whedos, with conspecifics from different sites occupying 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*) 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 (Figure 3.5). For *Ctenopoma petherici* mean trophic position was similar in whedos and 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 (Figure 3.5). Trophic position distributions of fish assemblages were similar between habitats. The distribution of trophic positions in the river channel had a higher mean and seemed to be more left skewed compared to distributions for floodplain habitats (river channel mean =3.1, whedo mean = 2.69, natural floodplain depression mean = 2.49, Figure 3.6). 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 to the natural floodplain depression. These findings indicate that fish assemblages of whedos had higher relative abundance of piscivores than natural floodplain depression.

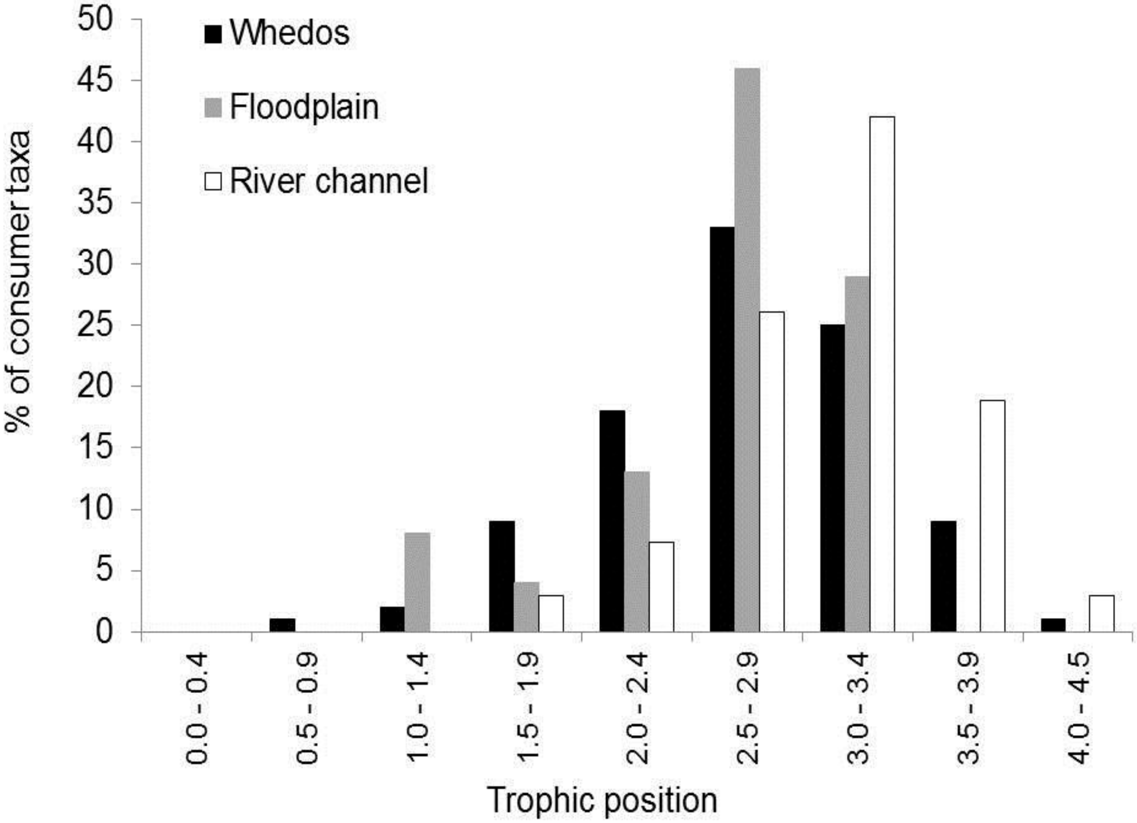


Figure 3.5. Mean trophic positions of three fish species based on samples from whedo, natural floodplain depression (floodplain), and river channel habitats.

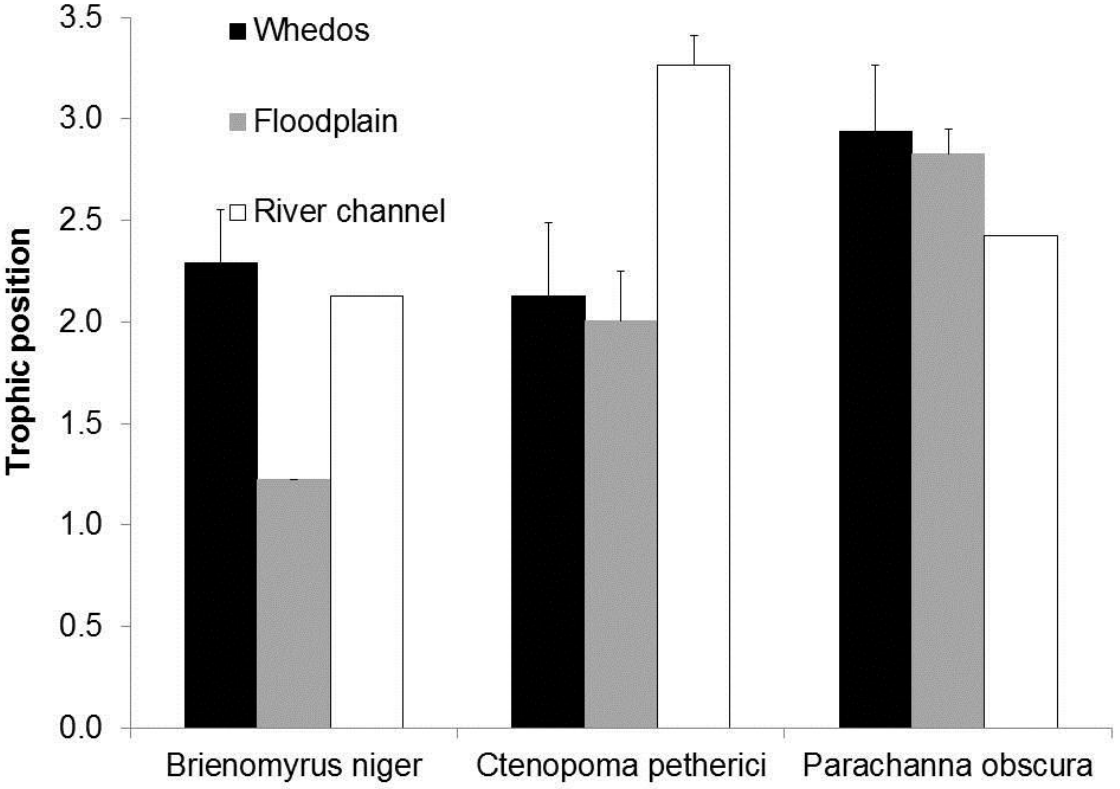


Figure 3.6. Distributions of trophic position values for fish assemblages inhabiting whedo, natural floodplain depression (floodplain), and river channel habitats.

DISCUSSION

MixSIR 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 microphytobenthos probably was an important basal production source supporting invertebrates and fishes in habitats of the Oueme River and floodplain. Consumer assimilation estimates for seston were high in the river channel, and it was low in whedos. Whedo habitats were covered by dense layers of aquatic macrophytes (average coverage 94%), that hindered algal production by shading. Though NPP in whedos was negative, indicating heterotrophy, periphyton (microphytobenthos) was collected from macrophyte leaves and roots near the water surface. Fishes inhabiting lentic floodplain habitats were largely supported by microphytobenthos and seston in addition to C_3 macrophytes. 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 Oueme River-floodplain ecosystem.

These results are in accord 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 et al. 1998, Bunn et al. 2003, Herwig et al. 2004). For example, Bunn et al. (2003) found that in turbid water holes in the Cooper Creek floodplain of Australia, microphytobenthos, 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, studies have stressed the low importance of C_4 grass as a food resource for metazoan consumers, probably due to its refractory nature (e.g., Thorp and Delong 1998, Herwig et al. 2004, Clapcott and Bunn 2003, Zeug and Winemiller 2008). For example, in oxbow lakes of the Brazos River, Texas, material derived from C_3 macrophytes from the riparian zone was estimated to constitute a large fraction of fish biomass, and C_4 grasses were of relatively little importance (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).

Although DIN concentrations were higher in whedos compared to the natural floodplain depression and river channel, and SRP concentrations in natural floodplain depression and river channel habitats were 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 ($P/R > 1$). Whereas whedos were net heterotrophic, concentrations of chlorophyll *a* in whedos indicate that algae were present. Overall, ecosystem metabolism in whedos was 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 were less than the level of a primary producer. 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 for some species. Another potential source of error would be if one or more important production source 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. Therefore, the likelihood is low that systematic bias skewed the major findings.

Average trophic position of floodplain fishes was lower compared to positions of fishes from the river channel sample. This conclusion is based on the comparison of frequency histograms of trophic positions estimated for fish assemblages from the various habitats. This finding is consistent with studies that have documented longer food chains in aquatic ecosystems supported largely by seston (phytoplankton) compared to those supported mostly by microphytobenthos (periphyton) and macrophytes (detritus) (e.g. Layman et al. 2005, Hoeinghaus et al. 2008). Mean fish trophic position tended to be high in whedos, and the majority (87%) of fishes captured in these habitats are clearly identified as piscivores. Whedo fish assemblages had a highly consistent composition (Chapter 2), probably because high fish densities and hypoxic conditions (resulting from aquatic macrophytes covering the surface of shrinking aquatic habitats) select for predatory fishes that possess adaptations for aerial respiration. After the onset of hypoxia, these apex predators dominated the species assemblages of whedos (Chapter 2).

Findings from whedos are consistent with studies that have documented high percentages of predatory fishes in isolated floodplain habitats (e.g. Lowe-McConnell 1964, Winemiller 1990, Montaña et al. 2011). For example, Montaña et al. (2011) found that in the floodplains of three rivers in Venezuela, fish assemblages became dominated by piscivores as aquatic habitats were reduced during the dry season and local populations of herbivorous and invertivorous fishes were reduced by predation. In a small forest stream in Costa Rica, following desiccation of surrounding floodplain habitats, aquatic organisms became more crowded and were preyed upon by predatory fishes, so that assemblages were dominated by predatory fish at the end of the dry season (Winemiller 1990).

The Flood Pulse Concept predicts that, during floods, fishes colonize productive aquatic habitats of floodplains, consume food resources derived from terrestrial plants, 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 Oueme 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 (i.e. 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 Oueme 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 probably limit fishery production in whedos: restriction of algal production by shading, and hypoxia caused by decomposition and respiration of aquatic macrophytes that only allows fish species having adaptations for aerial respiration to persist (Chapter 2). Because nutrient concentrations are relatively high in whedo habitats, control of aquatic macrophyte growth in whedos would presumably yield greater algal production and consumer biomass that includes harvestable fish stocks.

CHAPTER IV

GENERAL CONCLUSIONS

This thesis investigated fish assemblage and food web structure of whedos on the Oueme River floodplain in order to test conceptual models of metacommunity dynamics and food webs, and to explore the potential to increase the yield of whedos. Because significant correlations existed between aspects of assemblage structure and physicochemical parameters, our results indicate that fish assemblage and food web structure of whedos are strongly influenced by deterministic ecological processes. Fish assemblage structure and environmental characteristics were highly consistent among whedos. These findings suggest treatments resulting in higher yield during experimental manipulation could likely be applied to all whedos of the lower Oueme River floodplain with similar results.

Chapter II documented that whedo habitats were marked by conditions of low dissolved oxygen caused by high densities of aquatic macrophytes. Also, fish assemblages in whedos were dominated by piscivorous fishes that can tolerate conditions of aquatic hypoxia. These fishes were a small subset of the approximately 116 fish species known from the Oueme River Basin. Although it is likely that a more diverse assemblage of fishes colonize whedos during floodplain inundation (Welcomme 1979), by the time I sampled, all fishes that lack accessory respiratory adaptations and that were vulnerable to piscivores apparently had been eliminated.

Chapter III documented that whedo fish assemblages were strongly supported by algae (microphytobenthos) and C_3 plants, and C_4 grasses were not an important basal production source. Despite relatively high nutrient concentrations in whedos, water column and benthic net primary production were negative, indicating that dense coverage of aquatic macrophytes limits algal production in whedos through shading. Algae are a highly nutritious and labile basal production source that is important to fish biomass. I therefore suggest that an increase of algal biomass in whedos may translate into higher production of fish biomass.

The results obtained from my thesis research imply that control of aquatic macrophyte growth is a viable option for management of whedo fisheries. Reduction of macrophyte biomass would presumably allow for higher DO concentrations in whedos, which would in turn allow for more diverse local fish assemblages that contain species lacking special respiratory adaptations. These fishes enter whedos during flood pulses, but supplemental stocking during the low-water period also might enhance production. Hauber et al. (2011b) reported that some whedos in the Niger River floodplain in northern Benin were stocked with juvenile fishes captured from the floodplain. The most commonly socked species were *Clarias* spp., tilapine cichlids, and *Heterotis niloticus*. Some whedos received supplemental food (e.g., bran from rice, millet, maize and sorghum, kitchen waste, bone meal) on an irregular basis. It is unclear whether or not these management practices significantly enhanced fishery yields (Hauber et al. 2011b). *Clarias* spp. constituted 72% of the whedo catch overall, and this species normally is smoked and dried for preservation. Hauber et al. (2011a) suggested that harvesting whedos in the Niger floodplain earlier might increase the abundance and diversity of harvestable fishes. Supplemental feeding and early harvest could enhance whedo production, especially if nets are used with large enough mesh size to allow fingerlings to escape (Hauber et al. 2011b). I suggest that control of aquatic macrophytes would allow for more sunlight penetration in whedos presumably leading to increased algal production, which could support more productive and diverse fish assemblages and larger harvestable stocks.

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APPENDIX 1

Appendix 1. Means and 5-95th confidence percentiles (in parentheses) of estimated contributions of basal production sources to fish biomass in whedos, a natural floodplain depression, and the Oueme River channel from MixSIR models. Sample sizes for consumers are in parentheses next to species names.

Site	Taxa	C_3 plant	C_4 grass	Microphytobenthos	Seston
Whedo 1	*Brienomyrus niger* (3)	25 (4-62)	16 (11-21)	59 (23-81)	0 (0-0)
	Clarias agboyiensis (3)	16 (2-43)	23 (18-28)	61 (34-76)	0 (0-0)
	Clarias gariepinus (3)	25 (3-65)	21 (16-26)	54 (14-76)	0 (0-0)
	Ctenopoma petherici (3)	25 (3-68)	20 (14-24)	55 (13-77)	0 (0-0)
	Parachanna obscura (3)	21 (3-52)	30 (25-34)	49 (19-68)	0 (0-0)
	Polypterus senegalus (3)	31 (5-66)	20 (15-25)	49 (15-75)	0 (0-0)
	Sarotherodon galilaeus (2)	27 (4-65)	24 (18-30)	49 (12-73)	0 (0-0)
	Crab (2)	23 (3-47)	49 (44-53)	29 (4-49)	0 (0-0)
	Snail 1 (1)	37 (4-85)	7 (1-16)	55 (9-86)	0 (0-0)
	Hemiptera (2)	11 (1-34)	2 (<1-5)	87 (64-97)	0 (0-0)
Whedo 2	*Brienomyrus niger* (3)	50 (12-83)	7 (1-14)	43 (8-82)	0 (0-0)
	Clarias agboyiensis (3)	39 (7-73)	18 (10-25)	43 (7-78)	0 (0-0)
	Clarias gariepinus (3)	45 (9-80)	10 (3-17)	46 (7-83)	0 (0-0)
	Ctenopoma petherici (3)	37 (4-77)	15 (6-22)	48 (5-84)	0 (0-0)
	Hemichromis fasciatus (1)	38 (5-73)	22 (8-32)	40 (5-78)	0 (0-0)
	Parachanna obscura (2)	37 (5-71)	22 (12-29)	41 (6-77)	0 (0-0)
	Polypterus senegalus (2)	41 (8-71)	21 (11-28)	38 (6-75)	0 (0-0)
	Protopterus annectens (1)	44 (6-81)	13 (2-24)	43 (5-83)	0 (0-0)
	Xenomystus nigri (2)	49 (9-84)	8 (1-16)	43 (6-84)	0 (0-0)
	Snail 1 (2)	44 (5-89)	4 (<1-12)	52 (4-90)	0 (0-0)
	Hemiptera (2)	67 (6-95)	2 (<1-7)	31 (2-91)	0 (0-0)
Whedo 3	*Brienomyrus niger* (1)	27 (3-60)	12 (2-24)	33 (4-66)	25 (3-55)
	Clarias agboyiensis (3)	12 (1-54)	27 (18-33)	47 (4-64)	12 (1-32)
	Ctenopoma petherici (3)	26 (3-59)	10 (2-19)	40 (6-68)	23 (3-46)
	Erpetoichthys calabaricus (2)	17 (1-48)	32 (23-39)	34 (3-55)	15 (2-38)
	Malapterurus beninensis (1)	24 (3-56)	15 (2-27)	29 (3-62)	27 (3-61)
	Parachanna obscura (1)	22 (3-53)	18 (4-31)	26 (3-58)	28 (3-67)
	Polypterus senegalus (3)	9 (1-62)	17 (8-24)	61 (6-75)	11 (1-30)
	Crab(3)	20 (3-42)	25 (14-34)	25 (4-49)	29 (5-58)
	Snail 1 (3)	23 (4-47)	13 (2-24)	29 (5-56)	34 (6-62)
	Hemiptera (3)	30 (4-67)	5 (<1-12)	50 (10-78)	15 (2-30)

Appendix 1 cont'd.

Site	Taxa	C_3 plant	C_4 grass	Microphytobenthos	Seston
Whedo 4	*Brienomyrus niger* (3)	61 (28-84)	8 (1-14)	31 (5-68)	0 (0-0)
	Clarias agboyiensis (3)	39 (8-72)	17 (7-23)	45 (6-80)	0 (0-0)
	Clarias gariepinus (3)	70 (36-90)	4 (<1-9)	27 (4-62)	0 (0-0)
	Ctenopoma petherici (3)	22 (3-62)	16 (6-24)	63 (16-87)	0 (0-0)
	Parachanna obscura (3)	43 (13-63)	30 (23-35)	28 (4-62)	0 (0-0)
	Polypterus senegalus (3)	48 (17-68)	25 (17-30)	28 (4-64)	0 (0-0)
	Xenomystus nigri (3)	68 (10-95)	2 (<1-6)	31 (2-88)	0 (0-0)
	Crab (2)	26 (4-47)	46 (38-51)	29 (3-55)	0 (0-0)
	Snail 1 (3)	36 (7-76)	9 (2-17)	56 (9-87)	0 (0-0)
	Snail 2 (2)	46 (10-73)	18 (7-25)	37 (5-78)	0 (0-0)
	Hemiptera (2)	8 (1-27)	2 (<1-6)	90 (72-98)	0 (0-0)
Whedo 5	*Brienomyrus niger (3)*	43 (8-71)	9 (1-17)	27 (3-61)	20 (2-42)
	Clarias agboyiensis (3)	37 (5-62)	21 (12-29)	24 (3-56)	16 (2-40)
	Clarias gariepinus (3)	33 (3-67)	20 (12-27)	37 (4-68)	9 (1-28)
	Ctenopoma petherici (3)	10 (1-49)	11 (3-18)	70 (32-84)	7 (1-24)
	Erpetoichthys calabaricus (1)	19 (2-48)	30 (16-49)	15 (1-46)	26 (2-68)
	Parachanna obscura (3)	34 (5-58)	27 (18-36)	21 (2-53)	15 (1-39)
	Polypterus senegalus (3)	33 (5-58)	17 (7-28)	19 (2-49)	30 (4-59)
	Xenomystus nigri (3)	14 (1-41)	1 (<1-4)	81 (55-94)	2 (<1-9)
	Crab (3)	19 (2-47)	25 (12-38)	11 (1-37)	41 (5-77)
	Snail 1 (3)	36 (4-62)	23 (15-31)	27 (3-59)	13 (1-34)
	Hemiptera (3)	28 (3-86)	1 (<1-5)	66 (10-90)	3 (<1-11)
Whedo 6	*Brienomyrus niger* (3)	53 (17-80)	10 (2-19)	36 (4-80)	0 (0-0)
	Clarias agboyiensis (2)	39 (7-65)	24 (14-33)	36 (5-77)	0 (0-0)
	Clarias gariepinus (3)	54 (12-79)	11 (2-20)	34 (4-84)	0 (0-0)
	Ctenopoma petherici (3)	45 (11-72)	15 (5-24)	40 (6-82)	0 (0-0)
	Erpetoichthys calabaricus (1)	36 (4-64)	26 (14-36)	38 (4-78)	0 (0-0)
	Parachanna obscura (2)	39 (7-64)	25 (15-33)	36 (5-76)	0 (0-0)
	Polypterus senegalus (3)	57 (2-75)	19 (4-28)	22 (1-92)	0 (0-0)
	Xenomystus nigri (3)	72 (3-83)	16 (1-23)	10 (1-94)	0 (0-0)
	Crab (3)	36 (8-58)	32 (24-39)	32 (5-67)	0 (0-0)
	Snail 1 (3)	49 (17-76)	11 (3-20)	39 (7-79)	0 (0-0)
	Coleoptera (2)	85 (69-94)	8 (1-15)	6 (1-26)	0 (0-0)
	Hemiptera (3)	97 (90-99)	1 (<1-3)	3 (<1-9)	0 (0-0)
Whedo 7	*Brienomyrus niger* (3)	31 (4-70)	17 (14-20)	52 (12-80)	0 (0-0)
	Clarias agboyiensis (3)	34 (2-60)	36 (34-39)	30 (3-62)	0 (0-0)
	Ctenopoma petherici (3)	75 (4-83)	18 (14-22)	7 (1-80)	0 (0-0)
	Erpetoichthys calabaricus (3)	52 (2-66)	33 (30-36)	15 (1-66)	0 (0-0)
	Parachanna obscura (3)	63 (55-67)	34 (31-38)	2 (<1-11)	0 (0-0)
	Polypterus senegalus (3)	56 (2-67)	32 (29-36)	11 (1-67)	0 (0-0)
	Protopterus annectens (1)	32 (4-65)	29 (24-34)	38 (5-68)	0 (0-0)
	Crab (3)	27 (3-50)	45 (43-48)	28 (4-53)	0 (0-0)
	Snail 1 (3)	39 (3-71)	25 (22-28)	36 (4-74)	0 (0-0)
	Hemiptera (2)	50 (3-85)	11 (7-16)	38 (3-87)	0 (0-0)

Appendix 1 cont'd.

Site	Taxa	C_3 plant	C_4 grass	Microphytobenthos	Seston
Whedo 8	*Brienomyrus niger* (3)	10 (1-27)	16 (5-23)	75 (57-89)	0 (0-0)
	Clarias agboyiensis (3)	4 (<1-13)	30 (21-37)	65 (55-76)	0 (0-0)
	Ctenopoma petherici (3)	15 (2-36)	15 (6-22)	70 (48-87)	0 (0-0)
	Erpetoichthys calabaricus (3)	15 (2-35)	28 (20-34)	57 (36-73)	0 (0-0)
	Gymnallabes typus (1)	25 (3-53)	41 (29-47)	35 (4-63)	0 (0-0)
	Parachanna africana (2)	20 (2-47)	25 (15-32)	55 (27-77)	0 (0-0)
	Parachanna obscura (3)	23 (3-49)	24 (16-30)	53 (26-76)	0 (0-0)
	Polypterus senegalus (3)	14 (2-34)	27 (19-33)	59 (38-75)	0 (0-0)
	Crab (2)	32 (5-58)	37 (29-41)	32 (4-62)	0 (0-0)
	Snail 1 (3)	9 (1-24)	31 (23-37)	60 (45-73)	0 (0-0)
	Hemiptera (1)	38 (4-78)	14 (3-22)	49 (6-85)	0 (0-0)
Whedo 9	*Brienomyrus niger* (3)	17 (1-68)	23 (17-28)	49 (2-69)	8 (1-25)
	Ctenopoma petherici (3)	10 (1-63)	31 (26-36)	50 (2-63)	6 (1-19)
	Gymnallabes typus (2)	22 (2-55)	31 (24-37)	32 (3-55)	13 (1-35)
	Malapterurus beninensis (2)	20 (1-64)	27 (20-33)	42 (2-63)	9 (1-27)
	Parachanna africana (2)	17 (2-46)	24 (13-34)	18 (2-47)	35 (4-75)
	Parachanna obscura (3)	18 (2-44)	21 (12-30)	21 (3-46)	36 (5-69)
	Polypterus senegalus (3)	19 (1-61)	26 (19-31)	42 (3-63)	11 (1-30)
	Protopterus annectens (1)	32 (3-70)	7 (1-16)	38 (5-71)	21 (2-47)
	Crab (2)	20 (1-49)	42 (36-47)	27 (2-49)	8 (1-27)
	Snail 1 (3)	8 (1-67)	28 (22-33)	55 (1-67)	5 (<1-19)
Whedo 10	*Clarias agboyiensis* (3)	43 (9-71)	13 (2-25)	44 (5-88)	0 (0-0)
	Clarias gariepinus (1)	33 (4-61)	24 (11-36)	43 (5-82)	0 (0-0)
	Ctenopoma petherici (3)	76 (49-85)	13 (4-20)	10 (1-47)	0 (0-0)
	Erpetoichthys calabaricus (2)	32 (4-58)	27 (15-38)	41 (5-79)	0 (0-0)
	Oreochromis niloticus (1)	57 (24-82)	8 (1-19)	35 (4-74)	0 (0-0)
	Parachanna obscura (3)	38 (10-65)	16 (5-26)	46 (10-83)	0 (0-0)
	Polypterus senegalus (3)	39 (10-66)	16 (4-26)	46 (9-84)	0 (0-0)
	Protopterus annectens (3)	38 (9-65)	17 (6-27)	46 (9-84)	0 (0-0)
	Crab (3)	33 (5-58)	26 (15-36)	41 (6-79)	0 (0-0)
	Snail 1 (3)	59 (31-80)	9 (1-18)	32 (4-67)	0 (0-0)
Whedo 11	*Brienomyrus niger* (3)	53 (14-71)	17 (8-23)	14 (1-59)	12 (1-37)
	Clarias agboyiensis (3)	54 (30-67)	29 (18-31)	8 (1-36)	9 (1-29)
	Clarias gariepinus (3)	52 (12-72)	15 (6-21)	15 (1-61)	13 (1-39)
	Ctenopoma petherici (3)	57 (40-69)	25 (18-30)	7 (1-27)	8 (1-26)
	Parachanna obscura (3)	27 (3-52)	23 (14-30)	27 (3-56)	21 (2-48)
	Polypterus senegalus (3)	23 (3-51)	11 (2-20)	33 (7-60)	32 (4-58)
	Crab (2)	68 (59-76)	24 (18-29)	3 (<1-10)	4 (<1-13)
	Snail 1 (3)	41 (5-81)	1 (<1-4)	53 (11-89)	4 (<1-11)
	Coleoptera (1)	19 (2-49)	25 (10-36)	20 (2-50)	29 (3-74)
	Hemiptera (3)	88 (75-96)	1 (<1-3)	8 (1-21)	2 (<1-8)

Appendix 1 cont'd.

Site	Taxa	C_3 plant	C_4 grass	Microphytobenthos	Seston
Floodplain	*Aphyosemion bitaeniatum* (3)	47 (26-71)	5 (1-12)	20 (3-41)	27 (4-51)
	Brienomyrus niger (1)	23 (2-55)	19 (8-28)	25 (3-64)	27 (3-60)
	Brycinus longipinnis (3)	77 (61-91)	2 (<1-7)	7 (1-21)	10 (1-30)
	Clarias gariepinus (1)	31 (4-66)	7 (1-17)	23 (3-53)	35 (4-73)
	Ctenopoma petherici (3)	54 (23-72)	14 (3-22)	18 (2-58)	11 (1-29)
	Hepsetus odoe (3)	19 (2-47)	13 (6-19)	25 (4-49)	42 (12-64)
	Neolabias unifasciatus (2)	72 (54-88)	4 (<1-11)	10 (1-29)	10 (1-31)
	Oreochromis niloticus (2)	62 (40-84)	3 (<1-9)	10 (1-29)	21 (2-50)
	Parachanna obscurav (3)	29 (4-54)	18 (9-25)	27 (4-55)	26 (4-47)
	Polypterus senegalus (3)	53 (26-72)	13 (2-21)	19 (2-55)	12 (1-31)
	Crab (1)	19 (2-47)	30 (19-38)	22 (3-59)	23 (2-52)
	Snail 1 (3)	44 (42-69)	3 (<1-10)	16 (2-36)	35 (6-62)
	Coleoptera (2)	82 (67-93)	2 (<1-7)	5 (<1-19)	7 (1-25)
	Hemiptera (3)	60 (41-81)	3 (<1-9)	12 (1-30)	22 (3-48)
River Channel	*Bagrus docmak* (1)	28 (5-53)	21 (10-32)	16 (2-45)	30 (3-69)
	Brienomyrus niger (1)	54 (29-74)	13 (3-24)	10 (1-32)	18 (2-55)
	Brycinus macrolepidotus (2)	15 (2-34)	33 (26-40)	15 (3-36)	36 (6-58)
	Brycinus nurse (1)	33 (7-59)	17 (6-28)	16 (1-44)	29 (3-72)
	Chromidotilapia guntheri (3)	19 (4-33)	32 (23-39)	38 (27-53)	9 (1-28)
	Chrysichthys aluuensis (1)	46 (20-71)	8 (1-20)	14 (1-43)	25 (2-63)
	Chrysichthys ogooensis (2)	21 (4-41)	27 (21-35)	14 (2-38)	36 (4-65)
	Ctenopoma petherici (3)	43 (26-60)	15 (8-22)	13 (2-31)	28 (4-54)
	Distichodus rostratus (2)	72 (54-87)	3 (<1-10)	10 (1-31)	11 (1-31)
	Eleotris senegalensis (2)	22 (5-42)	26 (19-34)	14 (2-35)	37 (6-64)
	Hemichromis fasciatus (3)	40 (24-56)	18 (11-25)	18 (4-35)	23 (3-46)
	Hepsetus odoe (3)	32 (15-50)	20 (14-27)	13 (2-30)	35 (6-60)
	Heterobranchus longifilis (3)	26 (4-51)	23 (12-34)	18 (2-46)	28 (2-67)
	Hydrocynus vittatus (3)	37 (21-53)	21 (14-28)	19 (5-36)	22 (3-45)
	Hyperopisus bebe (3)	36 (19-51)	23 (16-30)	22 (8-38)	19 (2-42)
	Labeo brachypoma (1)	62 (36-83)	4 (<1-14)	13 (1-42)	15 (1-41)
	Macrobrachium sp. (3)	23 (8-41)	24 (18-30)	11 (2-28)	42 (10-64)
	Mastacembelus praensis (1)	19 (2-42)	30 (18-40)	19 (2-48)	27 (3-61)
	Mormyrops anguilloides (1)	21 (3-45)	27 (16-38)	19 (2-46)	28 (3-63)
	Mormyrus rume (3)	25 (8-42)	25 (19-32)	13 (2-31)	37 (6-61)
	Parachanna obscura (1)	18 (2-40)	32 (20-42)	20 (3-48)	26 (3-59)
	Pellonula leonensis (1)	32 (8-54)	16 (8-25)	10 (1-32)	39 (5-79)
	Pollimyrus isidori (3)	22 (6-36)	30 (21-37)	37 (26-52)	9 (1-28)
	Polypterus endlicheri (1)	25 (4-50)	23 (12-34)	18 (2-47)	29 (3-68)
	Sarotherodon galilaeus (3)	62 (45-78)	6 (1-14)	19 (3-38)	10 (1-29)
	Sarotherodon melanotheron (2)	32 (7-52)	12 (2-23)	48 (31-71)	6 (<1-22)
	Schilbe intermedius (3)	28 (11-47)	20 (14-27)	10 (1-28)	41 (8-66)
	Synodontis schall (6)	36 (25-46)	21 (15-27)	38 (29-48)	4 (<1-15)
	Tilapia cessiana (3)	48 (33-65)	14 (6-21)	20 (4-38)	16 (2-38)
	Tilapia guineensis (3)	20 (5-36)	32 (25-38)	23 (11-39)	24 (3-47)
	Tilapia mariae (1)	76 (42-91)	2 (<1-9)	10 (1-46)	8 (1-24)
	Crab (1)	27 (4-52)	21 (10-33)	17 (2-47)	29 (3-69)