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Louca, Vasilis (2009) *The ecology of fishes and mosquitoes of the lower Gambia River floodplains*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/2082/

The ecology of fishes and mosquitoes of the lower Gambia River floodplains

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Submitted for the degree of Doctor of Philosophy

February 2009

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Abstract

This study investigated aspects of the ecology of fishes and mosquitoes using floodplains in the lower reaches of the Gambia River, a semi-arid river system. The Gambia River, situated at the edge of the Sahel, represents one of the few remaining major river systems not to have been impacted by any impoundments. It was hypothesised that seasonal variations in physical variables particularly related to the pattern of flooding and drying influence fish species distribution; the presence of some of these species probably also influencing mosquito larvae distribution.

Fish and mosquito larvae were sampled along two lateral transects on the floodplain in The Gambia, from May to November 2005 – 2007. Water conductivity, pH and water depth all influenced fish species richness and bolongs (creeks) held greater species richness compared with other floodplain habitats, probably because they acted as conduits for fish moving on and off the floodplain. Species richness and catch biomass increased rapidly following the first rains and then declined. The Guinean tilapia, *Tilapia guineensis*, was the dominant species on the floodplains and its catches were positively associated with higher levels of conductivity and dissolved oxygen, shallower water and less vegetation cover. The Guinean tilapia is primarily an iliophage and the catches varied seasonally. Controlled experiments using *T. guineensis* in tanks with shallow water barriers showed that fish density plays a significant role in triggering fish emigration, whereas a lack of food available caused an increase in exploratory behaviour but with no impact on successful emigration.

The influence of fish on the distribution of mosquito larvae on the floodplains was investigated. Semi-field trials were used to test two possible mechanisms for this influence: direct predation and oviposition avoidance due to the presence of fish chemical cues. The presence of *T. guineensis* decreased the chance of finding culicine larvae in the field possibly due to culicine mosquito avoiding ovipositing in habitats with fish present as fewer culicines oviposited in experimental tanks with fish, suggesting that ovipositing culicine females avoid water with fish. In contrast, oviposition by anophelines was unaffected by fish. Both fish species tested, *T. guineensis* and a common insectivore, *Epiplatys spilargyreius* were effective predators removing all late-stage culicine and anopheline larvae.

In order to determine the relationships between mosquito distribution and the physical environment in an urban setting, mosquitoes were collected and environmental physical parameters were measured in and around Farafenni town, located at the edge of the foodplains in The Gambia. Levels of reactive phosphorus, distance from the nearest house, turbidity, amount of vegetation cover and the presence of algae all influenced the occurence of mosquito larvae collected in and around Farafenni town. *Anopheles arabiensis* was found closer to houses than *Anopheles gambiae* sensu stricto and the presence of algae was a strong indicator of the presence of anopheline larvae in general. Sites dominated by anophelines had higher turbidity levels compared to sites in which culicines dominated. Production of pupae was associated with high levels of reactive phosphorus concentrations.

The results are discussed in the context of world climate change, anthropogenic impacts on large rivers and increased urbanisation.

Acknowledgements

This thesis is the product of the contribution of a number of people. Special thanks go to my supervisors, Martyn Lucas and Steve Lindsay, who put faith in me and have trusted me with this project.

I would like to thank the Medical Research Council (MRC) in The Gambia for their support, particularly the staff based at the Farafenni MRC station where most of this work was carried out. The following people have participated and helped with the work: Musa Drammeh, Bambo Jawo, Tomarin Jadama, Biran Salleh, Ousman Bah, Abdoulie Bojang, Lamin Sanyang, Ousman Njie and Lamin Camara. Many thanks to Pierre Gomez for the provision of the rainfall data.

This work would not have been possible if it was not for the support of a number of my colleagues and friends: Margaret Pinder, Clare Green, Matt Kirby, Ann Kelly, Chloe Day, Erin Dilger, Silas Majambere, Rob Hutchinson, Balla Kandeh, Heleen Sombroek, Lamin Jarju and Mbye Njie.

Finally, many thanks for Chantima Piyapong and my family, as well as for my uncle Polys, who provided me with endless support and encouragement during the whole duration of my studies.

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Declarations

The material included in this thesis has not been previously submitted for a degree at the University of Durham or any other university. The study was funded by the National Institutes of Health (grant number: 1 VO1 AI058250-01) and in part by award of the Freshwater Biological Association Hugh Cary Gilson Memorial Award in 2005. The contributions of other people are listed below:

Chapter 1: General introduction: Vasilis Louca (VL) was responsible for writing the review.

Chapter 2: Fish community characteristics of the lower Gambia River floodplains

VL, Martyn Lucas (ML) and Steve Lindsay (SL) designed the study and VL implemented the field work assisted by two local assistants, Musa Drammeh (MD) and Biran Salleh (BS). Pierre Gomez (PG) provided the rainfall data and Silas Majambere (SM) the data of the floodplain flooding pattern. Chapter 2 was published in a modified format:

Louca, V., Lindsay, S. W., Majambere, S. & Lucas, M. C. (2009). Fish community characteristics of the lower Gambia River floodplains: a study in the last major undisturbed West African river. *Freshwater Biology* **54:** 254-271

Chapter 3: Habitat associations, reproduction and diet in the Guinean tilapia, *Tilapia guineensis*, on the floodplains of the Gambia River.

VL, ML and SL designed the study and VL implemented the field work assisted by MD and BS. Chantima Piyapong (CP) assisted with the identification of fish species. Chapter 3 was submitted in a modified format to the Journal of Fish Biology and is currently in revision.

Chapter 4: Factors triggering emigration of Guinean tilapia: Importance of fish density and food availability

VL, ML and SL designed the study and VL implemented the experimental work. Chapter 4 was published in a modified format:

Louca, V., Lindsay, S. W. & Lucas, M. C. (2009). Factors triggering floodplain fish emigration: Importance of fish density and food availability. *Ecology of Freshwater Fish* **18**: 60-64

Chapter 5: Role of fish as predators of mosquito larvae on the floodplains of the Gambia River.

VL, ML and SL designed the study and VL implemented the field work assisted by MD and BS. Clare Green (CG) carried out the PCR work on the mosquito larvae.

Chapter 5 has been accepted for publication in the Journal of Medical Entomology and is currently in press in a modified format.

Louca, V., Lucas, M. C., Green, C., Majambere, S., Fillinger, U. & Lindsay, S. W. (2009). Role of fish as predators of mosquito larvae on the floodplain of the Gambia River. *Journal of Medical Entomology* **In Press**

Chapter 6: Chemical and biological characteristics of malaria breeding sites in an urban town and surrounding area in The Gambia.

VL, ML, SL and Margaret Pinder (MP) designed the study and VL implemented the field work assisted by MD. Clare Green (CG) carried out the PCR work on the mosquito larvae.

Chapter 7: General conclusion.

Written by VL

Ethical approval

Ethical approval for this study was given by the Joint Gambian Government and Medical Research Council's Laboratories in The Gambia, Durham University and the NIH.

Verbal consent was obtained from the local Farafenni and surrounding villages' leaders, as well as from the Gambian Fisheries Department.

Chapter 1

General introduction

1.1 Floodplain ecology

The first theoretical models on river ecology and function were developed with a focus on the longitudinal processes of rivers. These models suggest that rivers present a continuous gradient of physical conditions from the headwaters to the mouth of the river, causing a number of responses from the resident biota including fish, which adapt to conform to the conditions presented at the particular stage of the river reach in which they live. This results in a consistent pattern of loading, transport and utilization of nutrients along the length of the river. This came to be known as the River Continuum Concept (RCC) (Vannote *et al.*, 1980). This model restricted itself solely to the longitudinal dimension of stream channels and was limited to lotic river habitats that are permanently submerged.

In the same way that these longitudinal responses take place, Junk *et al.* (1989) suggested that in large, unmodified river-floodplain systems, which are subject to predictable, annual flooding, similar lateral changes in physical, chemical and biological processes occur and named this the Flood Pulse Concept. Floodplains are distinguished from other aquatic systems by the distinct wet and dry phases (Welcomme, 1979), and Junk *et al.*, (1989) defines floodplains as: "areas that are periodically inundated by the lateral overflow of rivers or lakes, and/or by direct precipitation or groundwater; the resulting physiochemical environment causes the biota to respond by morphological, anatomical, physiological, phenological, and/or ethological adaptations, and produce characteristic community structures". During flooding, nutrients previously mineralised during the dry season are dissolved in the floodwater. High primary production and decomposition occur (assuming that day-length and temperature are not low) with production surpassing decomposition at the beginning of the rainy season, the opposite taking place during receding waters at the end of the rainy and beginning of the dry season. This nutrient recycling within the floodplain, triggered by the seasonal flooding, is considered to be the main driving force of ecological processes on floodplains (Junk *et al.*, 1989; Bayley, 1995).

Floodplain inundation occurs through direct local rainfall and overspill from the main river channel (Welcomme, 1979). Welcomme & Halls (Welcomme & Halls, 2001) described a number of important measurable parameters which describe a flood event (Fig. 1.1). These include the amplitude, duration and timing of flooding and can vary between river systems as well as along different stretches of the same river.

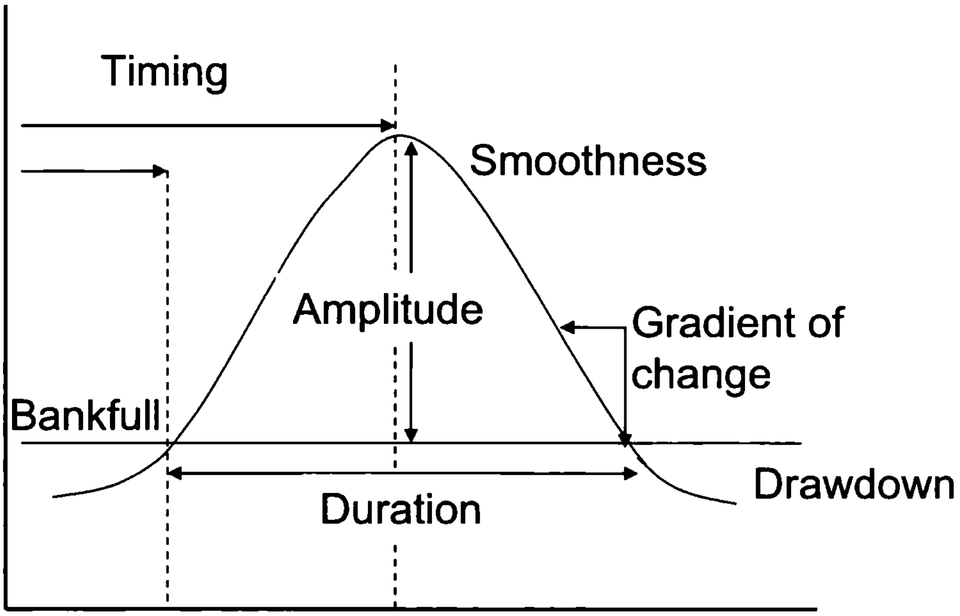


Figure 1.1 Flood parameters of biological significance. Adapted from Welcomme & Halls (2001)

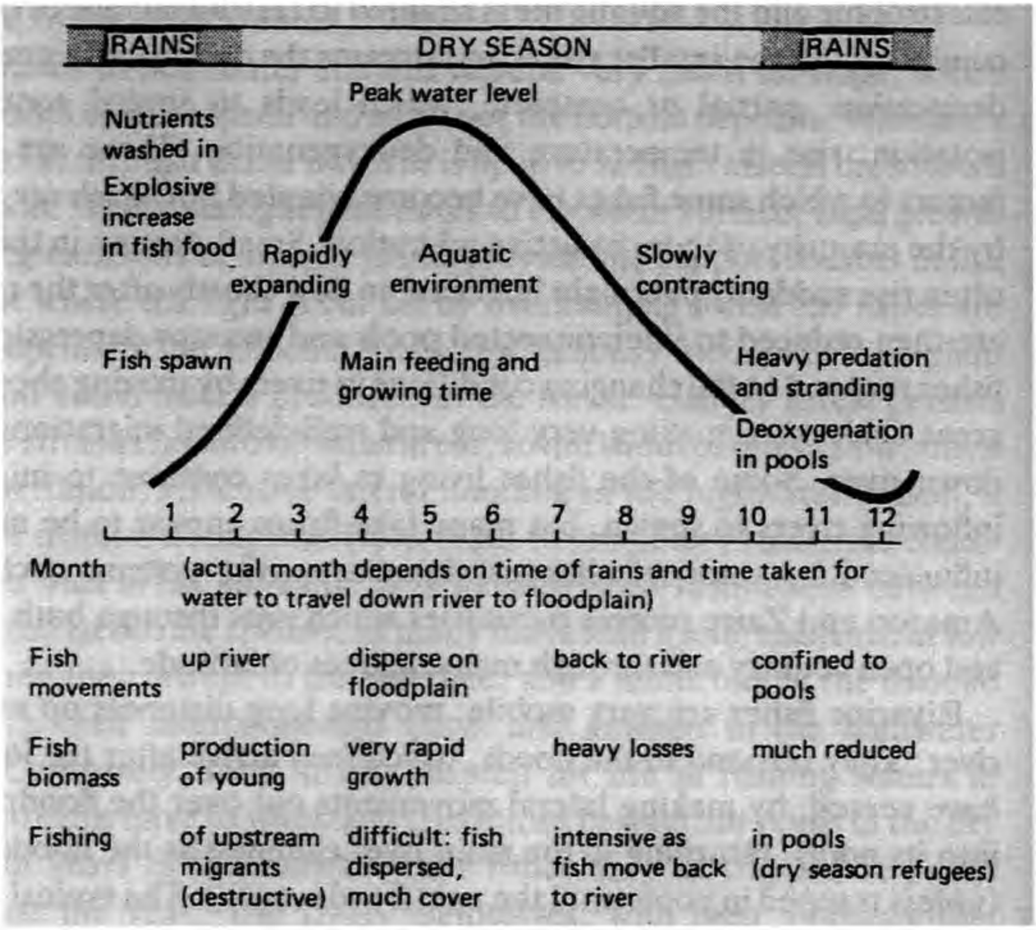
In areas with distinct rainy seasons, flooding can show a clear seasonal pattern, whereas in floodplains bordering the lower reaches of a river with substantial tidal input, the flooding may not only vary seasonally with the rainy season, but can also vary according to the tidal pattern (Welcomme, 1979). In some cases floodplains are inundated due to local rainfall as is the case with the seasonally flooded Argentinean Pampa grasslands (Perelman *et al.*, 2001).

Rivers may be classified into three categories depending on their hydrology; (1) temperate rivers with aseasonal flood pulses, (2) temperate with seasonal flood pulses and (3) tropical with seasonal flood pulses (Winemiller, 2004). Within the tropical group with seasonal flood pulses, a wide range of river-floodplain systems are encountered, which vary greatly in their ecology and hydrology depending on the local climatic conditions (Welcomme, 1979).

Floodplain habitats in temperate floodplains can include side channels, irrigation canals, floodplain lakes, pools, ponds, inundated alluvial grasslands and marshes (Poizat & Crivelli, 1997; King *et al.*, 2003). In tropical systems, floodplain habitats include flooded alluvial plains, floodplain creeks, mangrove swamps and reed beds (Giglioli & Thornton, 1965; Laroche *et al.*, 1997; Vidy *et al.*, 2004; Majambere *et al.*, 2008), floodplain lakes and seasonally flooded varzea forests (Petry *et al.*, 2003), floodplain pools and ponds (Benech *et al.*, 1992), flooded Amazonian meadows and gallery forests (Junk, 1983; Correa *et al.*, 2008) and nutrient-poor grasslands (Cotner *et al.*, 2006).

1.2 Floodplain ecology and fishes

Seasonal flooding of rivers can have a number of immediate effects on the fish that inhabit river drainage systems, the effects varying depending on the species of fish involved, the habitat complexity of the river and floodplains, the frequency and strength of the floods and the time of year (Lowe-McConnell, 1975; Welcomme, 1979; Mathews, 1998). In general this seasonal flooding modifies food availability as well as physical suitability of the habitat with fish species responding accordingly (Lowe-McConnell, 1975; Balcombe *et al.*, 2005). The seasonal cycle of events in tropical floodplains where floods coincide with conditions suitable for growth and reproduction have been summarised by Lowe-McConnell (1987) (Fig. 1.2).



Fish movements	up river	disperse on floodplain	back to river	confined to pools
Fish biomass	production of young	very rapid growth	heavy losses	much reduced
Fishing	of upstream migrants (destructive)	difficult: fish dispersed, much cover	intensive as fish move back to river	in pools (dry season refugees)

Figure 1.2 Seasonal variation in hydrological features in floodplain rivers and the consequent effects on fish populations. From Lowe-McConnell (1987).

During initial flooding at the beginning of the rainy season rapid decomposition of plant and animal material which has accumulated on the floodplain during the dry season leads to a massive influx of nutrients, which in turns helps the growth of bacteria, algae as well as macrophytes. These in turn support large numbers of invertebrates and overall leads to a large increase in available food for the fish, which migrate onto the floodplains to take advantage of these conditions. Following the decline of available food and the decrease in the levels of dissolved oxygen after the flood peak, fish migrate back to the main river channel or get trapped in isolated floodplain waterbodies (Lowe-McConnell, 1987; Leveque, 2005).

Similar responses to seasonal changes in the type and quantity of food available on the floodplains are observed between differing semi-arid floodplain systems. Tropical fish in the Rio Apure drainage basin, a tropical savannah environment in Venezuela, were dependent on algae and detritus as the main food items available during the peak of the dry season, but switched their diet to primarily aquatic invertebrates in the wet season (Prejs & Prejs, 1987). Similarly, in the arid Cooper Creek floodplain river in Australia, species diet was dominated by detritus and copepods during the dry season, but expanded significantly to include a range of aquatic and terrestrial invertebrates as well as other fish in the flood period (Balcombe *et al.*, 2005). This seasonal variation in food availability also has the effect of altering species interactions as the degree of diet overlap between species can vary greatly between the dry and wet seasons (Prejs & Prejs, 1987; Jepsen, 1997).

The predictable seasonal flooding of many floodplains has allowed fish to adapt and take advantage of the relatively abundant resources and seasonally available habitat for reproduction (Agostinho *et al.*, 2001; Paugy, 2002; Adite *et al.*, 2006) as floodplains can provide safe habitats with reduced predatory pressure for juvenile fish and are therefore extensively used as nursery habitats (Benech & Penaz, 1995; Carvalho de Lima & Araujo-Lima, 2004; Vidy *et al.*, 2004). In this way seasonal flooding also influences seasonal fish movement, this varying by species and floodplain system depending on the specific conditions (Lowe-McConnell, 1975; Chen *et al.*, 1983; Cucherousset *et al.*, 2007a; Cucherousset *et al.*, 2007b; Makrakis *et al.*, 2007). Moreover, river flooding has the effect of altering the habitat both in the main channel and on the floodplains, by altering the substrate through hydraulic sediment-transport processes, in ways that influence the spawning and feeding behaviour of certain species of fish (Berkman & Rabeni, 1987; Mathews, 1998). Flooding also has an effect on the algae and macrophytes both negatively, by washing out plants during peak flows, and positively, by inducing an influx of nutrients that helps their growth. Since algae can be a major carbon source in semi-arid floodplains as well as providing habitat structure for invertebrates and fish, it can have a direct influence on fish communities (Welcomme, 1979; Lewis *et al.*, 2000; Bunn *et al.*, 2003).

Floods have the effect of increasing water turbidity, which can interfere with sight-feeding fish (Junk, 1983; Mathews, 1998; Petry *et al.*, 2003). Moses (1987) and (2001) found that the annual catch of fish in the Cross River, Nigeria, was strongly correlated with the flooding of the previous year and the degree to which fish utilized allochthonous material in their diet. A similar pattern was observed in Cooper Creek, Australia, an arid floodplain system with seasonal flooding in which the catches of fish on the floodplain were highly correlated with the extent of floodplain inundation the previous year, as this determined the interconnectedness between the different floodplain habitats (Arthington *et al.*, 2005).

Water physical parameters tend to be extremely variable on floodplains, varying between habitat types, locations and stage of the rainy season. In the Amazon floodplain systems, white-waters, which originate in the Andes, can be fairly nutrient rich, turbid and have a pH of close to neutral. On the other hand, black-waters that arise in the central Amazonian lowlands are extremely nutrient poor, contain high levels of humic compounds and can be very acidic (pH 3.8-4.9) (Junk *et al.*, 1989). Due to these profound differences in the water chemistry between these two water types, as well as differences in topography and zonation, the fish communities are markedly different (Saint-Paul *et al.*, 2000; Hoeinghaus *et al.*, 2003). In the same way as with the Amazon blackwaters, large expanses of the Congo River basin floodplains are covered by black-waters with very low pH ranges (pH 3.5 to 5.2), are nutrient poor and exhibit low conductivities of 10 to 140 μS cm^{-1} (Laraque *et al.*, 1998). The water pH can also reach extremely low values, as low as pH 2) in tidal floodplains dominated by acid sulphate soils, as these soils generate sulphuric acid which leaks into the floodwater, this being common in tidal swamps and brackish lakes (Dent & Pons, 1995). In these cases pH values tend to be lower on floodplains compared to the main river channels (Welcomme, 1979). Acid sulphate soils are common in tide-dominated estuary floodplains in Australia (Lin *et al.*, 1995) and acid waters have been shown to present barriers to fish in accessing important floodplain nursery habitats (Kroon, 2005). Acid sulphate soils are known to be common on the Gambia River floodplains (Giglioli & Thornton, 1965; Webb, 1992) and this results in floodwaters with lower pH values compared to the corresponding water from the main river channel (Johnels, 1954).

Water conductivity can also vary between aquatic habitats and dry and wet seasons. Overall, conductivity tends to be higher in the dry season and lower in the wet season; the dilution of solutes due to the increased input of freshwater during the rainy season has been proposed as the main reason for these differences (Welcomme, 1979). However in tidal reaches of rivers, local effects of salt ingress and water evaporation may be more important. Differences in conductivity between aquatic habitats can be an important determinant of fish communities (Rodriguez & Lewis, 1997; Petry *et al.*, 2003). Dissolved oxygen (DO) can vary between habitats depending on the habitat size and amounts of photosynthesis and decomposition taking place, but more importantly DO tends to vary during the dry and rainy seasons (Welcomme, 1979). During the dry season, flooded areas become increasingly warmer and more isolated, leading to decreasing dissolved oxygen levels, which tend to force the fish to return to the main channel or more permanent floodplain habitats (Lucas & Baras, 2001). In the Amazon floodplain the species composition varies diurnally in hypoxic conditions as migrations between macrophyte stands occur as fish utilize the small amounts of oxygen entering the water by exudation from plant roots. Such conditions have a strong influence on the distribution, survival and susceptibility to predatory fish (Junk, 1983). The ability of fish to survive under severe hypoxic conditions is one of the driving factors determining the fish communities of the Sudd floodplains of the River Nile, with seasonal floodplains dominated by *Clarias*, *Polypterus*, *Heterotis* and *Channa* species, all with air breathing abilities (Springuel & Ali, 2005). Similar patterns are observed in the Murray-Darling floodplains of Australia as all floodplain-utilising species show high tolerance to hypoxia (McNeil & Closs, 2007).

1.3 Importance of wetland habitats in malaria transmission

Arthropods are responsible for the transmission of some of the most serious human diseases, including malaria, dengue, yellow fever and onchocerciasis. Malaria, caused by *Plasmodium* protozoans and transmitted by mosquitoes belonging to the *Anopheles* group, is one of the leading infectious diseases, responsible for over 2 million deaths every year (Gardiner *et al.*, 2005; Greenwood *et al.*, 2005; Grabowsky, 2008), and substantial economic burden to countries already stricken by poverty (Breman, 2001; Sachs & Malaney, 2002).

Mosquitoes belonging to the *Anopheles gambiae* sensu lato complex are considered to be the most important malaria vectors in sub-Saharan Africa (SSA). This species group consists of seven species: *An. gambiae* sensu stricto, *An. arabiensis*, *An. merus*, *An. bwambae*, *An. melas*, *An. quadriannulatus* and *An. quadriannulatus* B (Gilles & DeMeillon, 1968; Hunt *et al.*, 1998). The conventional wisdom is that mosquitoes belonging to the *An. gambiae* sl complex prefer to breed in shallow, open sun-lit pools usually associated with man-made aquatic habitats such as water storage tanks, drains, brick pits, hoof prints and tracks. In this way *An. gambiae* sl is regarded as a pioneer species in colonising newly flooded aquatic habitats and this was considered to be an adaptation against aquatic predators (Gilles & DeMeillon, 1968). Moreover, *An. gambiae* sl was always known to breed in aquatic habitats modified by humans for cultivation. Goma (1960) reported that the Papyrus swamps in Uganda were naturally free of *An. gambiae* but were colonised as soon as they were cleared and cultivated. In the same way, rice fields have always been known to be very important breeding sites for *An. gambiae* (Grainger, 1947; Gilles & DeMeillon, 1968). The importance of rice fields in the production of adult *An. gambiae* is now very well established (Lindsay *et al.*, 1995; Klinkenberg *et al.*, 2003; Diuk-Wasser *et al.*, 2004; Dolo *et al.*, 2004), but recent detailed studies investigating the factors that characterise mosquito breeding sites reveal that this species complex exhibits a very wide range of adaptations to a variety of environmental conditions; in Mbita, Kenya, *An. gambiae* sl has been observed to proliferate in both natural and man-made habitats and be equally abundant in recently flooded as well as well-established mature aquatic habitats (Fillinger *et al.*, 2004). Moreover, it is known to breed in unpolluted, natural floodplain habitats (Bøgh *et al.*, 2003; Majambere *et al.*, 2008), but is also known to be extremely abundant in polluted urban habitats (Robert *et al.*, 1998; Awolola *et al.*, 2007). Other habitat variables identified as being important for *An. gambiae* sl include the presence of algae (Rejmankova *et al.*, 1996; Minakawa *et al.*, 1999), vegetation cover (Stoops *et al.*, 2007), temperature (Bayoh & Lindsay, 2004; Munga *et al.*, 2006b) and distance to houses (Minakawa *et al.*, 1999; Mutuku *et al.*, 2006).

The association between wetlands and mosquitoes has long been known (Celli, 1933). Historically, one of the most important tools responsible for eradication of malaria from large parts of the world was environmental management, which included the draining of wetlands

(Gramiccia, 1964). Recently, the importance and benefits of wetlands as valuable habitats for a number of endangered species, their role in flood control and nutrient retention and cycling, as well as water purification has become increasingly appreciated (Moore *et al.*, 1989; Chapman *et al.*, 1996; Sheldon *et al.*, 2002; Van der Valk, 2006). This appreciation for wetlands has resulted in a recent interest in rehabilitating wetlands, mainly in temperate regions (Zedler & Callaway, 1999; Wan *et al.*, 2001). Wetland recreation, though, has raised issues with possible problems due to the creation of favourable mosquito breeding habitats (Russell, 1999; Willott, 2004), especially now that several vector borne diseases, such as malaria in Asia and dengue and yellow fever throughout the tropics, are on the increase (Gubler, 1998). Considering the harmful effects of traditional measures for controlling mosquito breeding in wetlands such as the use of Dichloro-Diphenyl-Trichloroethane (DDT) (Albanis *et al.*, 1995; Peters *et al.*, 2001) Organophosphates (OPs) (Pain *et al.*, 2004; Sereda & Meinhardt, 2005) and arsenic-based chemicals (Soper & Wilson, 1943), with persistent effects on the environment or on non-target species, as well as considering health risks associated with their use, interest in less environmentally harmful ways of controlling mosquito larvae has surfaced (WHO, 2003a). The World Health Organization (WHO) recommends the use of fish for controlling mosquitoes as an effective, sustainable, environmentally friendly (provided native species are used) and cheaper method of controlling mosquito larvae (WHO, 2003b; a). Fish have been used in the past as an important tool for the eradication of malaria from large parts of the world (Tabibzadeh *et al.*, 1970; Hadjinicolaou & Betzios, 1973; Sitaraman *et al.*, 1975), but after the introduction of DDT in the 1940s its use was reduced (Gabaldon, 1969). However, increased concern over pesticide impacts has resulted in a resurgence in the use of fishes for mosquito control.

Another one of these more environmentally friendly tools for controlling mosquito larvae has been the use of *Bacillus thuringiensis* var. *israeliensis* (Bti) and *Bacillus sphaericus* (Bs). These bacteria produce spores in water that release toxins which, when ingested by mosquito larvae (Culicidae) or black fly larvae (Simuliidae), are activated by the alkaline conditions encountered in the midgut of these invertebrate groups and cause their death (Charles, 1987; Karch & Charles, 1987). This relative specificity and effectiveness of these bacterial larvicides has spurred a recent interest in their large-scale use for controlling mosquito larvae (Skovmand & Sanogo, 1999; Fillinger *et al.*, 2003; Majambere *et al.*, 2007).

It is becoming increasingly apparent that a clear understanding of the ecology of floodplains, associations of floodplain species including fish and mosquitoes with the characteristic conditions encountered on floodplains and their responses to the seasonal changes as well as the identification and testing of possible, more environmental friendly mosquito control measures and the subsequent possible impacts of these control measures on the fish communities is of extreme importance.

1.4 The Gambia River: habitats, fish communities and malarial mosquitoes in the lower catchment

The Gambia River has a catchment area of 78,000 km^2 and originates in the Fouta Djalon plateau of Guinea. It flows 1,200 km through Senegal and The Gambia. Its floodplain borders the river channel along the lower 670 km, with the last 200 km being fringed by mangrove forest. The alluvial floodplains flood through rain runoff during the rainy season from the upland areas fringing the floodplains, water flooding over the banks of the river and creeks (locally known as bolongs) that directly connect the floodplain to the main river channel (Johnels, 1954; Lesack *et* *al.*, 1984). Tidal input on the floodplains can be considerable in the lower reaches of the river closer to the river mouth (Lesack, 1986), whereas direct input from local rainfall is more important further upstream with some floodplain habitats being completely rainfed (Svensson, 1933) (Fig. 1.3).

Roberts (1975) identified three main ichthyofaunal provinces in west and central Africa: the Nilo-Sudan province extending from Senegal to the Nile, the Upper Guinean which includes rivers from Senegal to Ghana and the Lower Guinean from Nigeria to Zaire. Leveque *at al.*, (1991) list 93 species of fish present in the Gambia River. Hugueny (1989) reported a direct linear relationship between river catchment and fish species richness for West African river systems and the Gambia River follows the same pattern as with the other West African rivers. The river fish fauna is described as Nilo-Sudanian, with the upper River Gambia colonised mainly by Guinean species. The fish fauna in the middle stretch of the River Gambia is Sudanese, but considered relatively poor in species diversity compared to the one encountered in the Senegal and Niger basins (Leveque *et al.*, 1991). The lower stretches of the river are dominated by estuarine and marine species that migrate up the river (Baran, 2000).

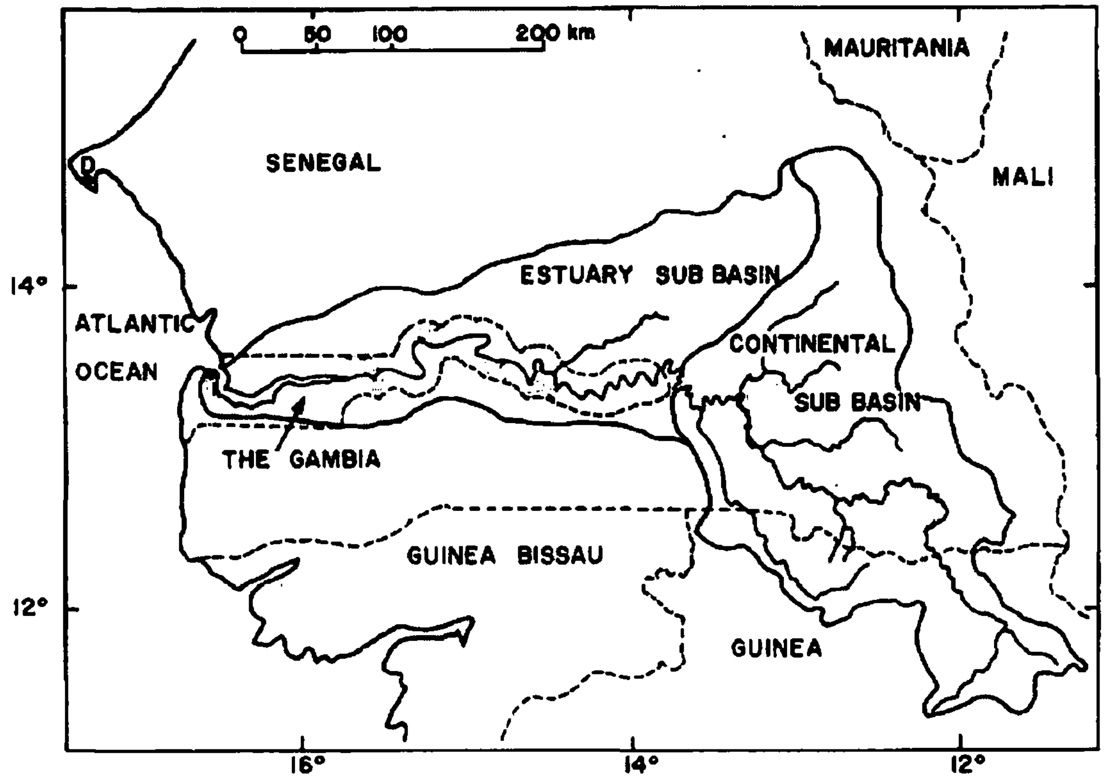


Figure 1.3 Map of the whole Gambia River catchment. From Lesack *et al.*, (1984)

Malaria is a major killer in The Gambia and reports suggest that it is responsible for 40% of deaths for children aged between 1 and 4 years (Alonso *et al.*, 1993). The main malaria vectors in The Gambia are *An. gambiae* s.s., *An. arabiensis* and *An. melas* (Bryan, 1983; Lindsay *et al.*, 1993; Coetzee *et al.*, 2000). Densities of *An. gambiae* s.s. are highly correlated with rainfall, whereas for *An. melas* the numbers are not influenced by rainfall (Bryan, 1983), probably due to the fact that *An. melas* breeds in more saline, mangrove habitats closer to the main river channel which tend to be present throughout the year (Bertram *et al.*, 1958; Giglioli, 1964). Bøgh *et al.*, (2003) identified aquatic habitats which are part of the Gambia River floodplain system to be the primary source of anophelines mosquitoes in rural villages bordering the floodplains, with the catches dominated by *An. melas* (81.5%), a species considered to be of minor importance to malaria transmission as it demonstrated low sporozoite rate (0.35%) compared to *An. gambiae* ss (3.5%) (Bryan, 1983). Adult mosquito catches in houses are usually dominated by *An. gambiae* ss and *An. arabiensis* during the rainy seasons (Lindsay *et al.*, 1989; Lindsay *et al.*, 1990; Bøgh *et al.*, 2001). Adult mosquito catches during the dry season are dominated by *An. melas*, but with no mosquitoes found positive for *Plasmodium falciparum* sporozoites, thus suggesting minimum or no malaria transmission during the dry season (Jawara *et al.*, 2008).

Major malaria intervention trials in The Gambia have so far focused on preventing biting by adult mosquitoes rather than controlling larvae (Lindsay *et al.*, 1989; Lindsay *et al.*, 1993; Kirby *et al.*, 2008) as well as a number of vaccine and drug trials (Doherty *et al.*, 1999; von Seidlein *et al.*, 2000; Sutherland *et al.*, 2003). Lindsay *et al.* (1989) showed that insecticide-treated bednets (ITNs) were effective in increasing the effectiveness of mosquito nets, as well as overall decreasing mortality (Alonso *et al.*, 1991). Another similar study showed a decrease in malaria cases as a result of the use of ITNs (Snow *et al.*, 1988a), but with no effect on malaria morbidity (Snow *et al.*, 1988b). An intervention study investigating the effectiveness of bacterial larvicides on mosquitoes on the Gambia River floodplains was planned to take place at the same timescale of this PhD. That study aimed to identify and describe the main anophelines breeding sites on the floodplains and determine whether bacterial larvicides are effective in controlling anophelines larvae and what the subsequent impact is on adult mosquito catches in neighbouring villages and on malaria.

The Gambia River floodplains, due to their unimpacted state provide aa ideal environment for studying the factors which influence the ecology of both fish and mosquitoes under natural conditions, as well as the interactions between these biota.

1.5 Study aims

This study hypothesises that the Gambia River floodplain fishes and mosquitoes respond to key environmental drivers which change seasonally in response to the seasonal flooding. The main aim is to improve the understanding of the ecology of fishes and mosquitoes of the Gambia River floodplains and understand what factors influence the structure of the fish communities and the distribution of the immature stages of the main malaria vectors (Fig. 1.4). This knowledge will improve our ability to predict possible impacts following the construction of a hydroelectric dam.

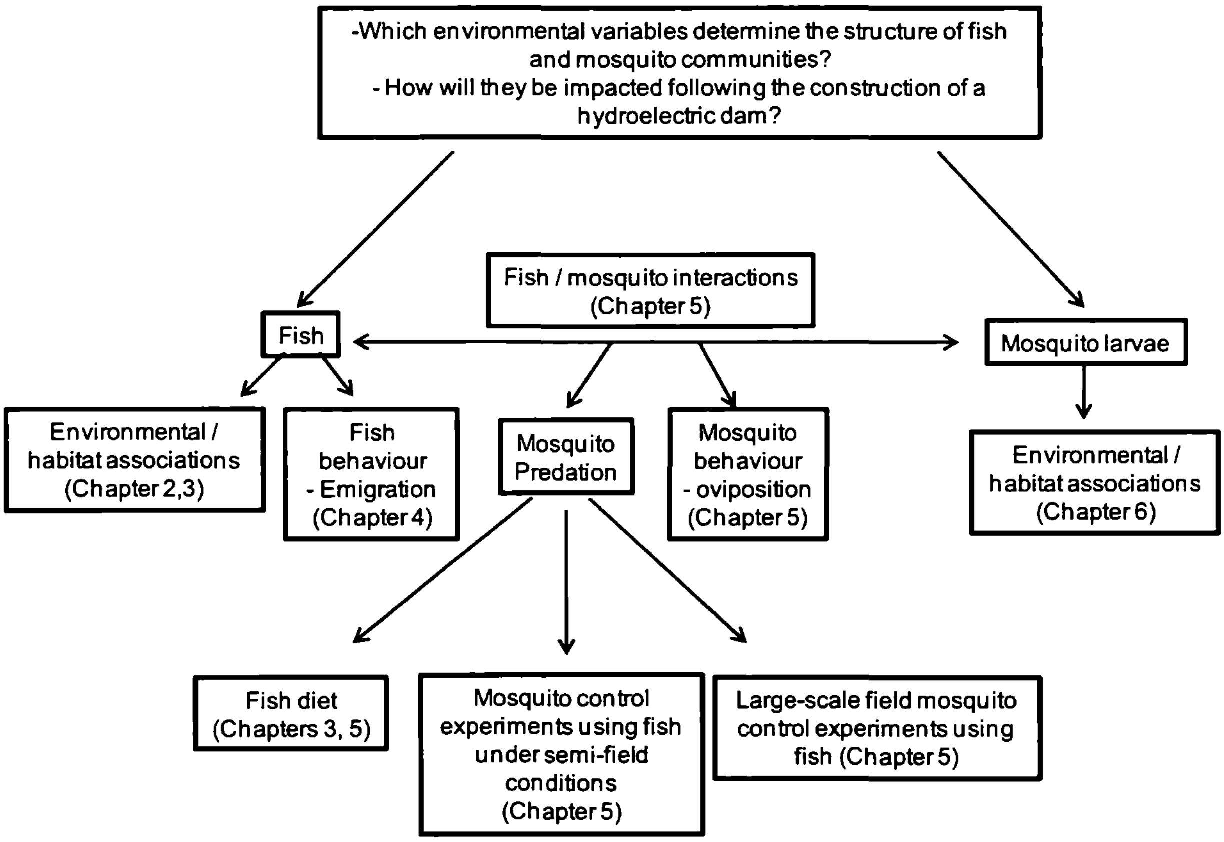


Figure 1.4. Thesis research plan

Chapter 2 identifies the key environmental parameters, which determine the structure of the floodplain fish communities and makes predictions on how the upcoming construction of a hydroelectric dam might impact them. Chapter 3 investigates in detail the biology of the dominant fish species on the floodplains in relation to habitat parameters, diet and reproductive patterns, in order to better understand the adaptations of this species utilising the seasonal floodplains. A further adaptation that is likely to be an important driver of population dynamics in emigration behaviour. Chapter 4 addresses how food abundance and density determine whether fish emigrate into newly flooded habitats.

Floodplains, contain important breeding habitats for malaria mosquitoes, whose distribution on the floodplains is potentially influenced by the presence of insectivorous fish. The diet of floodplain-utilising fish is described in Chapter 5 and the importance of two fish species as predators on mosquito larvae is investigated. The distribution of mosquito larvae might also be influenced by variation in water quality and this is investigated in Chapter 6.

Louca V, Lindsay SW, Majambere S, Lucas MC (2009). Fish community characteristics of the lower Gambia River floodplains: a study in the last major undisturbed West African river. *Freshwater Biology* **54**:254-271.

Chapter 2

Fish community characteristics of the lower Gambia River floodplains

Abstract

The Gambia River is the last major West African river that has not been impounded. However, a hydroelectric dam is being constructed and substantial changes to the hydrology and ecology of the system are expected. Little information is available on the impact of water impoundments in semi-arid regions on downstream floodplain fish communities, due to the scarcity of pre-intervention data. Because profound impacts on physical habitat, salinity and nutrient transport can occur downstream of such impoundments, a knowledge of the species-habitat associations of biota such as fishes is necessary for understanding likely changes and how to limit them or heir impacts.

Fish were sampled using cast- and hand-nets along two transects on the floodplain, and with fyke nets in two 'bolongs' (creeks) from May to November 2005 and 2006 in the lower reaches of the Gambia River, close to the salt water front where ecological changes due to the construction of the dam are likely to be pronounced. Greatest fish species richness was associated with low conductivity, low pH and deep water. Bolongs exhibited greater species richness compared with other floodplain habitats, probably because they acted as conduits for fish moving on and off the floodplain. Species richness and catch biomass increased rapidly following the first rains and then declined. Using a multivariate analysis, three main species

groups were identified on the floodplain; one associated with deeper water, one with less brackish water and one with shallow, open water. *Tilapia guineensis* was the most abundant species on the floodplains. The floodplains provide nursery habitats as many fish captured were immature, particularly for species where adults are mainly encountered in the main channel. Several small-sized floodplain specialists were also represented by a high proportion of mature individuals.

Impoundment is expected to reduce seasonal flooding of the floodplain in the lower Gambia River, downstream of the impoundment, resulting in reduced occurrence of aquatic habitats, especially bolongs. The expected lower dissolved oxygen and increased salinity, leading to alteration of the floodplain fish communities, benefiting salt-tolerant species, reducing overall species richness and probably reducing floodplain fish production.

2.1 Introduction

Rivers and estuaries are biologically diverse and complex systems (Sala *et al.*, 2000; Darwall & Vie, 2005) that provide important goods and services, such as food and transport, to human populations (Balmford *et al.*, 2002). Today, relatively few of these environments remain unaltered (Dynesius & Nilsson, 1994; Welcomme, 1995; Richter *et al.*, 1997b; Malmqvist & Rundle, 2002), although innovative approaches are being taken to improve protection of freshwater landscapes (Thieme *et al.*, 2007; Roux *et al.*, 2008). Among the most common modifications to large rivers are the construction of dams and levees. The direct impacts of such impoundments on migratory fish species are well documented in both tropical and temperate rivers (Baxter, 1977; Kapasa & Cowx, 1991; Halls *et al.*, 1999; Collares-Pereira *et al.*, 2000; Lucas & Baras, 2001; Anderson *et al.*, 2006). However, disruption of the natural hydrological regime, by construction of dams and other flow regulation devices, has far more pervasive effects on catchment function and ecological integrity and it is this that is considered to be the most detrimental human impact to river systems (Cowx & Gould, 1985; Ward & Stanford, 1989; Poff *et al.*, 1997; Richter *et al.*, 1997a; Amoros & Bornette, 2002).

The effects of dams on fish species that inhabit floodplains have sometimes been documented in Africa. On the Niger River in Mali, dam construction reduced the abundance of five fish species (*Gymnarchus niloticus, Polypterus senegalus, Gnathonemus niger*, *Citharinus citharus* and *Clarotes laticeps*), which use the floodplain for feeding and reproduction (Läe, 1995). Further downstream, in Nigeria, the construction of another dam lead to the disappearance of zooplanktivorous fish species from the floodplains (Nwadiaro, 1989). For most other African river systems, however, the direct and indirect effects of dams and barrages on floodplain species are poorly understood, mainly due to the lack of pre-impoundment data. The original composition of the fish communities was not well known for the Bia Basin in Cote d'Ivoire (Gourene *et al.*, 1999), the Zambezi River in Zambia (Karenge & Kolding, 1995) and the Kafue River, Zambia (Dudley & Scully, 1980).

Commonly, studies examining the impacts of dams on ecological communities have concentrated on the effects upstream of impoundments. However, in semi-arid regions some of the most profound impacts can occur a long distance downstream from the impoundment through, i) altered flow and high evapotranspiration leading to increased salinity, ii) alterations to physical habitat and iii) reduced silt and nutrient transport (Baxter, 1977; Saad & Abbas, 1985a; b; Stromberg *et al.*, 2007). Despite the ecological importance of such changes, little consideration has been given to determining the relationships between the assemblages of species and habitat characteristics in rivers of semi-arid regions, in zones sensitive to changes in hydrology. Such knowledge is fundamental for the provision of advice as to the likely impacts of upstream impoundments and how to ameliorate such effects.

The Gambia River is one of the last eight major (river length > 1000km) river systems in Africa to remain free flowing and the only one in West Africa (W.W.F., 2006). The last 500 km of the river has only a 1 m drop (Webb, 1992) and contiguous floodplains, seasonally inundated by floodwater (Lesack, 1986). This low gradient results in an extensive estuary and brackish water penetrates as far as 200 km from the river mouth. However, because of the strong seasonality of freshwater flow, the estuary is characterised by great seasonal fluctuations in salinity (0-33 PSU at 96 km from the estuary mouth), resulting in a dynamic mix of marine, estuarine and freshwater fish species in the main channel (Albaret *et al.*, 2004). The Gambia estuary is also the last in West Africa that is free from extensive human disturbances and retains a normal salinity gradient, unlike neighbouring estuaries (Albaret *et al.*, 2004). However, this is about to change as a hydroelectric power project funded by the African Development Bank is underway at Sambangalou on the Gambia River in Senegal with the flooding of the dam scheduled for 2011 (McNeil, 2006). This will be the first major impoundment project on the river and, as is the case for other West African rivers such as the Sine-Saloum and Casamance, it is expected to alter severely the hydrology of the river, affecting local fish populations and the wider ecological characteristics.

Although several studies have examined fish communities from the main channel of the Gambia River (Lesack, 1986; Albaret *et al.*, 2004; Vidy *et al.*, 2004; Ecoutin *et al.*, 2005), very little is known about those species inhabiting the floodplain. The only two studies to have described the fish fauna of the floodplains were based on expeditions to the lower river in 1931 (Svensson, 1933) and 1950 (Johnels, 1954). As has been the case with other major West African rivers (Barusseau *et al.*, 1985; Panfili *et al.*, 2006), it is likely that the effects of damming the Gambia River will include a reduction of floodplain inundation downstream and an increase in salt-water intrusion up-river. In order to understand probable impacts on the fish assemblages of the lower Gambia River floodplains, the aim of this study was to describe seasonal variation in the pre-impoundment fish community and its relationship to physical parameters (conductivity, turbidity, dissolved oxygen, pH and temperature) and habitat (ricefields, mud flats, bolongs) at floodplain sites near the upper limit of the salt front. This is the area downstream of the future dam that is as likely to be most sensitive to the impoundment. Through determination of species – habitat associations, predictions are made of likely fish community responses to changes in hydrology. Discussion is made on how this type of information could be used by national environment protection and development agencies to alleviate likely impacts.

2.2 Materials and methods

2.2.1 Study site

This study was conducted along two 2.3 km long transects and two adjacent bolongs on the floodplains east of Farafenni town in Gambia (13 ° 34'N, 15 ° 35'W), approximately 193 km and 209 km upstream of the estuary mouth (Fig. 2.1). This area approximates the upper limit of brackish water during the dry season. A brief description of the characteristics of the Gambia River is given in section 1.4.

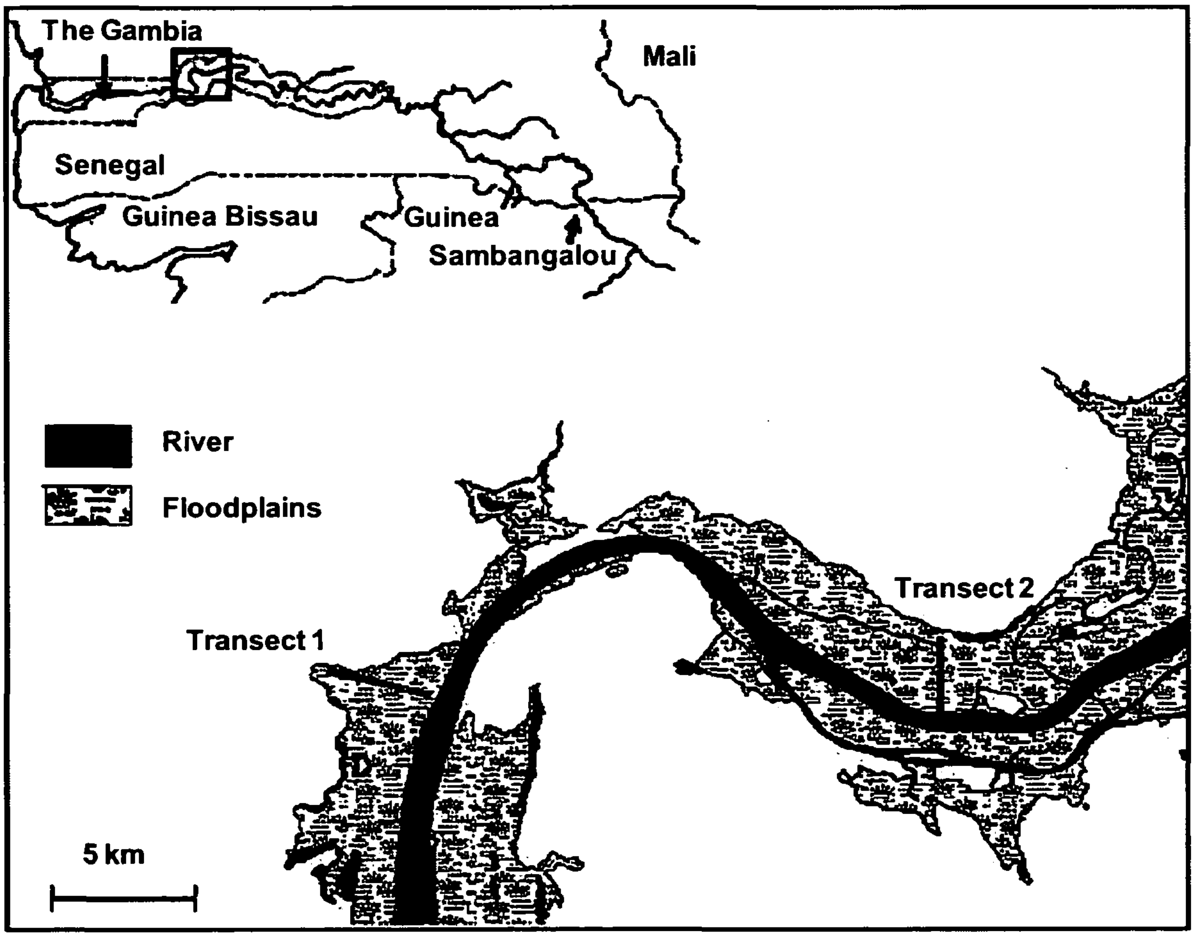


Figure 2.1 Location of the study sites along the Gambia River

No commercial fishing takes place in the two 100 km^2 zones of floodplain in which the study sites were based and there were just three artisanal fishermen catching food for local consumption. Therefore it is expected this limited fishing pressure had little influence on the species composition, relative abundance and size range of the fish community. The floodplains in this area are bordered by mangroves along the main river channel and some of the larger connecting bolongs. Landward of the mangroves are continuous areas of bare mudflats (Bøgh *et al.*, 2007), where there is prolonged desiccation during the dry season and a high salt content, mainly chlorides and sulphates (Giglioli & King, 1966). Ricefields are encountered sporadically on the floodplains, from the edge of the main river channel to the edge of the floodplain, depending on the relative access to the site by the local people (V.Louca, personal observation). Swamp rice is cultivated between 110-290 km from the river mouth, where the river is still tidal (Webb, 1992). The rice is grown first in rainfed nurseries away from the floodplains, and at the peak of the rainy season transplanted in to ricefields on the floodplains. No pesticides are used in the study areas. The farmers do not stock the ricefields with fish, and their colonisation is through natural dispersal. Neither do farmers normally harvest fish from these fields. Mudflats that receive periodic flooding in the dry season from the spring tides support the perennial *Sesuvium portulacastrum* L., as well as seasonal *Heleocharis* spp and beds of *Paspalum* spp (Giglioli & Thornton, 1965; Bøgh *et al.*, 2007). The area is therefore characterised by the presence of some saltmarsh vegetation, but also retains characteristic freshwater flora such as water lilies (*Nymphaea* spp.) in some habitats such as semi-permanent pools.

2.2.2 Sampling

The two transects (Balanghar-Ker Derry [BKD], 13° 39'N, 15° 23'W, Palaka [P] 13° 40'N, 15° 13'W) were sampled monthly in 2005 and 2006 from May to November, starting one month prior to the rainy season and continuing up to one month after the end of the rains, covering the period from minimum flooding, through maximum flooding and part-way through the period of decreasing inundation. Each transect started from the beginning of the floodwater to the main river channel or, as in the case of the Palaka transect, to the point where it was impossible to continue due to dense vegetation. Sampling took place with a cast net (diameter: 230 cm, mesh size: 10 mm) (Fig. 2.2) and a hand net (25 X 17 cm, mesh: 2 mm) every 150 m along each transect during the first 5 h of daytime. Prior to the start of the study, a number of sampling techniques (electric-fishing, minnow-traps and a seine-net) were tested, but all were ineffective, as relatively few fish were caught even when visual inspection showed them to be abundant. The cast net, a popular fishing technique in The Gambia, proved an effective method of catching a wide variety of fish in open floodwater, channels or gaps in vegetation. The hand-net was used to sample smaller fish species and juvenile fish in the shallower (<30 cm) vegetated areas. At each sampling point a cast-net was thrown at three different locations within 20 m of either side of the transect point. Five cumulative minutes of sweeping were also undertaken with the hand-net within the same sampling area. Although all sampling methods are, to some extent biased, combination of these two methods enabled sampling at different microhabitats, and therefore, better overall sampling of the habitats present. Together, these methods provided effort-standardised sampling throughout the study period along floodplain transects.

Choice of sample size at each sampling location was determined by the relationship between the number of species caught and sample size, the ability to sample undisturbed areas within each habitat patch (typically 200-300 m^2) at transect points, and time constraints. For the cast-net samples a doubling of sampling effort, from three to six cast net throws, resulted in a 15% increase in the number of species caught in mudflats and ricefields, and a 23% increase in the bolongs. Analysis of the sampling efficiency of the hand nets revealed that 5 minutes pushnetting caught 100% of species in 10 minutes in bolongs, 86% in mudflats and 66% in ricefields.

Figure 2.2 Sampling with cast-nets on the floodplains

The vegetation present at an aquatic site can influence the type and amount of food available for fish, as well as providing vital cover (Hickley & Bailey, 1987; Welcomme, 2002), and changes in vegetation cover due to the construction of the dam could therefore influence fish abundance and species composition. Seven vegetation types were defined; barren (areas with no vegetation), grass (*Paspalum* sp, *Sporobolus* spp), sedge (*Eleocharis* sp.), tall reeds (*Phragmites karka* Retz., *Cyperus papyrus* L.), sea purslane (*Sesuvium* spp.), cultivated rice (*Oryza sativa* L.) and water lilies (*Nymphaea* spp.). The dominant vegetation type was determined based on the emergent and/or submerged macrophytes which were most abundant within 20 m each side of each transect sampling point. In addition, the total percentage vegetation cover and number of vegetation types present at each point were recorded. Mangrove habitats (*Rhizophora* spp, *Avicennia* spp.) were only encountered as a thin strip at the edge of the main river channel and were not sampled as they were part of the main river channel and outside the scope of this study.

Each sample location on the transect was categorised as one of five aquatic habitat types: mudflats, rice fields, bolongs, pools (semi-permanent; rainfed and mostly not connected with the rest of the inundated floodplain except during short periods during heavy rainfall), and puddles (natural or man-made depressions less than 20 m in diameter, rainfed or filled with floodwater during high tides and lasting only a few days before completely drying out). Each water body was assessed as to whether it had a permanent connection to the rest of the floodwater or not. At each location water quality parameters (conductivity, pH, temperature, dissolved oxygen) were measured in the field with a multiparameter probe (WTW Multi 350i, Weilheim, Germany). Water samples were collected and taken to the laboratory for turbidity determination using a turbidity meter (HANNA HI 93703, Italy). Water depth was measured to the nearest cm with a metre rule at three different locations within the sampling area, and then averaged.

Two bolongs, each in close proximity to, but not part of a transect, were additionally sampled over a two-day period in the week after each transect sampling, because they provide important connections between main river and floodplain habitats. Doubling of sampling effort from one to two 24-h periods, resulted in an 18% increase in species richness for the fyke net catches, suggesting a two-day period to be a reasonable descriptor of community composition susceptible to capture by this method. The sampling locations for bolongs BKD and P were 1330 m and 970 m, respectively, from the main river channel. A two-way fyke net (mesh 10 mm) was placed in each bolong, connected with a 5 mm mesh leader net as described in Vidy *et al.* (2004). Nets were placed to obstruct and sample the entire width (BKD: 8m; P: 5m) of each bolong. However, on several occasions, during exceptionally high water flows, the bolong overflowed, so that some fish may have bypassed the net. Fykes were checked early in the morning (06:30 – 07:30) and evening (18:30 – 19:30). On all sampling occasions, the water depth was recorded to the nearest cm at three locations, in front of each fyke net and at the middle of the leader, and averaged. Water temperature, pH, turbidity and conductivity were all measured as described above. The study transects were located in the middle of two approximately 100 km^2 zones where detailed mapping of mosquito breeding sites has taken place (Majambere *et al.*, 2008). Detailed data on the percentage of flooded habitats for each month during 2005 and 2006 were collected as a measure of the extent of floodplain inundation. Rainfall data were collected at Farafenni town.

2.2.3 Processing of samples

Fish were preserved in 4% formalin and taken to the laboratory for subsequent identification, sexing and gonad analysis. Fish were identified to species using Paugy *et al.* (2003). Species were assigned to the bioecological categories of Albaret *et al.*(2004), which group West African fishes in terms of their marine and freshwater evolutionary origins and their reliance on freshwater, estuarine and marine habitats for part/all of their lifecycles. Bioecological categories, or environmental guilds, have been proposed as a way of assessing the ecological condition of rivers and as a reliable way of determining the impacts of river impoundments on biodiversity and fisheries management (Welcomme *et al.*, 2006).

Each fish was sexed and the reproductive status and maturity assessed by macroscopic observation using the classification stages of Panfili *et al.* (2006). The percentage of immature fish in catches was calculated to assess the use of the floodplains as a nursery habitat for juvenile fish, with species samples that comprised over 50% immature fish suggesting a high utilisation of floodplains as nursery habitats. This was expressed as the number of female fish of smaller standard length than the size at sexual maturity.

2.2.4 Statistical analysis

Repeated Measures ANOVA (SPSS version 15) was used to analyse differences in environmental variables between the aquatic habitat types. Transect catches from each sampling point and occasion were converted to Catch Per Unit Effort (CPUE) for each of the sampling methods for each species. Cast net data for each sample site and occasion were converted to the average number of fish (or biomass) of each species per cast throw, and hand-net data to number (or biomass) of fish for each species per minute of sweeping. The two CPUE values were added to provide a combined value for each sampling point, date and species, providing standardised CPUE data for comparison.

General Estimating Equations (GEE) were used to analyse the relationship between species richness and total catch biomass with abiotic variables, using SPSS version 15. This analysis extends generalized linear models (GLMs) to account for repeated measures and clustering of samples as well as allowing for linear and non-linear models (Horton & Lipsitz, 1999). Separate models were tested for species richness and catch biomass with environmental parameters in the bolongs and floodplains. Puddles and pools, water body types that were encountered on less than six sampling occasions, were excluded from the statistical analysis. A Gamma distribution model with a log-link was used to test the catch biomass. This non-symmetric function is appropriate for measures related to dimensions, including biomass. The Poisson distribution model is appropriate for counts of animal/plant units and therefore for testing species richness (Ter Braak & Smilauer, 2002).

Canonical Correspondence Analysis (CCA) (Ter Braak, 1986) was used to investigate the influence of environmental variables on species distribution from transect samples using CANOCO version 4.5. A partial CCA was undertaken with year, transect and transect points controlled for as covariables, so that repeated sampling effects were accounted for. To remove possible collinearity effects, only environmental variables explaining a significant additional proportion of the variance independent of other variables were used in the model. Forward selection was used to identify significant variables for inclusion and each was tested using a Monte Carlo permutation test with 999 runs. Data were log-transformed to prevent a few values from dominating a variable's contribution. Only species which were caught on more than three sampling occasions were used in the analysis to avoid undue influence of very rare species.

2.3 Results

2.3.1 Physical variables

Peak rainfall occurred in July in 2005 and August-September in 2006. The peak inundation of the floodplain occurred in July-August and the pattern of floodplain inundation suggests that flooding is a result of both increased local rainfall causing direct inundation of floodplain and also increased flooding from the main river channel originating from high flows due to rainfall in the upper catchment (Fig. 2.3).

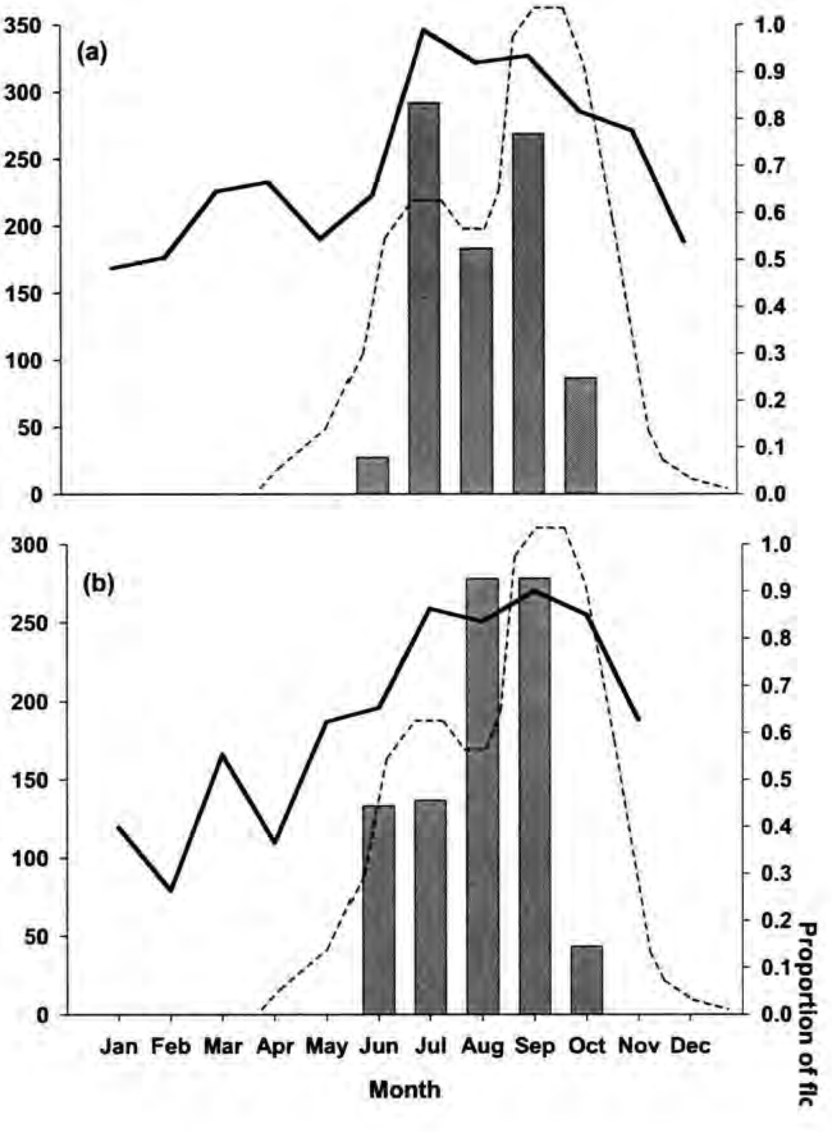


Figure 2.3 Seasonal changes in total monthly rainfall (bars), proportion of floodplain (sites BKD and P) inundated (solid line) and schematic of river discharge curve expressed as proportion of the maximum (dotted line) for (a) 2005 and (b) 2006. The seasonal river discharge curve is based on Lesack *et al.* (1984), and was measured 500 km from the river mouth.

Dissolved oxygen (DO) values ranged from 0.11–15.13 mg.L^{-1}, conductivity 0.044–33.7 mS cm^{-1} (approximately 0-21.5 PSU), temperature 20.5–39 °C, pH 3.1–9.5, turbidity 0.4-1000 NTU and water depth 2-79 cm. The high conductivity values encountered on the floodplains principally reflect increased salinity, associated with tidal influences, low rainfall and low river discharge. Temperature, DO, conductivity and turbidity, but not pH, differed significantly between aquatic habitats. Only waterbodies that were sampled on more than six occasions were used in the analysis, which thus excluded puddles and pools. Mean conductivity (ANOVA, d.f.=2 and 239, P<0.001) and DO (ANOVA, d.f.=2 and 239, P=0.008) were significantly lower in rice fields, temperature was significantly lower in bolongs (ANOVA, d.f.=2 and 239, P=0.005), turbidity was significantly higher in rice fields (ANOVA, d.f.=2 and 239, P<0.001) and bolongs were significantly deeper than other aquatic habitats (ANOVA, d.f.=2 and 239, P<0.001).

Physical variables changed markedly during the rainy season (Fig. 2.4). Bolongs and mudflat aquatic habitats were warmest at the end of the rainy season in September-October, whereas for rice fields this occurred immediately before the first rains in May. Turbidity peaked at the end of the rainy season for mudflats and bolongs. In ricefields, peak turbidity was experienced in the middle of rainy season, coinciding with rice transplantation. At the start of the rains, pH declined, with a minimum in August in all three habitat types. In floodwater and bolongs, pH rose progressively, reaching pre-rainy season values by the end of the season. Conductivity declined through the rainy season, whereas DO dropped following the first rains and then remained stable through the rainy season. Water depth showed no clear temporal pattern for the three aquatic habitat types, possibly reflecting greater tidal rather than seasonal influence on water depth.

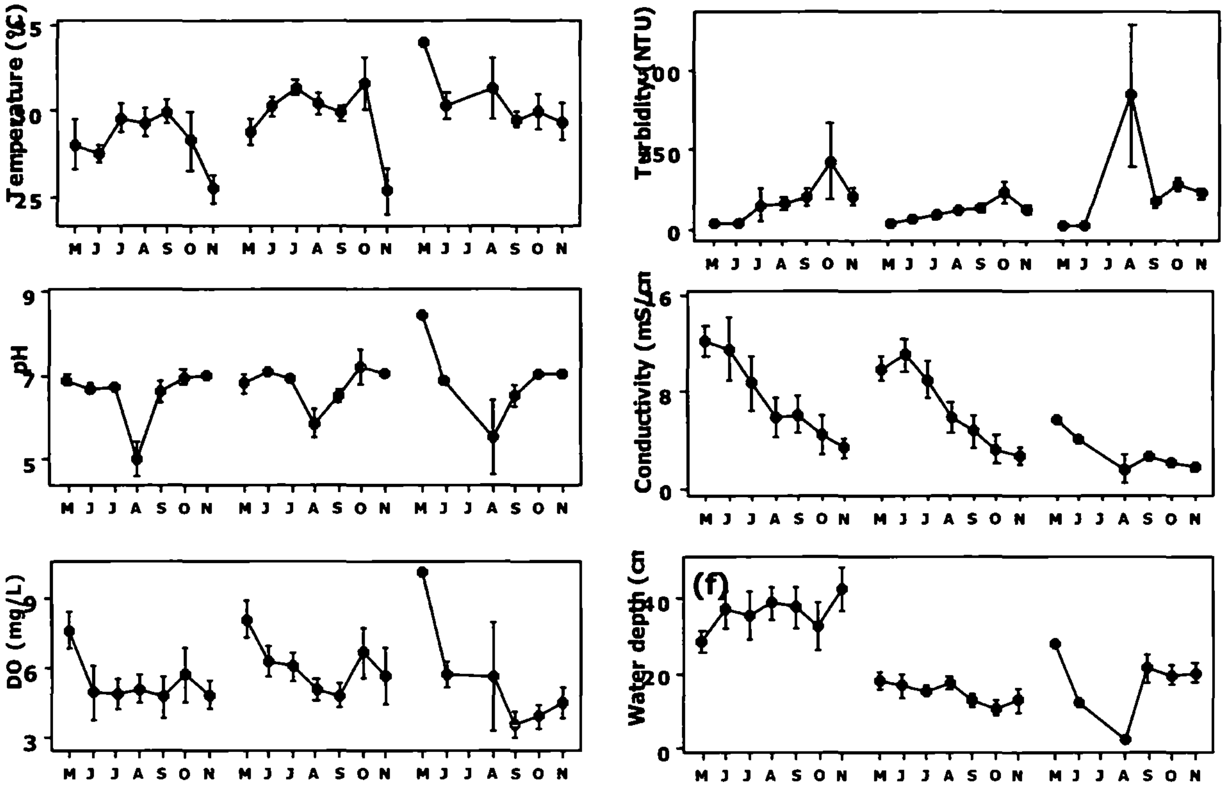


Figure 2.4 Temporal changes in means and 95% CIs of (a) water temperature, (b) turbidity, (c) pH, (d) electrical conductivity, (e) dissolved oxygen and (f) water depth for the three commonest aquatic habitats sampled on the Gambia River floodplains (data combined for 2005 and 2006).

2.3.2 Floodplain fish community composition – transect samples

Thirty-two species of fish belonging to 15 families were collected from the floodplain transects in 2005 and 2006 (Table 2.1). One species, *T. guineensis*, made up 72% of the catch by number. Similar proportions of species of estuarine/marine origin (ecological categories Ec, Em, Es, ME, see Table 1) occurred on the floodplain transects (65%) and in the bolongs sampled along the transects (62%, Table 2.1).

Table 2.1 Relative abundances and species abbreviations used in the CCA plot (Fig. 2.5) of all the fishes sampled in the Gambia River floodplain in 2005 and 2006. The percentage numbers of non-mature female fish are provided for those species with a sufficient sample size (n>20). Bioecological categories follow Albaret *et al.* (2004).: Co: continental species, occasional in estuaries; Ce: continental species from estuarine origin; Ec: estuarine species from continental origin; Es: strictly estuarine species; Em: estuarine species from marine origin; ME: marine-estuarine species, using estuaries as nurseries.

					2005				2006			
					Transect		Bolong		Transect		Bolong	
Family	Species	Abbr.	Cat.	% juv.	BKD %	P %	BKD %	P %	BKD %	P %	BKD %	P %
Elopidae	*Elops lacerta* Valenciennes	ELAC	ME	100	3	0	0	<1	1	<1	0	1
Clupeidae	*Pellonula leonensis* Boulenger	PLEO	Ec	21	1	<1	5	11	0	0	77	25
	Sardinella maderensis Lowe	SMAD	ME	-	1	0	0	0	0	0	0	0
	Ethmalosa fimbriata Bowdich	EFIM	Em	-	1	0	0	0	0	0	0	0
Hepsetidae	*Hepsetus odoe* Bloch	HODO	Co	-	<1	0	0	0	<1	0	0	0
Characidae	*Rhambdalestes septentrionalis* Boulenger	RSEP	Co	8	1	1	0	1	3	1	<1	3
	Brycinus nurse Rüppell	BNUR	Co	100	<1	1	1	4	<1	0	0	<1
	Alestes dentex L.	ADEN	Co	-	0	0	0	<1	0	0	0	1
Cyprinidae	*Barbus macrops* Boulenger	BMAC	Co	25	0	<1	0	1	0	<1	0	3
Bagridae	*Chrysichthys nigrodigitatus* Lacepède	CNIG	Ec	82	2	<1	41	54	1	<1	8	50
	Chrysichthys johnelsi Daget	CJON	Ce	100	0	0	2	2	<1	<1	<1	4
Schilbeidae	*Schilbe intermedius* Rüppell	SINT	Co	79	0	0	12	3	0	0	<1	1
Clariidae	*Clarias anguillaris* L.	CANG	Co	-	0	<1	0	1	0	0	<1	0
Mochokidae	*Synodontis schall* Bloch & Schneider	SSCH	Co	100	0	<1	10	12	0	<1	1	1
	Synodontis batensoda Rüppell	SBAT	Co	50	0	<1	7	1	0	0	<1	<1
Cyprinodontidae	*Poropanchax normani* Ahl	PNOR	Co	20	15	1	0	0	12	<1	0	<1
	Epiplatys spilargyreius Duméril	ESPI	Co	30	1	3	0	0	3	4	0	<1
	Epiplatys bifasciatus Steindachner	EBIF	Co	-	0	0	0	0	1	<1	0	0
	Aplocheilichthys spilauchen Duméril	ASPI	Es	-	0	0	0	0	0	<1	0	0
Gerreidae	*Eucinostomus melanopterus* Bleeker	EMEL	ME	-	0	0	0	0	0	0	<1	0
Sciaenidae	*Pseudotolithus senegalensis* Valenciennes	PSEN	ME	-	0	0	1	1	0	0	0	0
Monodactylidae	*Monodactylus sebae* Cuvier	MSEB	Es	100	<1	0	1	3	0	<1	2	2
Cichlidae	*Tilapia guineensis* Bleeker	TGUN	Es	57	56	90	6	2	72	91	2	<1
	Tylochromis jentinki Steindachner	TJEN	Es	100	4	0	4	0	2	0	3	<1
	Tylochromis intermedius Boulenger	TINT	Es	-	0	0	0	0	<1	0	0	0
	Oreochromis niloticus L.	ONIL	Es	-	0	0	0	0	0	<1	0	0
	Tilapia zilli Gervais	TZIL	Es	-	0	0	0	0	0	<1	0	0
	Hemichromis bimaculatus Gill	HBIM	Es	35	1	2	1	0	0	1	0	<1
	Hemichromis fasciatus Peters	HFAS	Ec	9	2	2	1	<1	3	1	1	1
Mugilidae	*Liza grandisquamis* Valenciennes	LGRA	Em	100	5	0	1	1	1	<1	0	3
	Liza falcipinnis Valenciennes	LFAL	Em	100	3	<1	0	0	<1	<1	0	<1
	Mugil cephalus L.	MCEP	ME	-	0	0	0	0	<1	0	0	0
Polynemidae	*Polydactylus quadrifilis* Cuvier	PQAD	ME	-	0	0	1	1	0	0	1	1
Gobiidae	*Gobionellus occidentalis* Boulenger	GOCC	Es	-	0	0	0	0	<1	0	<1	0
	Nematogobius maindroni Sauvage	NMAN	Es	100	2	<1	3	0	<1	<1	0	0
	Porogobius schlegelii Günther	PSCH	Es	25	1	<1	4	2	0	1	5	<1
	Periophthalmus barbarus L.	PBAR	Es	-	0	0	0	0	<1	0	0	<1
Anabantidae	*Ctenopoma kingsleyae* Günther	CKIN	Co	-	0	0	0	0	<1	0	0	0
Cynoglossidae	*Cynoglossus senegalensis* Kaup	CSEN	Em	-	0	<1	1	<1	0	0	0	0
Total Number					488	2850	209	355	923	3285	471	451

Fish species richness increased with lower conductivity (Table 2.2) and increasing water depth. When monthly catches were compared to the dry season (May) catches, species richness did not vary significantly, suggesting that it changed little with the progression of the rainy season and with inundation, although the species composition did change (section 2.3.5). Barren mudflats, which dominated the floodplains, were chosen as a reference 'vegetation' type for comparison with fish catches associated with other vegetation types. Four dominant vegetation types exhibited significantly higher fish species richness than barren mudflats; sedge (59% higher), rice (36% higher), reeds (36% higher) and water lilies (67% higher). Mudflats were the commonest habitat on the floodplain transects and were chosen as a reference group for statistical comparisons (Table 2.2). Bolongs exhibited significantly higher catch biomass (29% more) and species richness (15% more) than mudflats, whereas rice fields had 21% less catch biomass (borderline significance). Catch biomass and species richness increased with increasing water depth, whereas richness increased with decreasing conductivity. Waterbodies with a permanent connection to floodwater had 335% higher average catch biomass compared to ones with no permanent connection.

Catch per unit effort of the ten commonest species in the three main aquatic habitat types along transects, separated by sampling method are presented in Table 2.3. *Tilapia guineensis* was the commonest species in all habitats. The killifishes *Poropanchax normani* and *Epiplatys spilargyreius* were more commonly caught in hand nets; *P. normani* was encountered mainly in bolongs, and *E. spilargyreius* in rice fields. The characin *Rhambdalestes septentionalis* was mostly caught by cast nets in the bolongs.

Table 2.2 General Estimating Equations output for species richness and catch biomass with abiotic factors in the Gambia River floodplains (transect samples) and bolongs (fyke catches). OR refers to Odds Ratio, the relative importance of the measured variable in relation to the reference group for the nominal variables and the relative change in relation to one unit of change in the independent variable. Significant values are given in bold.

	Floodplains				Bolongs			
	Richness		Catch biomass		Richness		Catch biomass	
	OR	*P*	OR	*P*	OR	*P*	OR	*P*
Temperature	0.994	0.671	0.986	0.215	**0.925**	**<0.001**	0.992	0.770
pH	0.966	0.343	0.995	0.871	**0.943**	**0.012**	**0.983**	**<0.001**
Conductivity	**0.982**	**0.001**	1.004	0.650	1.010	0.483	0.993	0.464
Oxygen	1.006	0.565	1.010	0.265	**1.050**	**0.027**	**1.065**	**0.039**
Water depth	**1.008**	**0.002**	1.004	0.083	**1.005**	**0.001**	**1.009**	**<0.001**
Turbidity	0.999	0.265	1.002	0.122	1.000	0.701	0.998	0.588
No. of veg types	1.036	0.239	0.994	0.803	N/A	N/A	N/A	N/A
% veg cover	**0.996**	**0.006**	0.997	0.136	N/A	N/A	N/A	N/A
Catches:								
Day	N/A		N/A		**0.619**	**0.001**	**0.585**	**<0.001**
Night:	N/A		N/A		1		1	
Year:								
2005	0.889	0.223	0.847	0.094	1.060	0.794	0.923	0.405
2006	1		1		1		1	
Site:								
BKD	**0.823**	**0.014**	**0.706**	**0.001**	**0.858**	**<0.001**	**0.585**	**<0.001**
P	1		1		1		1	
Vegetation type:								
Barren	1		1		N/A	N/A	N/A	N/A
Grass	1.264	0.120	1.052	0.670	N/A	N/A	N/A	N/A
Sedge	**1.588**	**0.001**	1.064	0.649	N/A	N/A	N/A	N/A
Rice	**1.360**	**0.050**	1.239	0.171	N/A	N/A	N/A	N/A
Tall reeds	**1.362**	**0.043**	0.980	0.895	N/A	N/A	N/A	N/A
Water lilies	**1.674**	**0.004**	1.076	0.635	N/A	N/A	N/A	N/A
Aquatic habitat								
Floodwater	1		1		N/A	N/A	N/A	N/A
Rice fields	1.149	0.253	0.787	0.057	N/A	N/A	N/A	N/A
Bolongs	**1.287**	**0.003**	**1.148**	**0.047**	N/A	N/A	N/A	N/A
Month:								
May	1		1		1		1	
June	1.024	0.834	1.077	0.458	**1.277**	**<0.001**	**1.556**	**0.001**
July	1.050	0.687	1.110	0.269	**0.747**	**<0.001**	0.897	0.579
August	0.850	0.138	0.982	0.844	1.154	0.223	1.113	0.247
September	0.849	0.060	1.025	0.792	0.744	0.423	0.738	0.118
October	0.935	0.581	0.880	0.343	1.148	0.677	0.968	0.781
November	0.850	0.178	**0.730**	**0.043**	**0.690**	**<0.001**	**0.608**	**<0.001**
Connectivity:								
Yes	1.308	0.189	**3.351**	**0.012**	N/A	N/A	N/A	N/A
No	1		1		N/A	N/A	N/A	N/A

Table 2.3 Catch per unit effort (cast net: number of fish per cast net throw; hand net: number of fish per minute of sweeping) of the 10 commonest species compared between the Gambia River floodplain habitats of mudflats, rice fields and bolongs. Samples were taken by cast-net and hand-net over the whole study period.

Species	Mudflats		Rice fields		Bolongs	
	Cast net	Hand net	Cast net	Hand net	Cast net	Hand net
	(Mean ± S.E.)	(Mean ± S.E.)	(Mean ± S.E.)	(Mean ± S.E.)	(Mean ± S.E.)	(Mean ± S.E.)
Rhambdalestes septentrionalis	0.04 ± 0.01	0.00 ± 0.00	0.13 ± 0.05	0.00 ± 0.00	0.42 ± 0.16	0.00 ± 0.00
Chrysichthys nigrodigitatus	0.06 ± 0.02	0.00 ± 0.00	0.03 ± 0.02	0.00 ± 0.00	0.07 ± 0.03	0.00 ± 0.00
Poropanchax normani	0.04 ± 0.02	0.21 ± 0.06	0.03 ± 0.02	0.17± 0.06	0.06 ± 0.03	0.59 ± 0.14
Epiplatys spilargyreius	0.01 ± 0.01	0.30 ± 0.03	0.00 ± 0.00	0.35 ± 0.06	0.00 ± 0.00	0.17 ± 0.03
Tilapia guineensis	14.36 ± 3.2	0.18 ±0.02	9.99 ± 1.32	0.19 ± 0.04	4.91 ± 0.74	0.11 ± 0.02
Tylochromis jentinki	0.05 ± 0.01	0.00 ± 0.00	0.02 ± 0.02	0.00 ± 0.00	0.09 ± 0.03	0.00 ± 0.00
Hemichromis bimaculatus	0.16 ±0.03	0.04 ± 0.01	0.11 ± 0.03	0.02 ± 0.01	0.01 ± 0.01	0.04 ± 0.01
Hemichromis fasciatus	0.16 ± 0.03	0.01 ± 0.00	0.21 ± 0.05	0.02 ± 0.01	0.11 ± 0.03	0.01 ± 0.00
Liza grandisquamis	0.01 ± 0.00	0.00 ± 0.00	0.20 ± 0.09	0.00 ± 0.00	0.11 ± 0.04	0.00 ± 0.00
Liza falcipinnis	0.05 ± 0.03	0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.00	0.08 ± 0.03	0.00 ± 0.00

2.3.3 Habitat associations

Monte Carlo tests performed using CCA showed a significant contribution of four variables (conductivity, % vegetation cover, water depth and pH) to explaining fish species distributions (Table 2.4). Figure 2.5 summarises the relationship between the abundance of fish species caught on the floodplains in 2005 and 2006 and the factors included in the model, of which the first two axes accounted for 77.1% of the variance. A cluster of species, principally *Elops lacerta, Monodactylus sebae, Brycinus nurse, R. septentrionalis* and *P. normani,* was associated with deeper water habitats. *Periophthalmus barbarus* was associated with habitats with higher conductivity ranges, whereas *Synodontis shall, Chrysichthys nigrodigitatus, Liza falcipinnis, Tylochromis jentinki, Hepsetus odoe, Porogobius schlegelli* and *Pellonulla leonensis* were associated with lower conductivities. *Barbus macrops* and *Liza grandisquamis* were associated with habitats with sparse vegetation cover and *Epiplatys spilargyreius* and *Epiplatys bifasciatus* with dense vegetation cover. These species clusters were confirmed in part using cluster analysis (Fig. 2.6). Using CCA, no clear pattern of habitat associations of the different bioecological guilds identified above was observed.

Of the 21 species for which sufficient samples were taken on the floodplain by all sampling methods, more than 50% of females comprised reproductively immature fish in 13 species (Table 2.1). This group included one characin (*B. nurse*) and eight catfishes, with the rest being of estuarine/marine origin demonstrating the use of floodplains as nursery habitats for these species.

Table 2.4 Habitat variable loadings and ordination summary for the canonical correspondence analysis of the fish assemblages in the lower Gambia River floodplain for Axis 1 and Axis 2. Only the statistically significant (Monte Carlo significance test, 999 permutations) habitat variables were included in the model and are shown here; Water depth (*F*-ratio: 7.71, *P*=0.001), % vegetation cover (*F*-ratio: 1.98, *P*=0.010, Conductivity (*F*-ratio: 7.71, *P*=0.015), pH (*F*-ratio: 7.71, *P*=0.025).

	Canonical coefficients for environmental variables		Correlation of environmental variables with species axis	
	Axis 1	Axis 2	Axis 1	Axis 2
Water depth	0.90	- 0.03	0.53	- 0.01
% vegetation cover	0.50	0.53	0.29	0.18
Conductivity	- 0.24	0.75	- 0.14	0.25
pH	0.00	0.20	0.00	0.07

Summary statistics for ordination axis	Axis 1	Axis 2
Eigenvalues	0.12	0.04
Species-environment correlations	0.58	0.34
Cumulative % variance:		
species:	2.60	3.40
species- environment:	58.8	77.1
Sum of all eigenvalues:	4.69	
Sum of all canonical eigenvalues:	0.20	

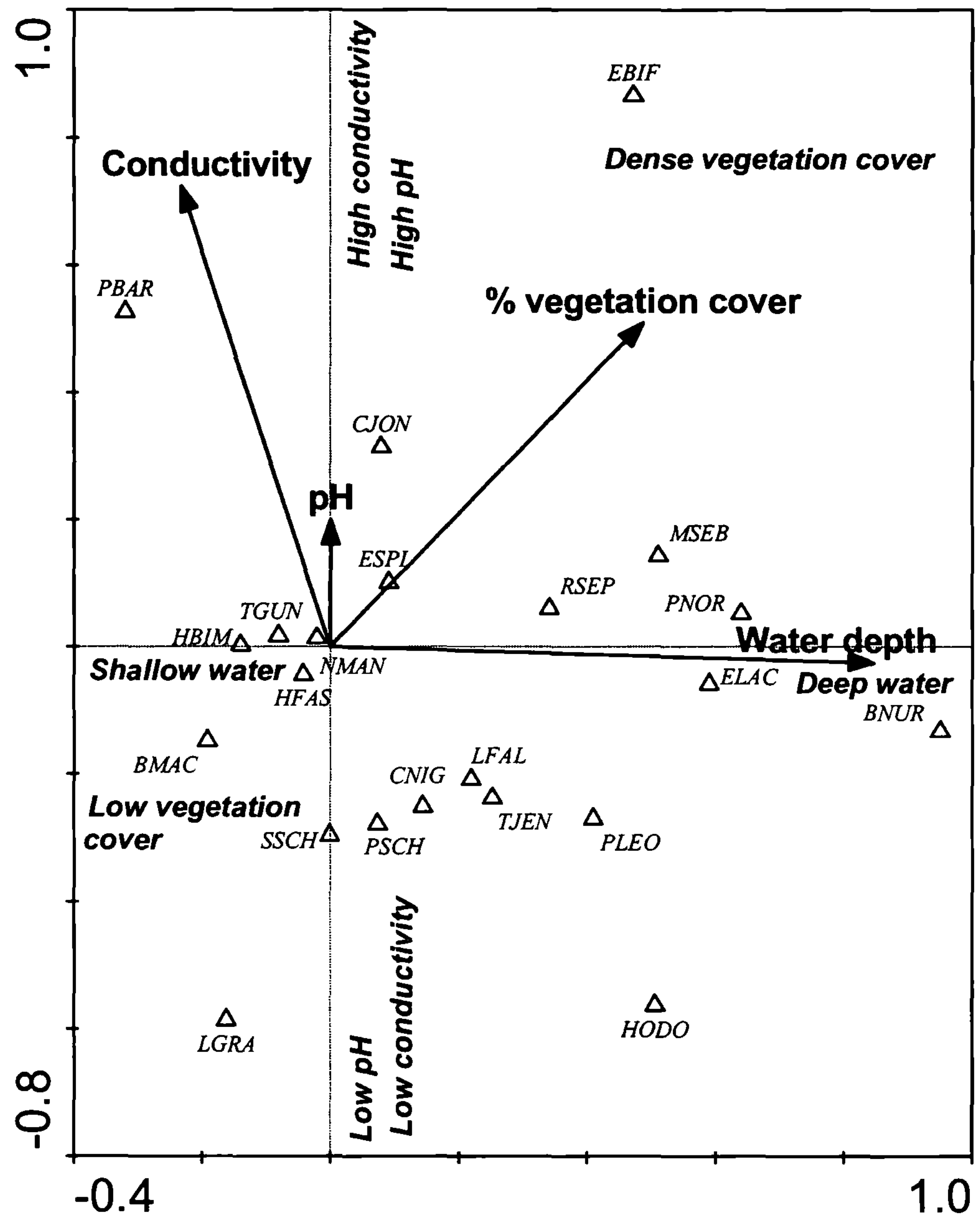


Figure 2.5 Canonical correspondence analysis biplot of the distribution of the 22 commonest fish species (Δ) and significant environmental variables (vector arrows) sampled on transects of the floodplain. The position of each species centroid indicates its association with the environmental conditions. The corresponding species name for the species acronyms are given in Table 2.1. Positive scores on axis 1 represent mainly deeper and more permanent water habitats generally with denser vegetation cover. Positive scores on axis 2 represent habitats associated with higher conductivity and pH.

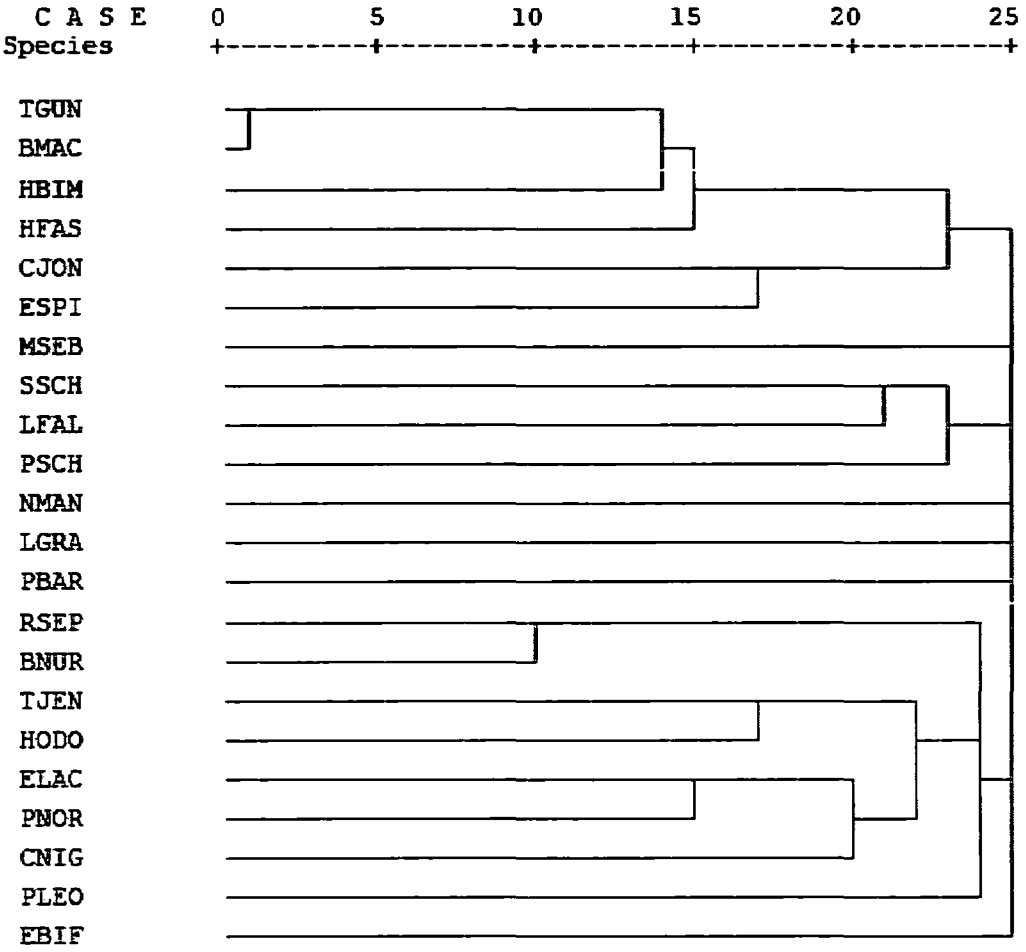


Figure 2.6 Cluster analysis output of species associations of the 22 commonest fish species. The corresponding species name for the species acronyms are given in Table 2.1

2.3.4 Bolongs – fyke net samples

In total, 29 species of fish belonging to 16 families were captured in fyke nets in the bolongs (Table 2.1). Two species, *P. leonensis* (a clupeid) and *C. nigrodigitatus* (a bagrid catfish), made up 64% of the total catch. Five species occurred mostly in night catches. These were four catfishes: *C. nigrodigitatus* (Wilcoxon Signed Ranks Test, *n*=536; day catches, median: 1, range: 0-20, night catches: median: 5, range: 0-149, *P*=0.002) *Chrysichthys johnelsi* (Wilcoxon Signed Ranks Test, *n*=38; day catches, median: 0, range: 0-0, night catches: median: 0, range: 0-9, *P*=0.001), *S. schall* (Wilcoxon Signed Ranks Test, *n*=67; day catches, median: 0, range: 0-3, night catches: median: 1, range: 0-16, *P*=0.001), *Synodontis batensoda* (Wilcoxon Signed Ranks Test, *n*=22; day catches, median: 0, range: 0-0, night catches: median: 0, range: 0-8, *P*=0.018) and the threadfin *Polydactylus quadrifilis* (Wilcoxon Signed Ranks Test, *n*=15; day catches, median: 0, range: 0-1, night catches: median: 0, range: 0-3, *P*=0.018). Species richness and biomass were tested against continuous variables using GEE analysis. Categorical variables (day/night catches, sampling bolong, year and month) were also incorporated into the model, with bolong accounted for as a repeated measure variable (Table 2.2). Fish catch biomass and species richness increased with decreasing pH, increasing DO and water depth, suggesting increased standing stocks in the bolongs through the main period of high river flow, but perhaps also due to high tide levels. Fish species richness in the bolongs was significantly higher in June than in dry season reference conditions in May and subsequently lower in July and November, suggesting that bolongs were mostly inhabited by fish following the first rains and that this use subsequently declined.

2.3.5 Temporal changes in species abundance

While species richness in the bolongs and the floodplain (combined data from all methods over 2005 and 2006) did not differ significantly between months, the catches of individual species showed marked changes during the rainy season (Fig. 2.7). Catches of four species, *L. qrandisquamis*, *R. septentrionalis*, *T. guineensis* and *Hemichromis bimaculatus* peaked immediately before the rainy season; catches of three species (*C. nigrodigitatus, P. leonensis, S. schall*) peaked in the first 2 months following the onset of the rains, whereas catches of *Schilbe intermediatus, T. jentinki*, *P. normanii* and *E. spilargyreuius* were highest in the middle and latter part of the rainy season. Catches of other species such as *H. fasciatus* varied little throughout the rainy season.

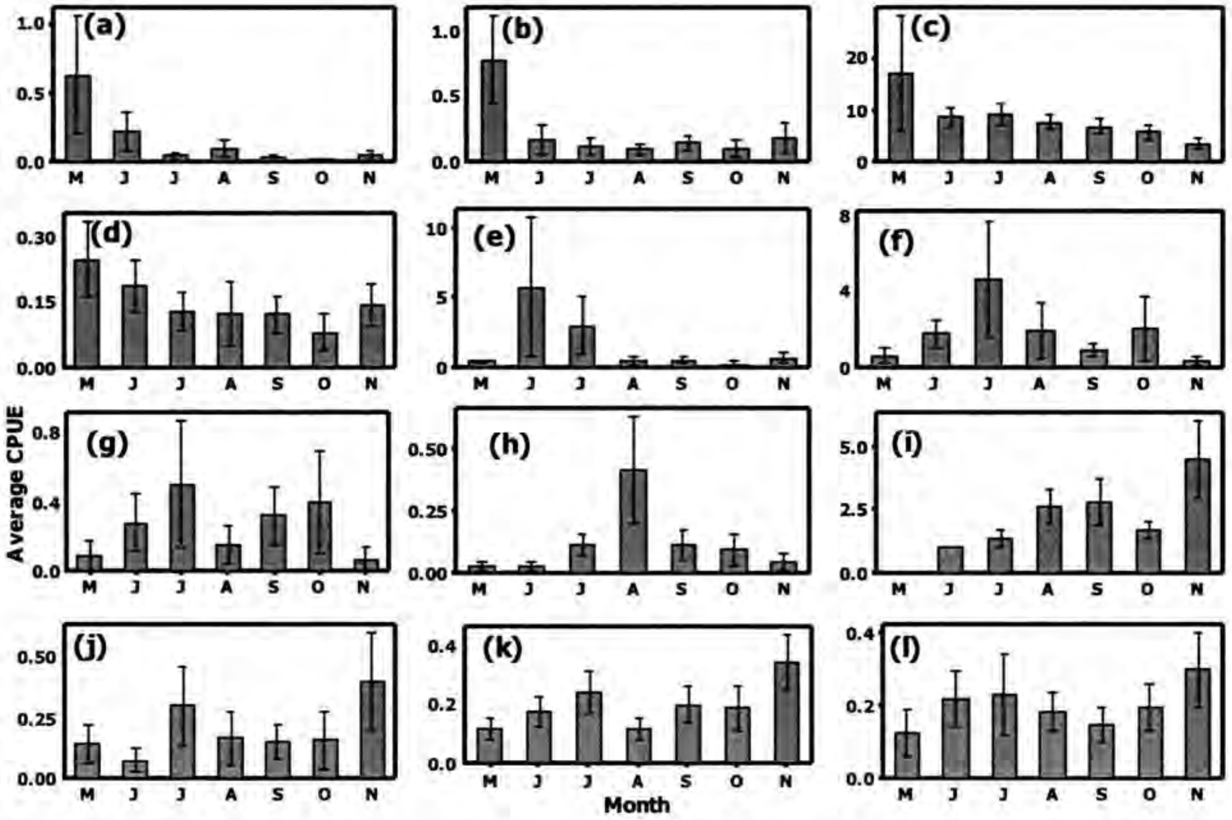


Figure 2.7 Temporal changes in mean and SE in the total catches of some of the commonest species caught in the floodplains and bolongs for 2005 and 2006; sampling effort was consistent between months: (a) *L. grandisquamis,* (b) *R. septentrionalis,* (c) *T. guineensis* (d) *H. bimaculatus* (e) *P. leonensis* (f) *C. nigrodigitatus,* (g) *S. schall,* (h) *T. jentinki,* (i) *S. intermedius* (j) *P. normani* (k) *E. spilargyreius* (l) *H. fasciatus*

2.4 Discussion

This is the most comprehensive study of fishes in the lower floodplains of the Gambia River, the last major river in West Africa without any impoundments, and provides baseline information on the structure of fish community and floodplain habitat in the vicinity of the head of tide before impoundment of the river by a hydroelectric dam. A lack of pre-intervention data is one of the common problems in determining the impacts of changes to aquatic environments, especially in equatorial regions, and this study will enable future impacts to be assessed. The study also demonstrates clear structuring of the fish assemblages by environmental factors that are predicted to change markedly downstream of the dam following impoundment (McNeil, 2006), suggesting that significant changes to the wetlands and their fish communities are likely. The effects of construction of the hydroelectric dam on downstream hydrology of the river, subsequent changes in environmental variables and impacts on the fish communities of the lower Gambia floodplains are summarised in a conceptual model (Fig. 2.8).

In total, 19 families and 39 species of fishes occurred on the lower floodplains, compared to 26 families and 95 species described for the whole of the Gambia River (Leveque *et al.*, 1991). This indicates that a substantial part of the river's fish fauna utilises the floodplains in the lower river. Six of the eight ecological categories sampled by Albaret *et al.* (2004) were present on the floodplains, with the two categories not encountered being marine ecotypes. This reflects the location of the sampling sites at the current upper limit of salt penetration, restricting the occurrence of strongly marine affiliated species in the locality. Twenty-six out of 39 species caught on the floodplains and bolongs were of estuarine/marine origin, indicating a strong influence of estuarine species on the fish communities of the floodplains. However, 12 strictly freshwater species also occurred, reflecting the current suitability of habitats for this ecological group, especially during the wet season flooding phase. No clear pattern of habitat associations of the different bioecological guilds identified above was observed in this study. This is probably because these bioecological categories were defined on the basis of the evolutionary origins and resultant salinity tolerance of each species (Albaret *et al.*, 2004). Even though these categories would be expected to be related to particular conductivity ranges, this was not always the case in this study. For example, species of freshwater evolutionary origin (e.g. *H. odoe*) and some species of marine origin (e.g. *L. falcipinnis*) were both associated with low conductivities.

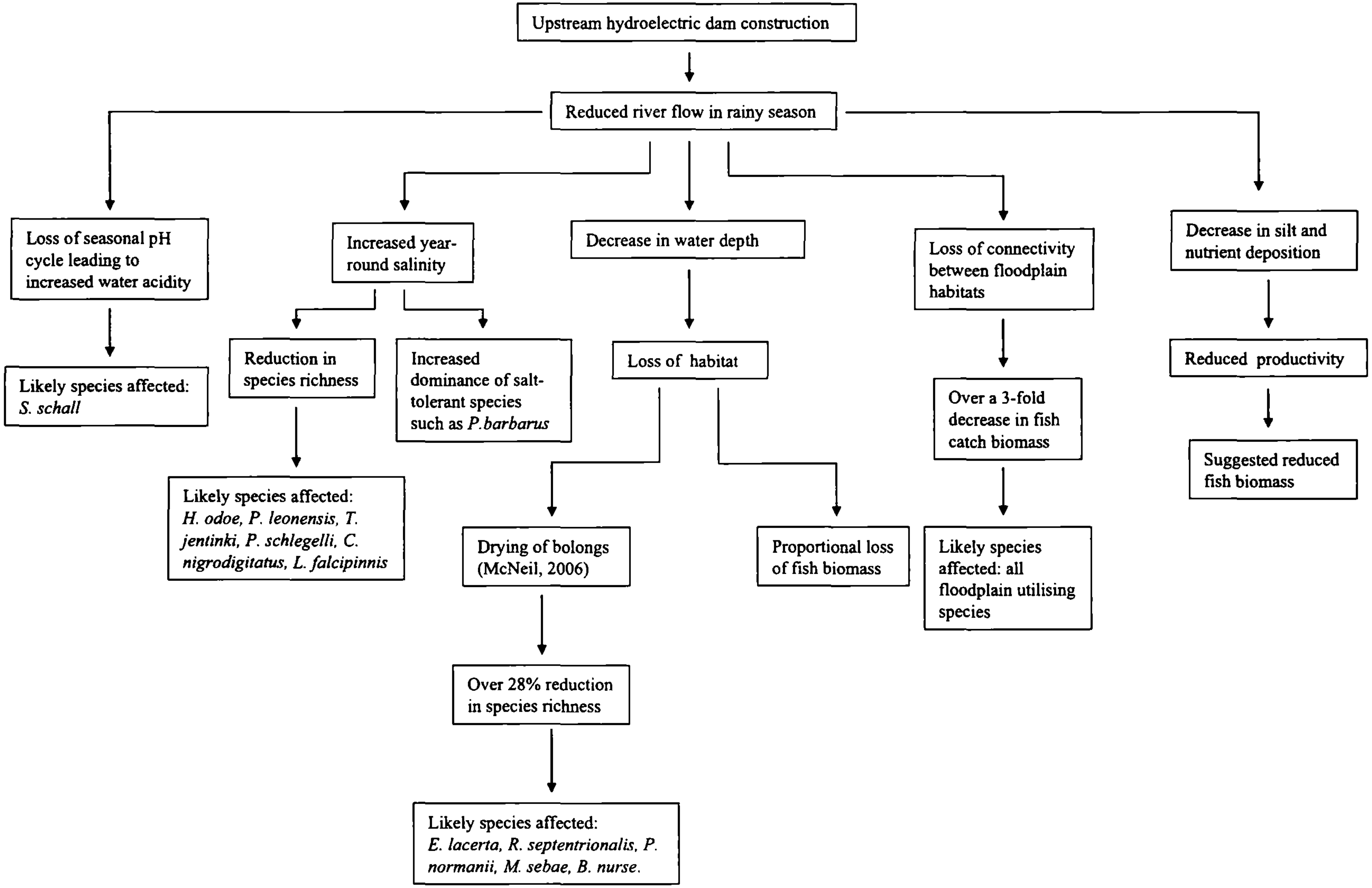


Figure 2.8 Conceptual model of the proposed effects of the hydroelectric dam on the fish communities of the lower Gambia River floodplains.

These results indicate that the fish communities of the lower floodplains are not random associations of species, but are governed primarily by four environmental factors (conductivity, pH, water depth and vegetation cover) all of which are expected to be affected after the completion of the hydroelectric dam. Reduced water flow downstream of the impoundment will result in a dramatic alteration of the flood curve of the river from the one described by Lesack *et al.* (1984), with an expected decrease in both the amplitude and the duration of the flood leading to lower water levels, increased conductivities caused by higher salt intrusion and alterations in vegetation cover and plant species composition (Fig. 2.8). Moreover, decreased connectivity between floodplain pools and the rest of the floodplain will restrict access and decrease both the number of fish species and fish biomass found in them (Fig. 2.8) as this study has shown that connectivity is a key factor affecting these attributes. Previous plans to dam the Gambia River in the late 1970s were rejected, mainly due to the anticipated changes in salinity and pH that would have severely impacted rice cultivation along the middle and lower reaches of the river (Webb, 1992). Plans for an anti-salinity barrage to block the saline intrusion were rejected, as this would have led to increased sediment acidity levels upstream of the barrage. High concentrations of iron sulphates in the mangrove soils reduce local sediment and water pH, but tidal currents limit the accumulation of this acidity (Giglioli & Thornton, 1965). The reduced tidal environment upstream of a barrage would increase retention of acidic materials and severely impact rice productivity (Webb, 1992). The results indicate that pH plays a significant role in controlling the structure of fish communities on the floodplains (Fig. 2.8), as well as possibly triggering the migration of species through the bolongs. The three commonest aquatic habitats show a clear seasonal variation pattern in pH, with lower values at the peak of the rainy season, indicating that pH is not only influenced by tidal fluctuations as suggested previously (Webb, 1992). Furthermore, higher DO values, deeper water and lower water temperature all associated with an increase in the number of species using the bolongs, with all of these parameters probably associated with higher water flows which result in increased water depth, greater oxygenation of the water, lower temperature and the washing off of iron sulphates from the soils to the water, resulting in lower pH.

These results concur with other studies from the region demonstrating the importance of water temperature and conductivity (Benech & Niare, 1998), and water level (Welcomme, 1979; Welcomme, 1985; Lowe-McConnell, 1987), as key drivers of fish migration in floodplain river habitats. The lower Gambia floodplains provide nursery or potential nursery habitats for many species and this is demonstrated by the high number of species comprising mostly immature individuals, including some of those for which adults occur mostly in the main channel rather than the floodplain (Albaret *et al.*, 2004; Ecoutin *et al.*, 2005). A fuller answer as to the importance of the lower Gambia River floodplains as nursery habitats requires analysis of the relative sources of juvenile recruitment to the adult populations, particularly for those species where the adults commonly inhabit the main channel. Species with a large proportion of mature fish tended to be small-sized (*P. leonensis, R. septentrionalis, B macrops, P. normani, E. spilargyreius, H. fasciatus, H. bimaculatus, P. schlegelli*), as these are more likely to benefit from the reduced predation pressure on the floodplains compared to the main river channel (Welcomme, 1979). Artisanal fishing in the area is not expected to be the reason for the large proportion of small-sized fish caught on the floodplains, as no commercial or large scale fishing takes place on the floodplains and in the main river channel in the area. This is also supported by Lesack (1986), who suggested that variations in fish catches in the Gambia River are due to changes in environmental variables influencing emigration and immigration, rather than fishing pressure.

The environmental impact assessment report on the hydroelectric dam project (McNeil, 2006) predicted that dam construction will result in many Gambian bolongs drying due to the reduced flows. This is expected to have a severe impact on the fish species that use the floodplain, since this study has shown that the bolongs hold the highest species richness and biomass indicating and that they are a vital aquatic habitat on the floodplains. Moreover, drying of the bolongs will restrict access of the fish onto the floodplain, decreasing further the number of species using other aquatic floodplain habitats, such as mud flats and ricefields (Fig. 2.8).

Tilapia guineensis was the commonest species encountered on the floodplains, comprising 72% of transect catches by number and was mainly encountered in mudflat and ricefield habitats (Table 2.3). It is a very important food source for people in rural areas adjacent to floodplains in The Gambia. Peak abundance of this species occurs in the first two months following the onset of the rains and then progressively declines. This is the start of the 'hungry season', when adults carry out hard manual labour in their fields waiting for the harvest at the end of the rains (Ceesay *et al.*, 1997). Consequently, reduced flows following the construction of the dam are expected to have a major impact on tilapia biomass and would, therefore, restrict a major protein supply for the local people at a particularly critical time of year.

Previous studies have shown that dam construction alters the frequency and degree of inundation of floodplains downstream of impoundments (Dumont, 1992), leading to less flooding, large increases in water salinity and decreases in DO, particularly within the tropics (Adams & Hughes, 1986). This, together with existing information (Webb, 1992; McNeil, 2006), suggests that the construction of the dam on the Gambia River could have a marked effect on the distribution and migration of the fishes in the lower Gambia floodplains since water depth, conductivity, oxygen and pH were found to be factors affecting distribution and seasonal changes in CPUE. It is anticipated that species associated with lower conductivities will disappear from the floodplains and overall decreases in DO will alter the timing of species migrations (Fig. 2.8). Salt water inundation is also likely to depress severely the cultivation of the swamp rice that is grown in large areas of the floodplains during the rainy season. Since rice is a staple diet of most Gambians, increased salinity is likely to have serious consequences for food production in the lower reaches of the river.

The construction of the dam is also likely to have a widespread impact on the ecology of the downstream area. Reduced flooding is expected to decrease the heterogeneity of the floodplains, reduce nutrient input and increase salt retention. West Africa forms part of the Palaearctic flyway and the Gambia River floodplains provide vital habitats for migrating and resident birds (Bos *et al.*, 2006). Anticipated changes in wetland vegetation and associated changes in invertebrates and fish production are expected to alter food availability for the different bird species, with possible long-term declines in avian biodiversity in the region.

Management of the dam after its construction will have to address these issues to minimise the impacts on the downstream habitats, fish and wider ecology, as well as other activities such as rice-growing. Maintaining high water flow during the rainy season in a manner that follows the natural flood regime of the river will slow down salt intrusion at the lower reaches of the river and ensure that at least some of the bolongs will stay connected with the main channel, thus allowing fish access. Moreover, periodic flushing with high water flow, ideally at the peak of the rainy season in August-September (as this coincides with the natural fluctuation in pH recorded in this study) should limit the accumulation of sulphates in the mangrove soils. Yet these activities are unlikely to be supported by a policy of maximising profitability from hydropower income generation, nor do they assist retention of water in the reservoir to support electricity generation during the dry season. Maintenance of catchment integrity and function across national boundaries can only be achieved by sensitive international cooperation and this will undoubtedly be needed in the case of the lower Gambia River.

This study identifies important factors influencing the structure of floodplain fish communities of an unimpacted, semi-arid, floodplain river system and demonstrates the sensitivity of fish communities to seasonal and spatial variations in environmental conditions. The sensitivity of species to anticipated changes in environmental conditions should always be taken into account in assessments addressing the potential impacts of impoundments on fishes and other biota. However, within semi-arid regions in particular, governments and development agencies need to take greater account of the potential impacts downstream of proposed dams, as some of the most profound environmental changes can occur a long distance from the site of intervention.

Chapter 3

Habitat associations, reproduction and diet in the Guinean tilapia, *Tilapia guineensis*, on the floodplains of the Gambia River

Abstract

The Guinean tilapia, *Tilapia guineensis*, is a common fish and food source in parts of West Africa. This species dominates the floodplain fish community of the lower Gambia River. To better understand the threat posed from the construction of a barrage across the river the ecology of this fish in the floodplains was studied, from the end of the dry season (May) to beyond the end of the rainy season (November) in 2005 and 2006. Fish were sampled using cast nets and hand nets along two transects on the river floodplains, 200 km from the river mouth. Catch Per Unit Effort of the Guinean tilapia was positively associated with higher levels of conductivity and dissolved oxygen, shallower water and less vegetation cover. The Guinean tilapia is primarily an iliophage and the peak of reproduction is at the beginning of the rainy season. Catch Per Unit Effort peaked in May, immediately before the first rains, and subsequently declined, probably reflecting increased movement into newly flooded habitat. Median size at maturity was 11.6 cm Total Length (L_T) for females and 12.5 cm L_T for males. Length-frequency analysis showed several juvenile cohorts present on the floodplains, together with very young fish in each month, suggesting continuation of reproduction throughout the rainy season.

The impending construction of a hydroelectric dam on the Gambia River is likely to negatively impact the Guinean tilapia through anticipated changes in the hydrology of the river.

3.1 Introduction

The Guinean tilapia, *Tilapia guineensis* (Fig. 3.1), is a widespread species in West African coastal rivers; its range extending from Senegal to Angola (Paugy *et al.*, 2003). This species is of substantial importance to artisanal floodplain fisheries in the region, providing an important food source for local people (Durand & Skubich, 1982). It has been proposed as a potential species for aquaculture in areas with variable salinities (such as estuaries) which prohibit the culture of other cichlids (Campbell, 1987; Legendre & Ecoutin, 1989). Nevertheless little is known of the natural ecology of this species (Campbell, 1987). The Guinean tilapia is primarily a fish of the floodplains and rarely occurs in the main river channel (Lesack, 1986; Ecoutin *et al.*, 2005). For this reason it is common on the extensive floodplains of the lower reaches of the Gambia River (Chapter 2), including brackish reaches, but is relatively less common in the middle reaches of the river (Reichard, 2008).

The floodplains of the lower reaches of the Gambia River show marked seasonal variations in inundation (Chapter 2). During the long and extremely hot dry season the flooded area contracts substantially, although side channels continue to connect with the main river. In the rainy season the rise of the river level combined with rainwater results in a 30-40% expansion of the flooded areas resulting in an extensive patchwork of shallow flooded areas and connecting channels (Lesack, 1986; section 2.3.1). In conjunction with this there are marked seasonal changes in dissolved oxygen, pH and salinity (Chapter 2). As the dominant fish species in the Gambia River floodplains and similar habitats, it is expected that the ecology of the Guinean tilapia is strongly influenced by the seasonal flooding pattern, as is common for floodplain fishes (Welcomme, 1979; Welcomme, 1985; Castro & McGrath, 2000).

Changes in the hydrology of river systems due to anthropogenic factors, such as the construction of dams can lead to profound changes in fish communities (see Chapter 2).

Considering that construction of a hydroelectric dam in the upstream reaches of the river is currently underway, with the flooding of the dam planned for 2011 (McNeil, 2006), this study presents an opportunity to study the natural ecology of this species on the floodplains of the Gambia River before impacts of the dam occur.

The aims of this study were to describe the spatial and temporal variation in the abundance of the Guinean tilapia on the floodplains of the Gambia River and investigate the reproductive and dietary ecology of this species and address the likely impacts of upstream impoundment on the species.

Figure 3.1 Picture of a Guinean tilapia collected on the Gambia River floodplains

3.2 Materials and methods

Fish were sampled along two 2.3 km transects (Fig. 2.1) between May and November in 2005 and 2006 as described in section 2.2.1. Measurements of water physical parameters and habitat descriptions are described in detail in section 2.2.2. Each sampling point was categorised as distinct habitat (mudflats, rice fields, bolongs, pools) as described in section 2.2.2.

3.2.1 Sample processing

Fish were preserved immediately in 4% formalin and identified using morphological keys (Paugy *et al.*, 2003). The Guinean tilapia hybridises with closely related species such as *Tilapia zilli* (Adepo-Gourene *et al.*, 2006; Nobah *et al.*, 2006), but due to the rarity of *T. zilli* or other closely related species in our sampling locations (Table 2.1), occurrence of hybrids was not a problem in this study. The total length (L_T) and body weight (W) were recorded.

3.2.2 Habitat use

General Estimating Equations (GEE) using SPSS (version 15) was used to identify which physical and habitat parameters influenced catches of the Guinean tilapia. This method extends generalised linear models to allow for repeated measures to be included in the analysis as well as allowing for data to be fitted to non-linear models (Horton & Lipsitz, 1999). Catch data were expressed as Catch Per Unit Effort (CPUE) by combining the average cast net catch (fish per cast net) and sweep net catch (fish per minute sweeping) for each sampling point on each occasion sampled. Because both methods were used at every site, on every occasion, in the same way, this combination is valid and integrates methods suited to catching small as well as large fish. The catch data followed a negative binomial distribution and were therefore fitted untransformed to a negative binomial distribution function with an identity link function.

Transect sampling point was accounted for as a repeated measure variable. Parameters analysed were water depth, conductivity, DO, water temperature, turbidity, percentage vegetation cover and vegetation type described in section 2.2.2

3.2.3 Reproduction and length-weight relationship

Sexual maturity of fish was determined by macroscopic examination of the gonads following the classification scheme of Legendre and Ecoutin (1989). Length at sexual maturity was determined by plotting the cumulative proportion of sexually mature fish against increasing total length and determining the median length at maturity (L_{50}) by fitting a 5-parameter sigmoid model, the model that provided the best fit to data, separately for males and females. Gonosomatic index (GSI), as a measure of reproductive condition, was calculated according to the following equation:

$$\mathrm{GSI} = 100\,(M_G / M_T)$$

where M_G is gonad mass in grams and M_T is total mass in grams.

The length-weight relationship for the Guinean tilapia was considered to follow the allometric growth model:

$$W = K\,L_T^{\,b}$$

where W is the weight in g, L_T the total length in mm and K is a constant of (10^{-5}) and b is the allometric coefficient. The parameters on the log-transformed data were obtained using least-squares analysis.

3.2.4 Population structure

Changes in population size structure of Guinean tilapia were assessed by length-frequency analysis of monthly samples. Bhattacharya's method in FiSAT (Bhattacharya, 1967;

Gayanilo *et al.*, 2005) was used to identify modes for the different size groups, using 1-cm classes. This method is an effective way of demonstrating the growth pattern and the number of cohorts and has been used for a variety of fish species (Bolland *et al.*, 2007; Nunn *et al.*, 2007; Spence *et al.*, 2007). Modal groups were distinguished on the basis of a separation index (SI), where an SI of two or more indicates a significant separation between size groups (Gayanilo *et al.*, 2005).

3.2.5 Dietary analysis

Stomach contents were examined for 1,525 tilapia, representing subsamples of a minimum of six randomly selected fish per 3-cm size category per sampling point and month from May to November. Stomachs were opened and the contents examined under a binocular microscope. Because samples were preserved in the field, progression of digestion was minimized. Although cichlids possess crushing throat teeth, which macerate food (Payne, 1978), for Guinean tilapia it was still possible to separate and distinguish the fragments of animal and plant tissue from sediment and organic detritus. Animal fragments were identified to taxonomic order with the aid of keys, while plant material was not subdivided further. Abundance of each food type identified in each fish was recorded as the wet weight of the material. Diet composition and feeding strategy was interpreted using the modified Costello method (Costello, 1990) of Amundsen *et al.* (1996). For each prey type the percentage occurrence ($\%F_i$) and the prey-specific abundance (P_i) were calculated as follows:

$$\%F_i = (N_i/N) \times 100$$

$$P_i = (\Sigma S_i/\Sigma St_i) \times 100$$

where N_i is the number of fish with prey i in their stomach, N is the total number of fish with stomach contents, S_i the stomach contents weight comprised of prey i and ΣSt_i the total stomach content weight in only those fish with prey i in their stomach. Prey abundance values for every prey item were obtained by the product of the percentage occurrence (%F_i) and prey-specific abundance (P_i), which is also represented by the area enclosed by the coordinates of the two axes on a %F_i versus P_i graph. In assigning this species to a trophic guild, prey types (starting from the commonest one) that totalled 50% of the total prey abundance were used to define the trophic guild.

3.3 Results

3.3.1 Catches and habitat use

A total of 6,524 Guinean tilapia were collected during the study. CPUE decreased during the rainy season, with highest catches recorded in May, immediately before the rains (Fig. 3.2). The Guinean tilapia was most abundant in mudflat habitats from May to August, with pools becoming more important in July relative to other habitat sites during the same month and rice fields of increased importance towards the end of the rainy season (Fig. 3.2). Using cast-net catches only, average Guinean tilapia densities in inundated mudflats were 11 fish m^{-2}, densities of 40-70 fish m^{-2} were commonly recorded and in floodplain pools densities of 500 fish m^{-2} occurred. Average catch biomass was 297g.m^{-2} (range 0-1960 g.m^{-2}).

There were marked seasonal patterns in physical parameters at the sites from which Guinean tilapia were sampled (Fig. 3.2). Conductivity and DO decreased steadily during the rainy season, whereas turbidity increased. The depth of water was shallow (average depth, 23cm), but fairly consistent throughout the rainy season. Water temperatures rose at the beginning of the rainy season with a peak in July, before a gradual decline, followed by a sharp decrease in November. There was a sharp decline in pH in August, with subsequent recovery by October. Higher Guinean tilapia catches were significantly associated with elevated DO and conductivity, shallow water and open water habitats (Table 3.1).

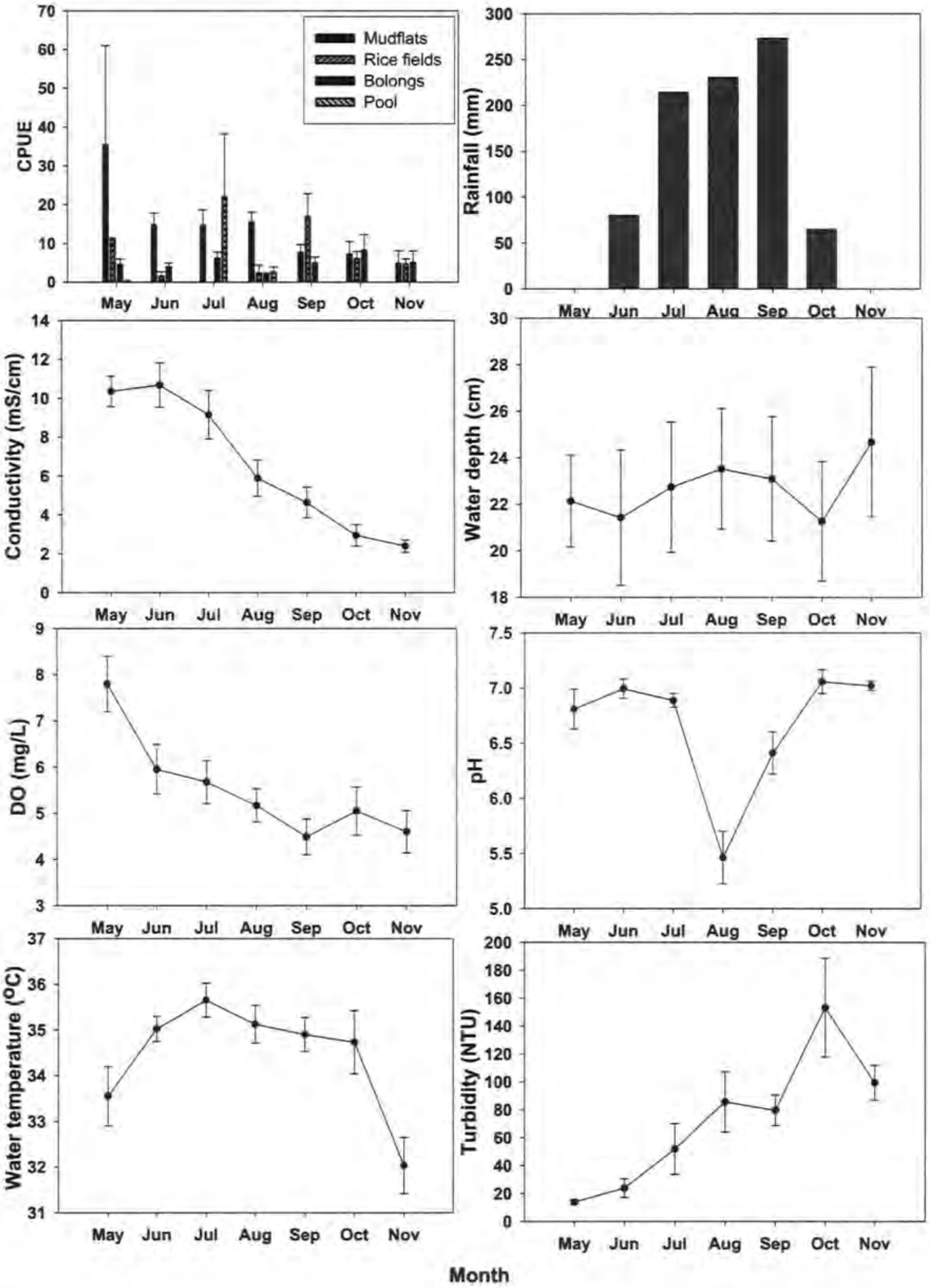


Figure 3.2 Temporal changes in CPUE (sum of catch per cast net throw and catch per minute of hand net sweeping at each site) of Guinean tilapia in relation to environmental variables during sampling periods in 2005 and 2006. Data are mean and SE except for rainfall, which is the average of the monthly totals for the two years.

Table 3.1 General Estimating Equations output for the relationship between *T. guineensis* CPUE in relation to habitat characteristics. Odd's Ratio measures the relative change in relation to one unit of change independent variables. Variation due to month and aquatic habitat were accounted for in the model.

Factors **CPUE**	**Odd's ratio**	**95% Wald C.I.** **Low**	 **High**	***P***
Temperature	0.96	0.92	1.00	0.07
pH	0.83	0.68	1.01	0.06
Conductivity	1.05	1.01	1.10	**0.02**
Water turbidity	0.99	0.99	1.00	0.23
Water depth	0.98	0.97	0.99	**<0.01**
No. of vegetation types	0.98	0.99	1.09	0.80
% vegetation cover	0.98	0.98	0.99	**<0.01**
Dissolved oxygen	1.07	1.02	1.13	**<0.01**

3.3.2 Reproduction and length-weight relationship

The median size at sexual maturity, L_{50}, was 11.6 cm L_T for females and 12.5 cm L_T males based on sample sizes of 784 females and 297 males. The smallest mature female was 5.8 cm L_T and the smallest mature male was 4.3 cm L_T. For further analysis, a L_T of 12cm was used to separate mature and immature fish for both sexes. There was a clear seasonal pattern in reproduction, with the highest proportion of mature females encountered in July, the first month of the rainy season (Fig. 3.3). The overall sex ratio of males to females was 1 : 2.46 for all fish caught, 1 : 2.45 for mature fish (those over 12cm L_T) and 1 : 2.47 for immature fish (fish less than 12 cm L_T). The sex ratio for immature fish stayed fairly constant during the rainy season, whereas for the mature fish, the highest proportion of males to females was 1 : 4.91 in July. This was followed by a steady decrease in the ratio, with the lowest value recorded in October (1 : 0.63; Fig. 3.4).

The length-weight coefficient for males was 2.97 (n=553, $r^2 = 0.97$), for females 3.08 (n=1372, $r^2 = 0.98$) and for both sexes together 3.04 (n=1925, $r^2 = 0.99$).

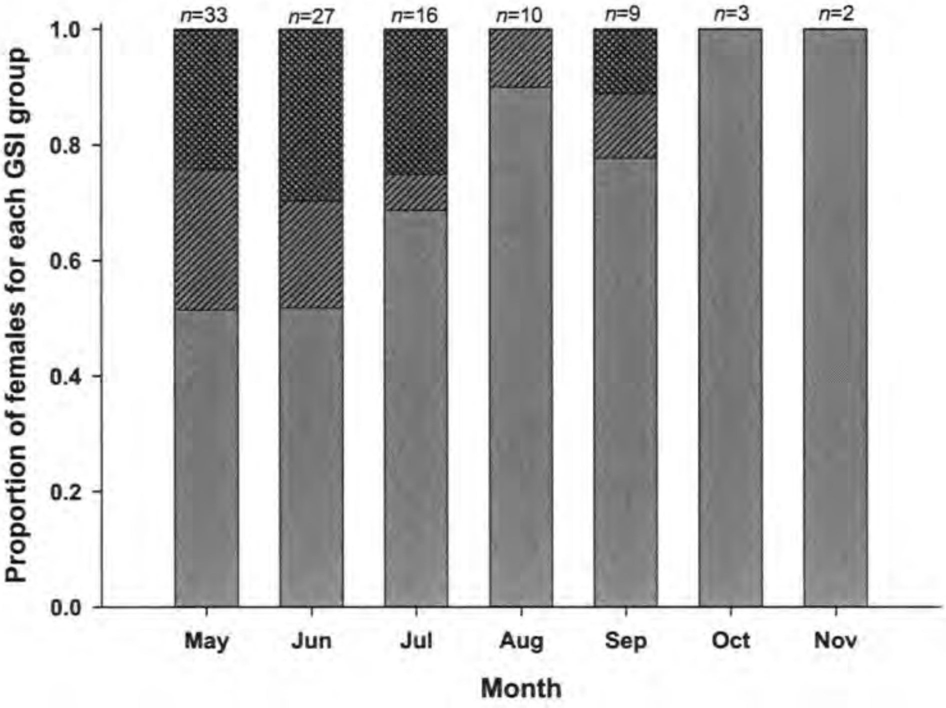


Figure 3.3 Seasonal variation in the proportion of adult female Guinean tilapia within each of three GSI groups: shaded bars (GSI: 0-0.99%), hatched bars (1-2.99%) and cross-hatched bars (≥3%). To avoid the influence of immature fish, only data from females over the median size at first maturity are shown.

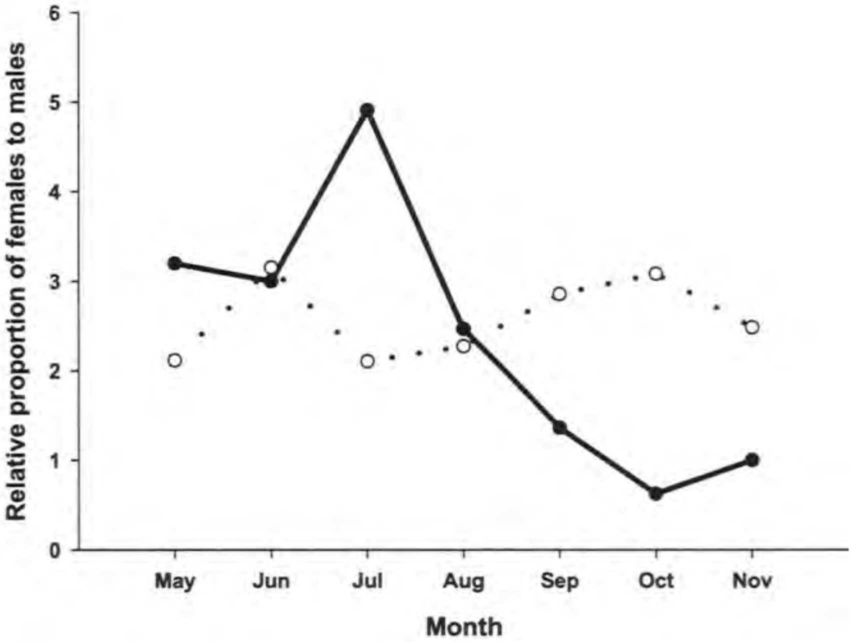


Figure 3.4 Temporal variation in sex ratio for mature (≥12cm L_T, solid line, *n*=325) and immature (< 12cm L_T, dotted line, *n*=1609) Guinean tilapia.

3.3.3 Population structure

Inspection of length-frequency plots and analysis of modal groups by month for 2005 and 2006 (Fig. 3.5) demonstrated the occurrence of several cohorts for much of the rainy season in both years. Very small fish (1-cm group) were present in June 2005 and confirm breeding at the start of the rainy season. Most of the significant modes defined by FiSAT were for immature length ranges, typically 4-7 cm L_T, 8-9 cm L_T and 11-12 cm L_T, suggesting that multiple cohorts of immature fish were present within the same season. For some months, a peak of mature fish with a L_T of 14-16 cm also appeared but numbers were normally low (Fig. 3.5).

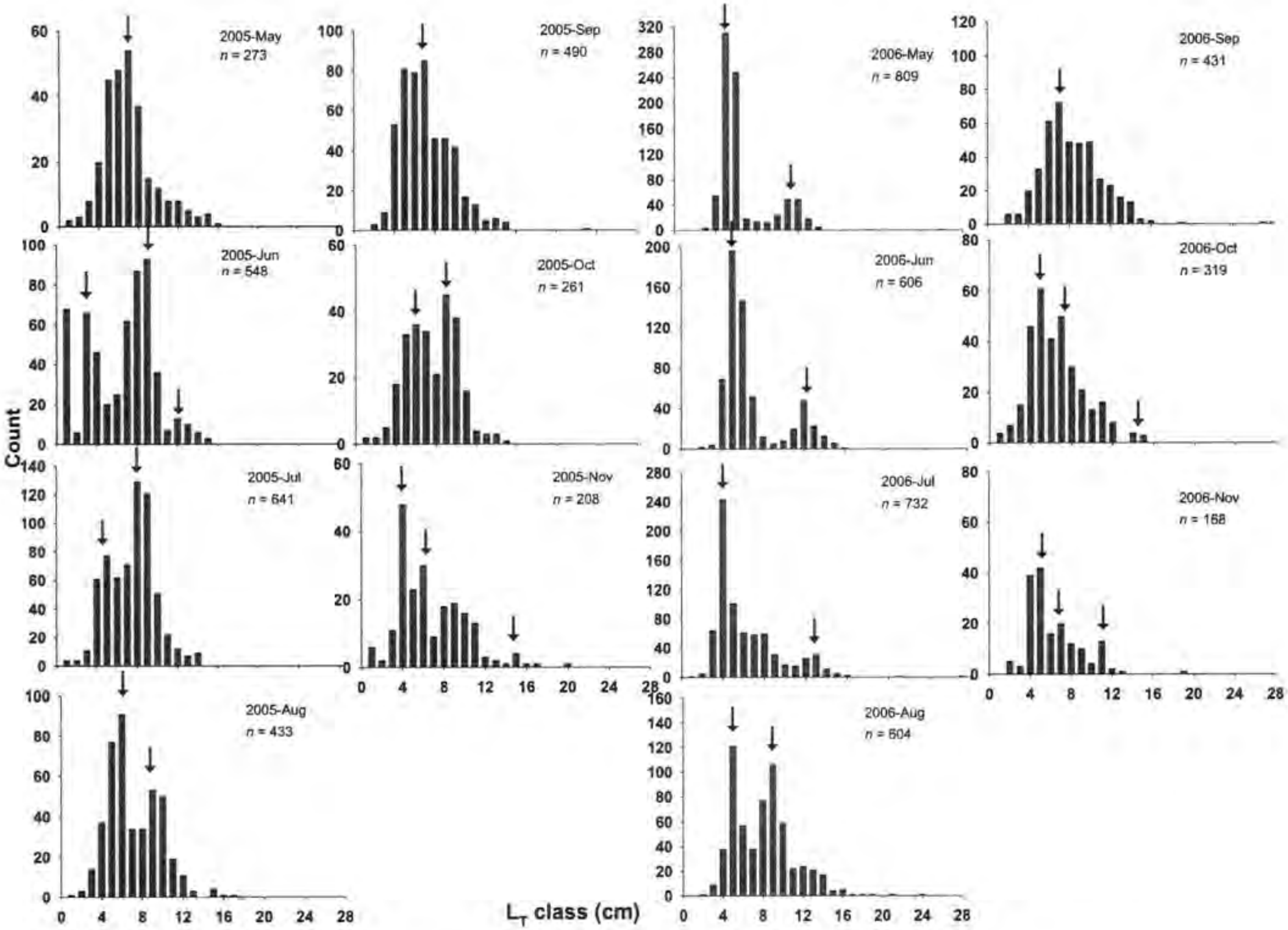


Figure 3.5 Total Length (L$_T$) frequency histograms of Guinean tilapia (both sexes combined) during the sampling period (May – November in 2005 and 2006). Arrows indicate modes identified as exhibiting significant separation by modal group analysis.

3.3.4 Diet

Diet analysis showed that Guinean tilapia is primarily an iliophage species as it feeds largely on silt, although small amounts of plant material, aquatic and terrestrial invertebrates, zooplankton, animal eggs and fish remains were also recorded (Fig. 3.6). Of the 1,525 fish analysed (mean L_T: 8.3 cm, SE: 0.1cm), 8.1% had empty stomachs, which were excluded from the analysis. For further analysis fish were divided into three size groups: 1-5 cm L_T (immature fish, size group 1), 6-11cm L_T (fish approaching maturity, size group 2) and over 12cm L_T (mature fish, size group 3) on the basis of the length at maturity data. The proportion of the diet comprising food items other than silt differed between the groups (Kruskal Wallis, n=1525, $P\leq$ 0.01), but not between months (Kruskal Wallis, n=1525, $P>$ 0.05). Size group 1 had a higher proportion of their diet comprising non-silt food items compared to both group 2 (Mann-Whitney, n=1213, Mean group 1= 0.20, Range=0.0-1.0; Mean group 2=0.09., Range= 0.0-1.0; $P\leq$ 0.01), and group 3 (Mann-Whitney, n=1213, Mean group 1= 0.20, Range=0.0-1.0; Mean group 3=0.07. Range= 0.0-1.0; $P\leq$ 0.01). No difference was observed between groups 2 and 3 (Mann-Whitney, n=1282, P>0.05), so these data were combined for presentation on Fig. 3.6. Increased, but still relatively low occurrence of non-silt dietary items by the smallest tilapia is demonstrated in Fig. 3.5. The proportion of non-silt food items in the diet varied by month for group 1 (Kruskal Wallis, n=243, $P\leq$ 0.01), but not for the other two groups (Kruskal Wallis, group 2: n=970, p> 0.05; group 3: n=312, $P>$ 0.05). Focusing on group 1, the proportion of the diet comprising non-silt food items increased from May to July, as flooding occurred, and subsequently decreased with the most silt-dominated diet observed in the last month of the rainy season in October (Fig. 3.7).

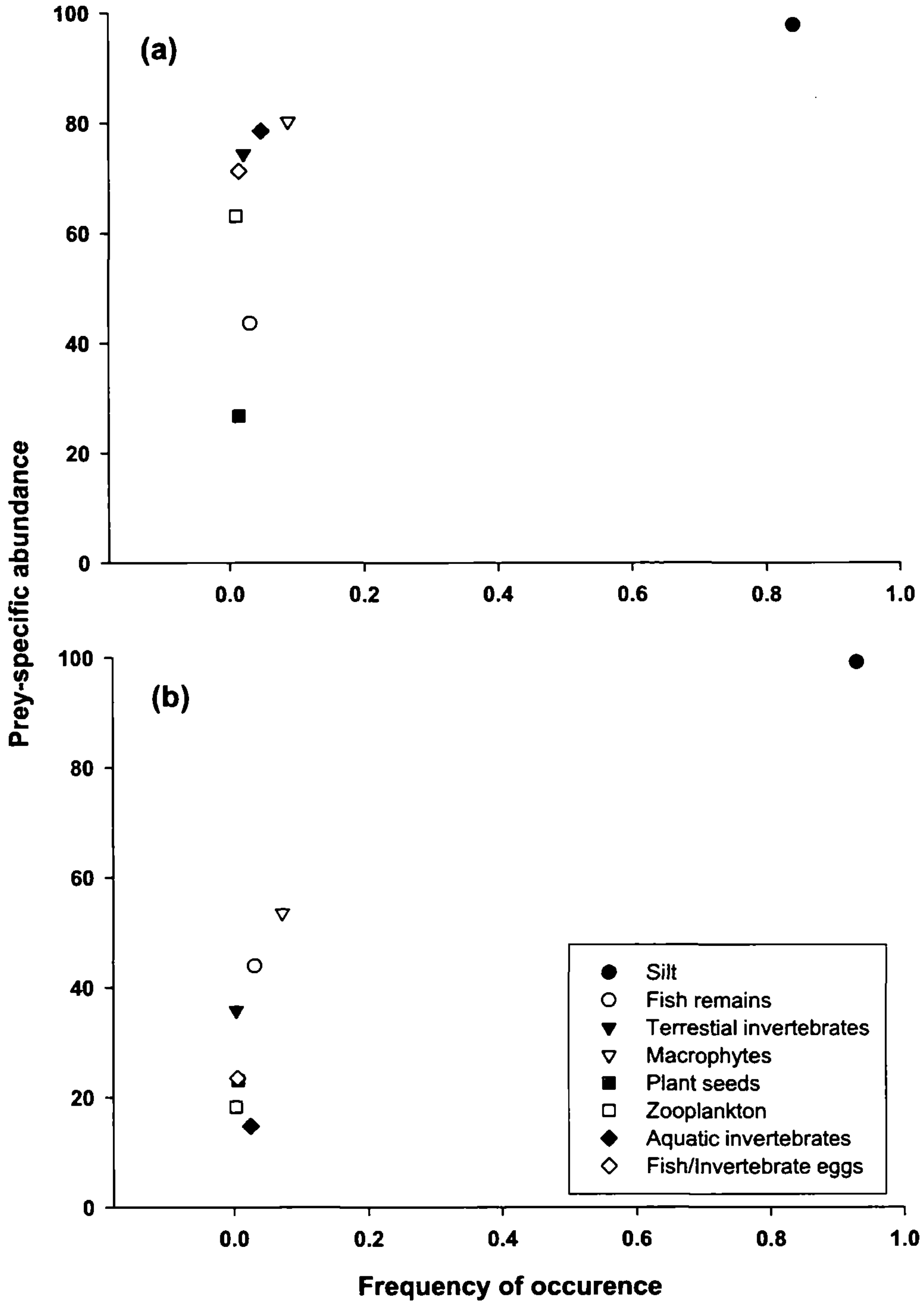


Figure 3.6 Graphical representation of the dietary composition of two size groups of Guinean tilapia: (a) 1-5 cm L_T and (b) 6 cm L_T and above.

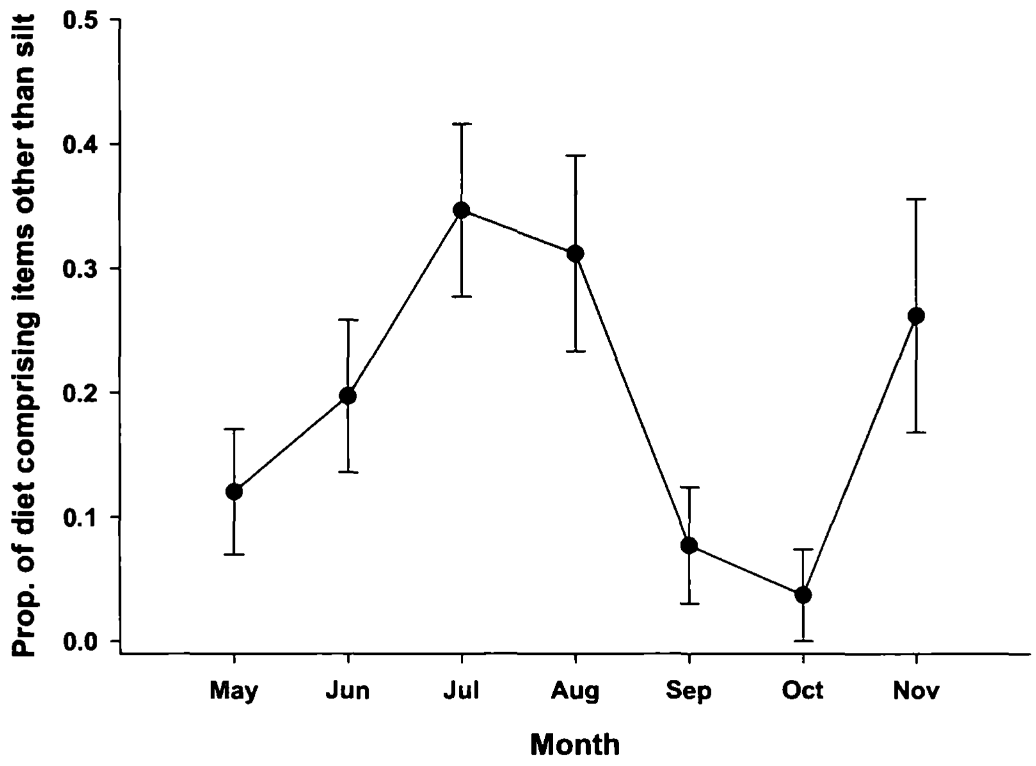


Figure 3.7 Temporal variation in the proportion of diet (by wet weight) comprising food items other than silt for 1-5cm L_T Guinean tilapia (May *n*= 42, Jun *n*= 42, Jul *n*= 47, Aug *n*= 34, Sep *n*= 30, Oct *n*= 27, Nov *n*= 21). Data are means and SEs.

3.4 Discussion

The Guinean tilapia is the dominant fish species of the floodplains of the lower Gambia River, constituting over 85% of the fish caught (Chapter 2). The flooded areas resemble salt marsh at the start of the rainy season with strongly brackish water, as well as very high temperatures, often around 35°C, although elements of freshwater habitat, such as lily beds always remain. The Guinean tilapia showed clear seasonal patterns in abundance in this harsh habitat. The highest tilapia CPUE occurred in May, immediately before the onset of the rainy season, after which there was a trend of decreasing CPUE. This reduction in catches is probably due to the 30-40% expansion of the flooded areas during the rainy season. This allows tilapias to spread over larger areas, leading to a subsequent reduction in density, reflected in reduced CPUE. The behaviour of Guinean tilapia appears highly geared to dispersal into new habitat (Chapter 4), supporting this interpretation.

Additionally, this pattern in CPUE might reflect increased numbers of Guinean tilapia moving from the edges of the main river onto the floodplain at the beginning of the rainy season. Welcomme (1979) reported that African floodplain-utilising tilapia species migrate earlier onto the floodplains than other species. This behaviour by Guinean tilapia might reflect opportunistic exploitation and reproduction in the newly flooded areas and perhaps also avoidance of the more hypoxic conditions encountered later on during the rainy season. Catches of Guinean tilapia were strongly correlated with DO (Table 3.1). Dissolved oxygen progressively declined during the rainy season (Fig. 3.2), probably due to the increased decomposition of organic matter which accumulates on the floodplains during the dry season. Dissolved oxygen is an important fish limiting factor in wetlands (Welcomme, 1979; Henning *et al.*, 2007) and can play a crucial role in limiting tilapia numbers at the later stages of the rainy season when it is at the lowest levels.

Guinean tilapia preferred shallow water habitats, as found further upstream in the Gambia River (Reichard, 2008). High Guinean tilapia catches were associated with elevated conductivity, reflecting their tolerance of strongly brackish conditions compared to many other cichlids (Legendre & Ecoutin, 1989). Tilapia catches were not affected by pH despite the low pH values encountered in August. The increased flooding, which occurs during the peak of the rainy season, causes flushing of iron sulphates from the mangrove soils resulting in a subsequent sudden increase in water acidity (Thornton & Giglioli, 1965). The Guinean tilapia CPUE was not affected by pH, suggesting that this species exhibits high tolerance of acidic water, a trait also reported elsewhere for this species (Campbell, 1987).

Guinean tilapia were more abundant in mudflat habitats in May before the first rains and subsequently moved into other habitats such as ricefields and pools as they became available with the expansion of the flood water. Pools were particularly important in July, coinciding with the first peak rainfall. This suggests that tilapias must have readily migrated into these pools at times of heavy rainfall when these pools were briefly connected to the rest of the floodplain. This is supported by evidence that under experimental conditions Guinean tilapia can successfully negotiate shallow water paths and emigrate into new aquatic habitats when they become available, particularly when at high fish densities (Chapter 4). Rice fields became more important towards the end of the rainy season, during the time when rice is transported from the rice nurseries to the newly created ricefields on the floodplains (Jarju L. unpublished data).

The median size at first maturity was 11.6 cm L_T for females and 12.5 for females, these being intermediate sizes to those reported elsewhere: (159 mm fork length in the Ebrie Lagoon, Ivory coast) (Legendre & Ecoutin, 1989) and 8 cm standard length for fish from the Niger Delta (Campbell, 1987)). The overall sex-ratio (males : females) for the Guinean tilapia on the floodplains was 1 : 2.46. The dominance of females on the floodplains is unlikely to be due to sex-biased sampling, since the species appears to be mostly restricted to the floodplain, where it was sampled in large numbers, and is uncommon in main channel habitats (Lesack, 1986; Ecoutin *et al.*, 2005). Since adults of both sexes take part in nest guarding and ventilating (Campbell, 1987) during the breeding period, one would expect to collect both sexes with equal ease. Also, thermal sex-determination can not be the reason for the female-skewed sex ratio. Although thermal sex determination occurs in fish including tilapia, high temperatures seem to favour production of males (Azaza *et al.*, 2008) and therefore would not generate the female-skewed sex ratios observed. At the whole population level, the bias in females may reflect relatively higher mortality of males. For the younger, non-reproductive fish of less than L_{50} (= 12cm L_T), the overall sex ratio did not fluctuate markedly through the rainy season. By contrast, for adults, at the start of the rainy season there were five times as many females as males captured, followed by a shift to a predominance of males later in the season. The most likely explanation for the temporal changes in sex ratio of adult Guinean tilapia is a difference in timing of movement between sexes on the floodplains. Welcomme (1979) reported that in the Kafue River floodplains, the females of certain tilapia species migrate earlier than the males. Such a pattern would fit the data here, particularly if associated with elevated mortality of females after spawning.

The Guinean tilapia exhibits relatively low GSIs compared to other tilapias and this is consistent with other studies on the reproduction of this species (Legendre & Ecoutin, 1989). Guinean tilapia reproduce primarily at the beginning of the rainy season, as most of the females with the highest GSI were collected from May-July (Fig. 3.3). This is in line with Panfili *et al.* (2006) who recorded that for 20 fish species, including the cichlid *Sarotherodon melanotheron*, reproducing in the Sine Saloum and the Gambia main river channels, all reproduced exclusively just before, or at the beginning of the rainy season.

However, the length-frequency data for all fish show that very young fish (3 cm and smaller) were present from the end of the dry season to the end of the rainy season. The same data also suggest strongly that multiple cohorts of juveniles were present within a single rainy season. Therefore, it seems that while reproduction in this species is concentrated at the start of the rainy season, it persists well after that in at least a portion of the population. It is possible that the absence of females with high GSI later in the rainy season was due to the modest sample of mature females (Sept-Nov $n = 14$) or that mature females at that time were inaccessible or unavailable for capture.

The Guinean tilapia is primarily an iliophagous species with silt dominating its diet. It is perhaps unsurprising that an iliophage should dominate an environment that is abundant in inundated mudflat areas. Although fish remains were found in some stomachs, these were mainly scales and bone fragments thought to be have been ingested incidentally with silt, rather than the digested remnants of eaten fish. Young tilapia exhibited a greater variation in their diet with macrophyte material, invertebrates, zooplankton, invertebrate/fish eggs and plant seeds each comprising over 60% of prey-specific abundance. The proportion in non-silt food items in the diet of young tilapias increases during the first half of the rainy season, before declining. As flooding occurs and new aquatic habitats form, productivity and subsequently the density of aquatic macrophytes and invertebrates normally increases (Junk *et al.*, 1989) and on the Gambia floodplains this appears to be reflected in the diet of some of the young tilapia. The more diverse diet of young tilapia, with animal protein elements, is likely to assist early development and growth and is widespread in tilapias (Campbell, 1987).

This study, demonstrates that the Guinean tilapia is well adapted to the seasonal floodplains of the Gambia River. The species is widespread across available habitats, but especially in shallow inundated areas. It exhibits clear seasonal timing in reproduction and it appears to have a strong capacity for rapid dispersal to newly available habitat. The current construction of the hydroelectric dam on the Gambia River upstream from the study area is expected to reduce overall river flow (McNeil, 2006). This will cause marked reductions downstream in the extent of seasonally flooded habitat and result in changes in environmental conditions such as an overall increase in water salinity due to the extended saline intrusion as well as a decrease in DO due to reduced levels of water movement (Adams & Hughes, 1986; Webb, 1992; McNeil, 2006). Because the Guinean tilapia is a floodplain species, the reduction in available habitat is likely to impact populations considerably.

This study shows that variations in DO and conductivity are important in determining CPUE of Guinean tilapia. The overall anticipated increase in salinity due to the construction of the dam might have a positive effect on Guinean tilapia abundance as higher catches in this study were associated with elevated conductivity. On the other hand, Panfili *et al.* (2006) showed that in the highly impacted Sine Saloum estuary in Senegal, which has an inverse salinity gradient in the estuary and high levels of salinity (>70 PSU), fish species exhibit lower size at first maturity than the same species living in the normal, unimpacted River Gambia estuary. Moreover, the more hypoxic conditions that will develop on the lower Gambia floodplains, following inundation upstream, as well as the disruption of the natural hydrological cycle, may impact reproduction and survival. It is therefore suggested that the construction of the dam will overall have detrimental effects on the populations of Guinean tilapia in the floodplains of the lower Gambia. The availability of locally-caught tilapia as food for villages may also be impacted and it seems likely that total fish production on the lower Gambia floodplains will decrease (Chapter 2).

Louca V, Lindsay SW, Lucas MC (2009). Factors triggering floodplain fish emigration: Importance of fish density and food availability. *Ecology of Freshwater Fish* **18**:60-64.

Chapter 4

Factors triggering emigration of Guinean tilapia: Importance of fish density and food availability

Abstract

Emigration is a widespread phenomenon among fish species in seasonal habitats, but little is known about the factors that trigger this behaviour. In controlled experiments using *Tilapia guineensis*, a species widely occurring in the seasonal floodplains of West Africa, density of fish played a significant role in triggering fish migration, whereas a lack of food available caused an increase in exploratory behaviour but with no impact on successful emigration. The impact of fish density and subsequently interactions between individuals on emigration suggests that this may be an important causal factor of emigration in fish species exhibiting social interactions.

4.1 Introduction

Migration is one of the commonest behavioural adaptations of animals living in seasonal environments and occurs in a variety of taxa including mammals, insects, birds and fish (Kennedy, 1951; Wolff, 1994; Lucas & Baras, 2001; Makrakis *et al.*, 2007; Castello, 2008), but surprisingly little is known of the factors that trigger individuals to emigrate to new habitats (Taylor & Norris, 2007). Emigration is defined as a one-way movement from the home area (Lidicker & Stenseth, 1992; Dingle & Drake, 2007) and suggested cues that trigger this exploratory behaviour include unfavourable environmental conditions, lack of resources, predation pressure and intra- and interspecific competition (Bell, 1991).

The relative strength of the different factors that trigger emigration may vary between species and particular environments. The proximate food limitation hypothesis assumes that territories are only important as a mechanism of capturing food (Marschall & Crowder, 1995), suggesting that only food availability truly determines the individual's decision to migrate. By contrast other studies suggest that a wider range of factors such as water temperature, flow and cover availability can trigger fish emigration (McMahon & Hartman, 1989; Keeley, 2001). Under controlled conditions McMahon & Tash (1988) recorded increased emigration rates of the desert pupfish, *Cyprinodon macularius*, in response to a doubling in densities and a consequent halving of available food and cover. Keeley (2001) found both food and density, rather than either exclusively, to be important components of demographic changes (emigration and mortality) in steelhead trout, *Oncorhynchus mykiss*. It is important to tease apart individual factors that influence fish migratory behaviour so that their relative influence can be assessed. Due to difficulties in isolating causal factors for emigration in the field, it has been suggested that only well-controlled laboratory studies can identify the truly significant factors (McMahon & Tash, 1988; Matter *et al.*, 1989; McMahon & Matter, 2006). Yet, these same experiments, on fish and non-fish taxa, have mostly been carried out on species which do not exhibit well-defined seasonal migration patterns (McMahon & Tash, 1988; Matter *et al.*, 1989; McMahon & Matter, 2006). Emigration behaviour is considered to be at least partly genetically determined (Dingle, 1980; Lidicker & Stenseth, 1992) and therefore experiments testing factors that influence emigration should also consider species adapted to seasonal environments.

Floodplain habitats are highly seasonal and provide dynamic conditions, some of which may present threats to fish and in other cases, advantages. Whilst fish may become concentrated into isolated pools or channels as water levels recede, floodwater also provides access to new habitat, which can be important for reproduction and/or feeding. Exploitation of seasonal floodplains by fishes may, therefore, be triggered by specific environmental conditions. The Guinean tilapia, *Tilapia guineensis*, is widely distributed on West African floodplains (Campbell, 1987). It is the commonest fish species encountered on the highly seasonal Gambia River floodplains, and readily colonises new habitats which become available during the rainy season (Chapters 2,3). Although most cichlids have very limited migratory habits (Hert, 1992; Lucas & Baras, 2001), this is not the case in cichlids living in seasonal floodplains habitat (Benech & Penaz, 1995). While average Guinean tilapia densities in inundated floodplain have been recorded as 11 fish m^{-2}, densities of 40-70 fish m^{-2} are not uncommon and in floodplain pools densities of 500 fish m^{-2} can occur (Chapter 3). In this species, the strongest territorial behaviour is exhibited by adult reproductive individuals which defend small areas from conspecifics (Campbell, 1987), and this is consistent with cichlid behaviour in general in which social interactions between siblings of juvenile cichlids start as simple physical encounters and avoidance and progress to elaborate lateral posturing and finally to strong sexual and dominance interactions (Valerio & Barlow, 1986; Keenleyside, 1991).

This study examined, under controlled conditions, the role of food availability and fish density in emigratory behaviour of the tropical floodplain fish, the Guinean tilapia. It was hypothesised that exploratory behaviour leading to emigration would increase with elevated density and reduced food, due to increased competition for space and food resources.

4.2 Materials and methods

4.2.1 Study site and test fish

The study was carried out at the Medical Research Council's field station at Farafenni town, The Gambia (section 2.2.1). It lies in an open flat Sudan savannah dominated by the Gambia River and the highly seasonal floodplains that border it (Svensson, 1933; Pages & Citeau, 1990).

Juvenile Guinean tilapia were collected from local floodplains using cast nets in 2007. Specimens were kept in large holding tanks for a minimum of 2 weeks to acclimatise the fish and accustom them to being fed on aquarium dried flake food (Tetramin, fed *ad libutum*). The total length of the fish collected varied from 5 to 7cm, a range that represents non-breeding individuals (Chapter 3). Young Guinean tilapia do not show any sexual dimorphism (Paugy *et al.*, 2003), so sexes were not differentiated in the study.

4.2.2 Emigration experiments

Six cement tanks were constructed under a shed with open sides so that the tanks would be exposed to the natural day/night variations in shade temperature and light, but prevent any changes in the water level of the tanks due to rainfall. Each tank was divided into two parts, each 1.0 m long and 1.0 m wide, with a water depth of 0.75 m, and a connecting ramp in the middle (Fig. 4.1; 4.2). Fish were placed on one side of the tank (A) and a clear tube (length, 7 cm, diameter, 3 cm) connected to the narrowing ramp (length, 15 cm) (Fig. 4.1), prevented return of fish which moved to the opposite side of the tank. Following introduction of fish into the holding tank, the water level was raised using a hose pipe and kept constant at 0.5 cm at the ramp (about one third of fish body depth), so as to make fish movement across the ramp challenging, so that only those individuals with sufficiently strong motivation to emigrate would do so (McMahon & Matter, 2006). Preliminary observations showed that tilapia readily approached and accessed the ramp and those that successfully traversed it did not return to the holding tank (cumulative increase in numbers in receiving compartment B and no recorded incidences of fish accessing the ramp via the tube). The effect of fish density on emigration was tested with high (40 fish m^{-2}), medium (25 fish m^{-2}) and low (10 fish m^{-2}) density treatments, densities naturally encountered in the wild, all of which were fed standard aquarium flake at a ration of 5% of fish biomass/day (Legendre & Ecoutin, 1989). Experiments lasted 7 days and comprised 12 tank replicates per treatment. For the food treatment, 25 fish per tank were used for treatment and control groups. Food (standard aquarium flake, 5% of average fish biomass/day) was provided for the control group and no food was given to the treated group for the whole 7-day duration of each experimental round. There were 12 tank replicates each for the food and control treatments.

Preliminary observations showed that fish approached and traversed the ramp throughout the day, but the lack of light prevented night-time observations. Behavioural observations were therefore carried out daily between 14:00 and 17:00, for 90 minutes in one randomly selected tank per treatment and the exploratory behaviour of the fish in that tank was assessed by counting the number of times fish moved onto the ramp (an individual fish exposing its whole body on the ramp). As the ramp was the area of the tank that became newly available at the start of the experiment, it was considered that an individual fish's effort to move onto the ramp was a good indicator of increased exploratory behaviour. The total number of fish that crossed into the emigration section over 24 hours was recorded daily at 17:00 from counts of fish in the emigration section of each tank. No mortality or loss of fish was recorded during the study. Individual fish were used only once to avoid problems related to learned behaviour.

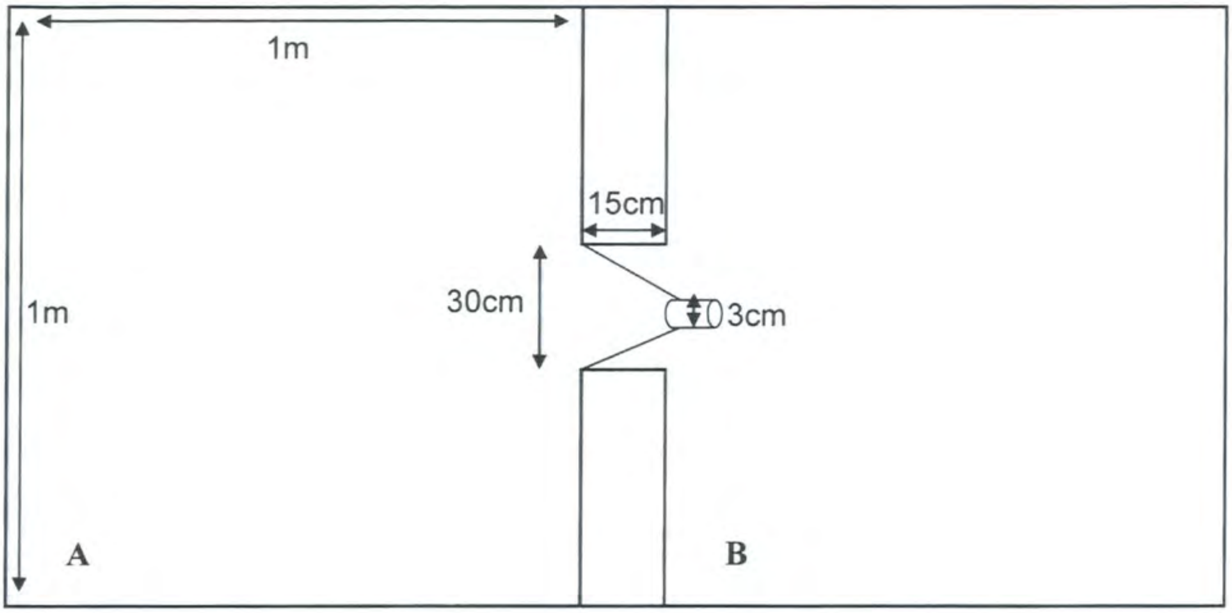


Figure 4.1 Experimental setup of the emigration test tanks. Fish were introduced on side A (75 cm deep), and emigrating individuals moved across the ramp (water depth at the ramp, 0.5 cm) to side B. The clear tube at the end of the ramp stopped fish from moving back to side A.

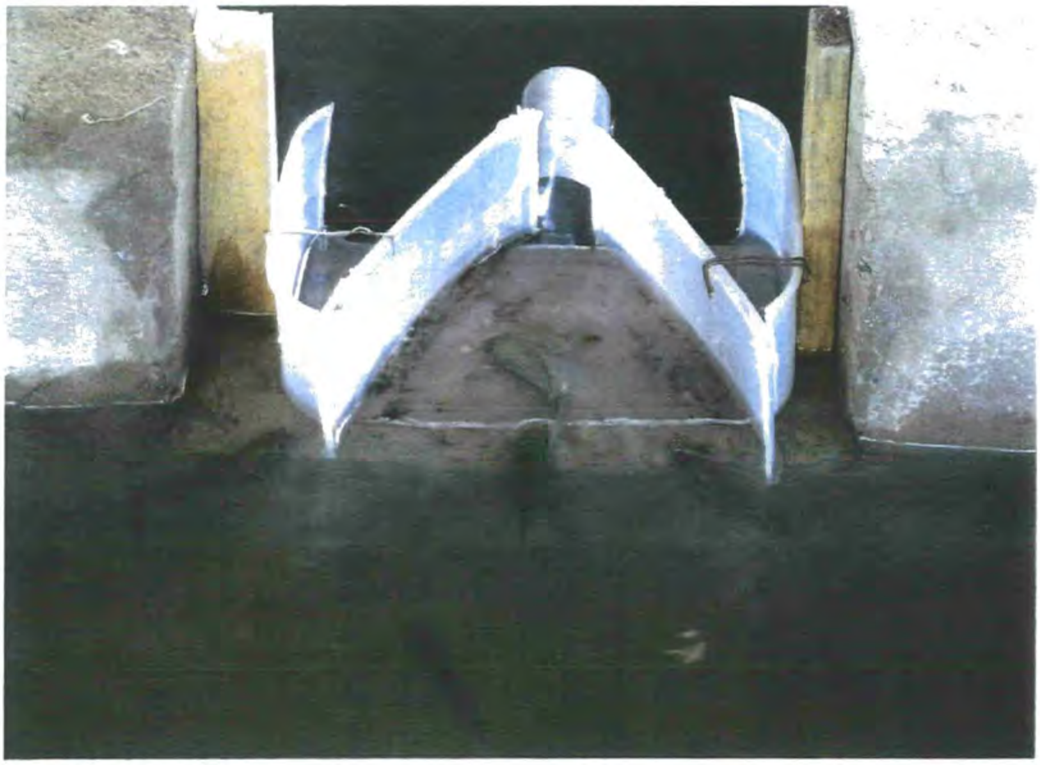


Figure 4.2 Guinean tilapia attempting to cross the shallow-water conduit.

4.2.3 Statistical analysis

The impacts of the density and food treatments on the number of fish which migrated and the number of attempted crossings were analysed using General Estimating Equations (GEE) (section 2.2.4). This analysis extends generalized linear models (GLMs) to account for repeated measures and clustering of samples as well as allowing for linear and non-linear models (Horton & Lipsitz, 1999). Since tanks were repeatedly sampled daily, it was important to select a method that accounts for repeated measures. Tank number was incorporated into the model as a repeated measures variable assuming an exchangeable correlations matrix. Data were fitted to a negative binomial distribution with a negative binomial link function as untransformed data followed a negative binomial distribution. All analysis was performed in SPSS version 15.

4.3 Results

The starting fish density in the holding tank had a highly significant effect on the proportion of fish that migrated ($P < 0.01$, Table 4.1) with the highest emigration rate observed with an initial density of 40 fish m^{-2}, with a relative odd's ratio (O.R., the proportional change relative to the reference group of 20 fish m^{-2}) of 1.48, whereas there was no significant difference between medium and low densities (Table 4.1). By contrast, food availability had no impact on the proportion of fish emigrating (Table 4.1). Both food availability (O.R. = 1.22) and the highest fish density (40 fish m^{-2}; O.R. = 1.13) caused a significant increase in the relative level of exploratory behaviour (Table 4.1). Relative levels of exploratory behaviour per fish, both for fish kept with and without food did not vary significantly over time (Table 4.1), but there was a significant decrease in the daily proportion of fish migrating for the medium (25 fish m^{-2}) fish density.

Table 4.1 Comparisons of the proportion of Guinean tilapia that successfully migrated across the ramp and relative frequency of exploratory movements onto the ramp per fish in relation to fish density and food availability. C.I. refers to confidence interval. Significant values are given in bold.

Factors		**Median**	**Range**		**Odds' ratio**	**95% Wald C.I.**		***P***
			Min.	**Max.**		**Low**	**High**	
Emigration (proportion of fish over 7-day experimental period)	High density	0.54	0.02	0.92	1.48	1.24	1.75	**<0.01**
	Med. density	0.02	0.00	0.76	1.23	0.97	1.55	0.09
	Low density	0.00	0.00	0.20	1.00	-	-	-
	No food	0.20	0.00	0.92	1.04	0.84	1.31	0.70
	Food supplied	0.02	0.00	0.76	1.00	-	-	-
Change in emigration over time (Days)	High density	0.03	0.00	0.63	0.99	0.99	1.00	0.11
	Med. density	0.00	0.00	0.62	0.98	0.97	0.99	**0.04**
	Low density	0.00	0.00	0.20	0.99	0.98	1.01	0.15
Ramp explorations (during 90-minute observation period)	High density	0.09	0.00	2.60	1.13	1.00	1.28	**0.05**
	Med. density	0.00	0.00	0.29	0.95	0.79	1.19	0.60
	Low density	0.00	0.00	0.60	1.00	-	-	-
	No food	0.15	0.00	5.50	1.22	1.05	1.41	**0.01**
	Food supplied	0.00	0.00	0.29	1.00	-	-	-
Change in ramp explorations over time (Days)	No food	0.15	0.00	5.50	0.99	0.99	0.98	0.21
	Food supplied	0.00	0.00	0.29	0.98	0.94	1.02	0.34

4.4 Discussion

For animals exhibiting social interactions, recent models based on emigration behaviour argue against resource availability as a driving force for emigration, but suggest social interaction to be a far more important factor (Wolff, 1994). However, others argue that resource availability, habitat use and social interactions and their effects on emigration are closely intertwined (McMahon & Matter, 2006). Cichlid fish are known to exhibit complex behavioural patterns with a variety of different interactions between individuals including juveniles (Keenleyside, 1991). In this study high fish density was shown to be a primary factor triggering emigration. During the dry season, the floodplains of the Gambia River are reduced to small water bodies with high densities of fish taking refuge in them (Svensson, 1933; chapters 2,3). Interactions between tilapias with established territories within those shrinking habitats and other individuals that find refuge in them during the dry season are likely to be a major factor driving fish out on to newly flooded areas at the beginning of the rainy season.

These results show that a lack of food induces increased exploration (Table 4.1), probably to find food, but there is no indication from the experimental set-up used that lack of food over the timescale of the study triggers them to make the extra effort needed to negotiate a shallow-water conduit and emigrate to a new habitat (Table 4.1). This finding is also in accordance with Mesick (1988) who concluded that food is not a strong trigger of emigration in stream-dwelling trout. These processes may be considered in the context of a mechanistic model whereby the availability of resources (e.g. food, cover, territorial space) affects the exploratory behaviour of individuals, such that elevated motivation of individuals and increased exploratory behaviour will lead eventually to emigration (Sale, 1969; McMahon & Matter, 2006). In this study the exploratory behaviour for fish with and without food did not vary over time suggesting that food availability is a relatively weak motivation for fish to emigrate. Emigration patterns in fish that occupy more permanent habitats, for example salmonids in streams and tropical fish in coral reefs are mostly well understood. Dominant fish hold territories and subordinate individuals exhibit increased exploratory behaviour and emigration, with subsequent high costs for the emigrating individuals, which often move to areas of poor quality habitat where energy gain may be low and predation risk high (Clarke, 1970; Larson, 1980; Marschall & Crowder, 1995; Keeley, 2001). However, if local resource availability is low, substantial costs can also be involved for fish that do not emigrate (McMahon & Tash, 1988), so there is a potential trade off of fitness costs and benefits to emigration. In the case of species such as the Guinean tilapia, which utilise seasonally flooded areas, emigrating into newly flooded, high-quality habitat unoccupied by other fish and with few aquatic predators can be expected to increase their survival chances (Welcomme, 1979; Lowe-McConnell, 1987; Lucas & Baras, 2001). In these habitats emigration may, therefore, be a characteristic of strong fitness benefit.

Louca V, Lucas MC, Green C, Majambere S, Fillinger U, Lindsay SW (2009). Role of fish as predators of mosquito larvae on the floodplain of the Gambia River. *Journal of Medical Entomology* **In Press**.

Chapter 5

Role of fish as predators of mosquito larvae on the floodplains of the lower Gambia River

Abstract

This study examined the potential of using native fish species to regulate mosquitoes in the floodplains of the Gambia River, the major source of mosquitoes in rural parts of The Gambia. Fishes and mosquito larvae were sampled along two 2.3 km long transects, from the landward edge of the floodplains to the river from May to November, from 2005 to 2007. A semi-field trial was used to test the predatory capacity of fish on mosquito larvae and the influence of fish chemical cues on oviposition. In the field there was less chance of finding culicine larvae where *Tilapia guineensis*, the commonest floodplains fish, was present; although the presence of anophelines was not related to the presence or absence of any fish species. In semi-field trials both *T. guineensis* and *Epiplatys spilargyreius* were effective predators removing all late-stage culicine and anopheline larvae within one day. Under semi-field conditions, fewer culicines oviposited in sites with fish, suggesting that ovipositing culicine females avoid water with fish. In contrast, oviposition by anophelines was unaffected by fish. These studies demonstrate that *T. guineensis* is a potential candidate for controlling mosquitoes in The Gambia as it achieved a high reduction in early instar anophelines, but can only be used in confined sites where water persists for substantial periods.

5.1 Introduction

The use of fish for controlling mosquitoes was an important tool in the pre-DDT era (Floore, 2006; Walker & Lynch, 2007). Typically fish were introduced into all potential mosquito breeding habitats, including ricefields, marshes, dams, canals and ponds (Hadjinicolaou & Betzios, 1973; Motabar, 1978). However, the introduction of DDT in the mid-1940s led to a significant decrease in the use of biological control (Gabaldon, 1969). Nevertheless, following concerns regarding the harmful effects of chemicals on non-target species and the development of insecticide resistance by mosquitoes (Milam *et al.*, 2000), interest in the biological control of malaria vectors has been rekindled (Killeen *et al.*, 2002b; Killeen, 2003).

Fish have been used successfully for controlling both culicine and anopheline mosquitoes (Tabibzadeh *et al.*, 1970; Victor *et al.*, 1994) but used relatively infrequently in sub-Saharan Africa (Walker & Lynch, 2007). Mosquito control using fish has focused on a limited number of species, primarily *Gambusia affinis*, and *Poecilia reticulata* that have traditionally been used for controlling mosquito larvae (Sitaraman *et al.*, 1975; Gall *et al.*, 1980; Cech & Linden, 1987; Homsky *et al.*, 1987; Blaustein, 1992; Valero *et al.*, 2006; Walton, 2007). One of the most important concerns when introducing exotic fish for mosquito control is their impact on native species (Benigno, 2001; Hoddle, 2004). In Greece the introduction of *G. affinis* led to a decline of the endemic fish species *Valencia letourneuxi* (Economidis, 1995), with similar findings reported elsewhere (United States (Leyse *et al.*, 2004), Spain (Garcia-Berthou, 1999), Australia (Arthington, 1991)). The problems with introducing exotic species have spurred interest in the use of native species for controlling mosquitoes (Romand, 1985; Mancini & Romi, 1988; Fletcher *et al.*, 1992; Fletcher *et al.*, 1993; Frenkel & Goren, 1999; Lee, 2000; Kusumawathie *et al.*, 2006a; Marti *et al.*, 2006; Yildirim & Karacuha, 2007).

Using fish for mosquito control can be unpredictable with several failures reported in the literature (Bence, 1988; Blaustein, 1992). However, the number of failures may be larger due to publication bias, over-representing successful trials. The importance of mosquito larvae in the natural diet of fish, exclusions of mosquitoes from aquatic habitats due to predation or avoidance by ovipositing female mosquito have rarely been investigated, with studies often reporting contradictory results. In Colombia, larvae of *Anopheles albimanus*, were found to be negatively associated with fish as well as predatory invertebrates, such as dragonfly and mayfly nymphs (Marten *et al.*, 1996). This phenomenon is thought to be far more widespread in nature with predatory fish influencing the distribution of many species of aquatic invertebrates (Wellborn *et al.*, 1996; Maddrell, 1998). In contrast in Pakistan, larvae of *Anopheles subpictus*, were positively related with the presence of aquatic predators including fish, although the authors were unable to provide an explanation for this (Herrel *et al.*, 2001).

Several aquatic invertebrate taxa have evolved avoidance behaviors to minimize predation risk (Kerfoot & Sih, 1987; Tjossem, 1990; Resetarits, 2001; Abjornsson *et al.*, 2002). This behavior has also been reported in mosquito species, mainly culicines, in response to both invertebrate and vertebrate (mainly fish) predators (Spencer *et al.*, 2002; Kiflawi *et al.*, 2003; Angelon & Petranka, 2004; Bond *et al.*, 2005; Munga *et al.*, 2006a). Identifying whether mosquitoes detect and avoid ovipositing in habitats containing fish is important as it affects the efficacy of fish to control mosquitoes since gravid female mosquitoes may select alternative breeding sites. Considering the importance of African anopheline mosquitoes in the transmission of malaria and the renewed interest in using fish for mosquito control, it is surprising that no studies have been carried out to determine whether *Anopheles gambiae* s.l., the principal vector of malaria in Africa, avoids fish. Whilst several studies have examined the potential of native fish species to control African malaria vectors, the importance of these species in the ecology of the mosquito has been overlooked (Kumar & Hwang, 2006). This study, therefore, tested the hypothesis that native fish species can be used for mosquito larval control in West Africa. The following predictions were tested: 1) the absence of aquatic stages of mosquitoes will be associated with the presence of certain floodplains fish species under natural conditions, 2) the diet of these fish species will include mosquitoes, 3) the presence of insectivorous fish will reduce oviposition by female mosquitoes under semi-field conditions, and 4) insectivorous fish will be efficient predators of mosquitoes under semi-field conditions as well as larger-scale rice field plots.

The study was carried out in the floodplains of the Gambia River, the major source of anopheline mosquitoes in rural parts of The Gambia (Bøgh *et al.*, 2007; Majambere *et al.*, 2008). This study formed part of a larger project investigating the use of microbial larvicides for controlling malaria vectors and, taking into account the lack of published information on the indirect effects of microbial larvicides on fish communities in lentic systems, allowed an investigation at a pilot-study scale whether this activity affected fish populations in the floodplains.

5.2 Materials and methods

5.2.1 Study area

This study was conducted along two transects, as described in Chapter 2 (Fig. 2.1). The transects were chosen to cross all vegetation zones typical of the floodplains. Rains occur from June to October, with the highest long-term rainfall recorded in August. Baseline data were collected in 2005 when no sites were treated with larvicide. In 2006, transect 1 was treated with *Bacillus thuringiensis* var. *israelensis*, followed by transect 2 in 2007 (Majambere *et al*, in prep).

Each transect was located at the center of a zone approximately 100 km^2 in area, where all aquatic sites were treated at weekly intervals from May to November. In 2006 approximately 2,200 Kg of Bti WDG and 1,200 Kg Bti CG was applied in spray zone 1, with 3,200 Kg Bti WDG and 3,700 Kg Bti CG in 2007 in zone 2. The floodplains in this area was characterized by a stretch of mangroves along the main river channel and some of the larger connecting creeks. Behind the mangroves were continuous areas of mudflats which were often entirely barren because of the prolonged desiccation during the dry season and high content of soluble salts, mainly chlorides and sulphates (Giglioli & King, 1966). Ricefields occurred in two belts on the floodplains, one along the landward edge of the floodplains and the other closer to the river. Mudflats that receive periodic flooding in the dry season from the spring tides support the perennial *Sesuvium portulacastrum*, as well as seasonal *Heleocharis* spp and beds of *Paspalum* spp (Giglioli & Thornton, 1965; Bøgh *et al.*, 2007). The area was therefore characterized by the presence of some salt marsh vegetation, but also retains characteristic freshwater flora such as water lilies (*Nymphaea* spp.) in some habitats, such as semi-permanent pools.

5.2.2 Field mosquito and fish sampling

The two transects (Fig. 2.1) were sampled monthly from May to November in 2005, 2006 and 2007, beginning approximately one month before the rains and ending one month after the rains. Mosquito larvae were sampled by taking ten dips with a standard mosquito dipper (350 ml capacity dipper, Clarke Mosquito Control Products, Illinois, USA) every 150 m along each transect between 07:00 and 13:00h. Dips were made within 20 m either side of the transect point. The presence or absence of anopheline and culicine larvae at each sampling site was recorded. Late anopheline larvae were transferred to plastic containers with water from the sampling site and transported to the laboratory and allowed to emerge for subsequent identification.

Fish sampling took place along the transects within 20 m of the mosquito-sampling locations using a cast net and hand nets as described in section 2.2.2. Together these two methods provided effort-standardized sampling throughout the study period along floodplain transects. Fish were preserved in 4% formalin and taken to the laboratory for subsequent identification. Fish were identified to species using Paugy *et al* (2003b). The aquatic habitat type at each sampling location on the transect was categorised as described in section 2.2.2.

5.2.3 Diet analysis

The modified Costello method (Costello 1990) of Amundsen et al. (1996) was used to describe the feeding habits of the different fish species and to identify the insectivores, the feeding guild most likely to prey on mosquito larvae. This methodology is described in section 3.2.5. The diet guilts were: detritivores (feeding primarily on organic detritus); insectivores (aquatic/terrestrial insects); piscivores (feeding on other fish); molluscivores (feeding on mollusks); illiophage (feeding on silt).

5.2.4 Semifield – Predation experiment

This experiment was based on a setup that had been used previously for testing the efficacy of microbial larvicides in the field (Fillinger *et al.*, 2003; Majambere *et al.*, 2007). Twenty-five plastic bowls with an upper diameter of 53 cm, a lower one of 40 cm and a height of 40 cm (70 L volume) were sunk into an open sunlit area on the MRC field station in Farafenni with the lip protruding 5 cm above the soil. Bowls were set out in a grid 2 m apart, with five rows of five bowls (Fig. 5.1). Overflow holes were created in each bowl, 35 cm from the bottom, to allow excess water to run-off during heavy rains. These holes were 1 cm in diameter and were covered with untreated nylon mosquito netting (mesh: 0.2 mm) to prevent larvae and fish from escaping. A collar of netting (inner diameter: 25 cm, mesh: 1 mm) was placed around the rim of each bowl, directed inwards and upwards at a 45° angle, to prevent any fish present from jumping out of the bowls.

Each bowl was filled with soil to a depth of 5 cm and 30 cm of unchlorinated tap water. The soil was thoroughly mixed beforehand to prevent variations in the soil conditions between bowls. Bowls were allowed to be colonized by mosquitoes for eight days and for late instar larvae to develop. Subsequently, the 25 bowls were ranked in terms of their anopheline larval densities at the end of the 8-day period. The 18 bowls with the highest densities were kept and the rest emptied. Subsequently, these bowls were separated into six groups of three each with similar anopheline densities. The two treatments, addition of six *E. spilargyreius* (average biomass: 0.45 g/70L) or six *T. guineensis* (average biomass: 26.3 g/70L) per bowl, and controls, with no fish, were assigned randomly within each one of these six groups.

Epilatys spilargyreius was selected for this experiment since this species was most frequently found with mosquito larvae in its stomach and was also the most common insectivore species and a surface feeder, while *T. guineensis* was selected because it was the most abundant fish in the floodplains (Table 5.1), a bottom feeder and is known to readily emigrate and colonize newly available floodplain habitats (Chapter 2; Chapter 3). Over 200 individuals of both species were collected from the floodplains. Each fish species was kept in separate stock containers and fed on standard aquarium flake food (Tetramin, fed *ad libitum*) prior to use in the experiments. Individual fish were used only once during the experiment to avoid the influence of learned behavior on mosquito predation. Fish of similar sizes were used to avoid variations within, but not between species in the predatory capacity due to size differences. The size range for *E. spilargyreius* was 3-5 cm total length (L_T: tip of snout to margin of caudal fin), and for *T. guineensis*, the range was 5-7 cm L_T. This represents the most appropriate sizes that can survive adequately in the experimental bowls used for this project, but also includes the size at which these fish are commonly found in floodplain habitat.

The experiment was run for a further 12 days. Mosquito sampling took take place daily between 17:00 and 19:00. Five dips were taken from each bowl using a standard dipper, four from the sides and one from the center. The presence or absence of anopheline and culicine larvae was noted and recorded as early (first and second instar), late (third and fourth instar), or pupae. All larvae were replaced, whilst pupae were removed for subsequent species identifications as described below. Any dead fish were replaced with fish kept in the holding bowl.

Figure 5.1 Predation semifield setup

5.2.5 Semifield – Oviposition cues

Nine bowls were placed 4 m apart in a grid arrangement in the same location as described above for the predation experiment. The greater distance between bowls than in the predation experiment was used to reduce the possibility of mosquitoes confusing chemical cues between bowls. Each bowl, including controls had a 20 x 20 x 20 cm netting cage (mesh size: 0.2 mm) suspended in the middle of the bowl, approximately 1 cm below the water surface. Three randomly chosen bowls contained six *E. spilargyreius* placed within the cage, three had six caged *T. guineensis* and three without fish served as controls. Dipping for mosquito larvae was carried out as described above for seven days after first colonization, while the bowls were left open and oviposition continued. Three separate trials were carried out. New bowls were used between trials and experiments to avoid cross-contamination of fish chemical cues.

5.2.6 Mosquito identification

All pupae collected from the semifield experiments and late anopheline larvae from the field study were placed in separate individual mosquito cages and allowed to eclode. Adult anophelines were identified morphologically using Gillies and DeMeillon (1968). Culicine mosquitoes were identified as *Culex quinquefasciatus* Say, *Toxorhynchites spp*, *Aedes vittatus* Bigot and other culicines. Sibling species of the *An. gambiae* complex were subsequently identified by amplification of ribosomal DNA using the polymerase chain reaction (PCR) (Scott *et al.*, 1993).

5.2.7 Ricefield pilot study

Studies were undertaken in natural ricefields to assess the effectiveness of *T. guineensis* to control mosquito larvae under natural conditions. The ricefields were located in Tamba Koto Village (UTM coordinates: 1331776N, 1530990W), 11 km east of Farafenni town, an area that flooded for 9 weeks in the previous year and where anopheline larvae were found close to the landward edge of the floodplains (Jarju *et al.*, in prep). One ricefield was divided into 16, 5 x 5 m plots by constructing 50 cm high embankments around each plot using soil collected from the same area. Eight randomly selected plots served as controls and in the rest, 50 *T. guineensis* were introduced into each plot (size range 5-7 cm L_T, as in section 5.2.4), following the natural flooding by rainfall of all plots. One emergence trap (1 m^2) was placed in the centre of each plot to estimate the average weekly abundance of adult mosquitoes and other emerging invertebrates (details of the methodology can be found in Fillinger *et al.* (in prep.)). Furthermore, larval surveys were implemented using a standard dipper as described above for the field sampling.

5.2.8 Statistical analysis

Data were entered using EpiInfo version (TM). Due to the large number of sites sampled for which zero counts of mosquito larvae were obtained, mosquito data were transformed to presence or absence of larvae. Canonical Correspondence Analysis (CCA) (Ter Braak, 1986) was used to analyze the influence of environmental variables (habitat type, treated/untreated with larvicides, transect, year, distance from the floodplain edge, percentage vegetation cover, sampling month and presence/absence of each of the four commonest insectivore fish species, as well as the commonest fish species, *T. guineensis*), on the presence/absence of anophelines and culicine larvae. A partial CCA was undertaken with sampling point controlled for as a covariable to account for repeated measures. Only environmental variables explaining a significant additional proportion of variance were used to avoid possible collinearity effects. Forward selection was used to identify significant variables and each variable was tested using Monte Carlo permutation test (999 runs). The CCA multivariate method is a descriptive approach that does not quantify the impact of each of the variables on the mosquitoes individually. Therefore, the impact of each of the variables identified using CCA on the presence/absence of anophelines and culicines was tested with General Estimating Equations (GEE) using SPSS version 15 (section 2.2.4). A binomial distribution with a logit link function was used to test the effect of those variables identified by

CCA as having a significant impact determining the distribution of positive and negative anophelines and culicine sites on each of those mosquito groups separate. All *P*-values were adjusted to account for the number of comparisons carried out.

For those fish species that significantly influenced the distribution of mosquitoes in the field, separate analyses were carried out using only the hand-net samples, as these were collected from the edges of aquatic habitats where mosquitoes were also sampled, reflecting a better representation of possible interactions between fish and mosquito.

Semifield data were incorporated untransformed in a mathematical model and analyzed using GEE analysis. Bowl identity was accounted for as a repeated measures variable assuming an exchangeable correlations matrix. For the predation semifield experiment the presence of anopheline and culicine mosquito was tested against the two fish treatments using a binomial distribution with a logit link function to test the predatory capacity of the two fish species.

In the oviposition experiment, larval densities (number of larvae per dip) were tested against the two fish treatments using a normal distribution and a log link function as a better goodness of fit was achieved with this distribution model compared to using a binomial model and testing presence/absence of mosquito. Comparisons between treatments were made only when at least one bowl was colonized by mosquitoes. The percentage reduction in larval mosquito densities was calculated using the formula of Mulla *et al* (1971):

$$\%\ \text{Reduction} = 100 - (C_1/T_1 \times T_2/C_2) \times 100,$$

where C_1 and C_2 describe the average number of larvae in the control tanks pre and post treatment, T_1 and T_2 describe the average number of larvae in the treated with fish tanks pre and post treatment.

A Poisson probability distribution with a log link function was used to test the impact of spraying with microbial larvicides on the fish species richness (number of fish species caught). The Poisson distribution model is appropriate for counts of animal/plant units and is therefore appropriate for testing species richness (Ter Braak & Smilauer, 2002). Catches of the commonest six fish species followed a negative binomial distribution, therefore a negative binomial distribution model, with a negative binomial link was used to test the impact of microbial larvicide spraying on the abundances of these species.

5.3 Results

5.3.1 Mosquitoes and fish feeding habits

A total of 11,013 fish were caught along the transects between 2005 to 2007 (Table 5.1). *T. guineensis* was the dominant species comprising over 86% of the combined catch with an average density of 11 fish/m^2 (range: 0-518 fish m^{-2}) and an average catch biomass of 296 gm^{-2} (range: 0-1959 $g.m^{-2}$) (see also Chapter 3). As most species were rare, with only a few individuals caught, reliable diet data could only be obtained for 12 species. For *E. spilargyreius*, the second species tested under semifield conditions, the average density was 0.1 fish/m^2 (range: 0-1 fish m^{-2}) and average biomass of 0.02 gm^{-2} (range: 0-0.1 gm^{-2}). Fish belonging to several feeding guilds were identified (Table 5.2), but only three species were collected with mosquitoes in their stomachs. Adult mosquitoes were observed in stomachs of *Rhambdalestes septentrionalis* and anopheline larvae in *Ctenopoma kingsleyae*, while culicine larvae occurred in *E. spilargyreius* and *R.. septentrionalis*. The insectivores mostly consumed aquatic Hemiptera, adult stages of terrestrial insects (Diptera, Coleoptera), larval/pupal stages of non-mosquito Diptera and Odonata nymphs (Table 5.2).

Table 5.1 Relative percentage of catches of all fishes sampled in the Gambia River floodplains from 2005 to 2007. The two species used in predation and oviposition tests are given in bold.

Family	Fish species	% catch	Mean catch biomass (g/m^2)
Elopidae	*Elops lacerta*	0.32	0.18
Clupeidae	*Pellonulla leonensis*	0.05	0.06
	Sardinella maderensis	0.03	<0.01
	Ethmalosa fimbriata	0.04	<0.01
Hepsetidae	*Hepsetus odoe*	0.04	0.27
Characidae	*Rhambdalestes septentrionalis*	1.13	0.09
	Brycinus nurse	0.04	0.04
Cyprinidae	*Barbus macrops*	0.05	<0.01
Bagridae	*Chrysichthys nigrodigitatus*	0.39	0.31
	Chrysichthys johnelsi	0.04	0.06
Clariidae	*Clarias anquillaris*	0.05	0.01
Mochokidae	*Synodontis schall*	0.03	0.05
	Synodontis batensoda	0.02	0.05
Cyprinodontidae	*Poropanchax normanii*	4.10	0.01
	Epiplatys spilargyreius	2.35	0.02
	Epiplatys bifasciatus	0.18	<0.01
	Aplocheilichthys spilauchen	0.01	<0.01
Gerreidae	*Eucinostomus melanopterus*	0.01	<0.01
Monodactylidae	*Monodactylus sebae*	0.03	0.01
Cichlidae	***Tilapia guineensis***	86.32	296
	Tylochromis jentinki	0.40	0.31
	Tylochromis intermedius	0.01	0.04
	Oreochromis niloticus	0.01	0.03
	Tilapia zillii	0.02	0.06
	Hemichromis bimaculatus	1.29	0.43
	Hemichromis fasciatus	1.20	1.97
Mugilidae	*Liza grandisquamis*	0.43	0.49
	Liza falcipinnis	0.44	0.89
	Mugil cephalus	0.01	<0.01
Gobiidae	*Gobionellus occidentalis*	0.01	0.01
	Nematogobius maindronii	0.14	<0.01
	Porogobius schlegelli	0.71	0.03
	Periophthalmus barbarus	0.14	<0.01
Anabantidae	*Ctenopoma kingsleyae*	0.02	<0.01
Cynoglossidae	*Cynoglossus senegalensis*	0.01	0.02
Total Number		11,013	

Table 5.2. Diet guilds (both sexes together) are provided for fish species with sufficient sample size (*n*>20), sampled in 2005-2006. Percentage abundance of each prey item is provided (%F_i X Pi). The prey item/items which add up to a minimum of 50 % of prey abundance and therefore determine the diet guild in which a species belongs are highlighted in bold: D, detritivores; I, insectivores; P, piscivores; M, molluscivores; L, illiophage

Fish species	Diet (*n*)	Fish	Molluscs	Terr. Arthropods	Aq. Invert.	Zooplankton	Fish/ Invert. eggs	Fish remains (Scavenging)	Detritus	Silt	Macro phytes	Plant seeds	Diet guild
Elops lacerta	29	**78.28**	21.72	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	P
Rhambdalestes septentrionalis	60	0.00	0.00	**41.85**	**31.87**	21.81	1.89	0.67	1.92	0.00	0.00	0.00	I
Chrysichthys nigrodigitatus	31	4.87	7.31	0.19	**81.62**	0.02	0.00	5.98	0.00	0.00	0.00	0.00	I
Poropanchax normanii	353	1.95	0.85	3.54	14.83	5.30	0.63	0.26	**69.51**	0.00	2.82	0.29	D
Epiplatys spilargyreius	108	0.00	0.00	**36.46**	**39.44**	7.16	0.00	0.00	16.94	0.00	0.00	0.00	I
Epiplatys bifasciatus	26	11.11	0.00	**66.66**	11.12	11.11	0.00	0.00	0.00	0.00	0.00	0.00	I
Tilapia guineensis	1431	0.00	0.38	0.78	3.78	1.72	0.29	2.36	0.00	**86.91**	3.60	0.19	L
Hemichromis bimaculatus	39	0.00	4.06	4.07	**79.68**	0.00	4.06	0.00	4.06	0.00	0.00	4.09	I
Hemichromis fasciatus	29	**66.67**	0.00	0.00	33.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	P
Liza grandisquamis	32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**97.18**	2.82	0.00	L
Liza falcipinnis	26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**100.00**	0.00	0.00	L
Porogobius schlegelli	39	0.00	**75.00**	0.00	25.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	M

5.3.2 Mosquito distribution

Canonical Correspondence Analysis identified five significant variables (percentage vegetation cover, sampling month, distance from floodplain edge, the presence or absence of *T. guineensis* and larvicide application) which determined the distribution of sites with or without anophelines or culicines (Fig. 5.2). The impact of these variables on the presence or absence of anopheline and culicine larvae was further tested using GEE analysis. Larviciding significantly decreased anophelines by 62% and culicines by 74% (Table 5.3). The presence of *T. guineensis* was associated with a 38% decrease in culicine mosquito (Table 5.3). Anophelines were associated with habitats with higher vegetation cover (Fig. 5.1, Table 5.3). Mosquito control using microbial larvicide did not have a significant impact on the fish species richness on the floodplains and no impact was determined in terms of the abundances of the commonest fish species encountered on the floodplains (Table 5.4).

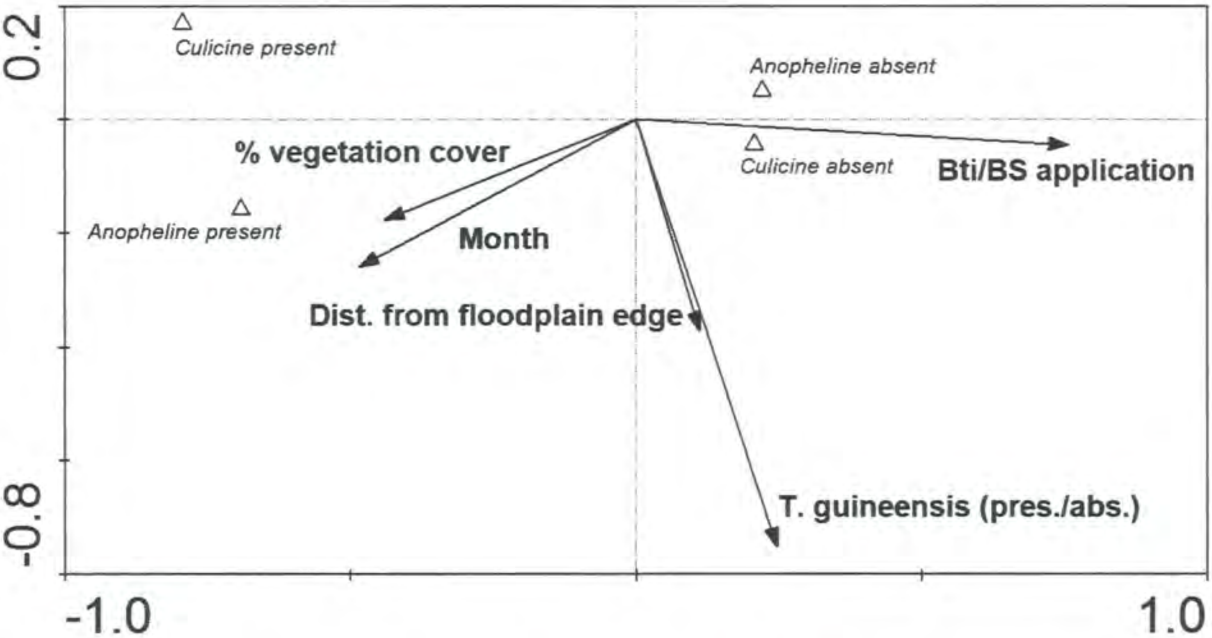


Figure 5.2 Canonical Correspondence Analysis biplot of the distribution of positive and negative sites for anophelines and culicine larvae (Δ) and significant environmental variables (vector arrows). The position of each centroid indicates its association with environmental variables.

A sub-sample (n=173) of late instar anopheline larvae collected along the transects were brought back to the laboratory to dentify them after emergence of the adults. Of these 41.6% were *An. coustani* s.l., 31.8% *An. gambiae* s.l., 11.6% *An. funestus*, 9.8% *An. pharoensis*, and 5.2%, *An. squamosus*. Those mosquitoes identified as *An. gambiae* s.l. (n = 55), were further identified to species by PCR analysis and 76% were identified as *An. gambiae* s.s., 12% *An. arabiensis* and 12% *An. melas*.

Table 5.3 Factors associated with the presence and absence of anopheline and culicine larvae during the 2005, 2006 and 2007 rainy seasons. Only those variables identified as significant by the CCA were included in the model. C.I. is 95% confidence interval. Significant values in bold.

Factors		**Odds ratio**	**95% Wald C.I.**		***P***
Anophelines			**Low**	**High**	
Intervention	Non-sprayed	1.00	-	-	-
	Sprayed	0.38	0.24	0.59	**<0.001**
T. guineensis	Absent	1.00	-	-	-
	Present	1.12	0.87	1.44	0.36
% vegetation cover		1.01	1.01	1.02	**<0.001**
Sampling month		0.96	0.92	1.00	0.05
Distance from floodplain edge		1.00	1.00	1.00	0.85
Culicines					
Intervention	Non-sprayed	1.00	-	-	-
	Sprayed	0.26	0.17	0.38	**<0.001**
T. guineensis	Absent	1.00	-	-	-
	Present	0.62	0.45	0.84	**0.002**
% vegetation cover		1.01	1.00	1.02	0.03
Sampling month		1.01	0.98	1.04	0.43
Distance from floodplain edge		1.00	1.00	1.00	0.95

Table 5.4 Influence of application of microbial larvicides on fish species richness (number of species) as well as abundances of the commonest fish species. C.I. is 95% confidence interval. Significant values in bold.

Factors		**Odds ratio**	**95% Wald C.I.**		***P***
			Low	**High**	
Fish species richness	Non-sprayed	1.00	-	-	-
	Sprayed	0.81	0.64	1.03	0.09
Year	2005	1.00	-	-	-
	2006	0.96	0.75	1.21	0.72
	2007	0.57	0.42	0.78	**<0.001**
Transect	1	1.00	-	-	-
	2	1.01	0.67	1.53	0.94
T. guineensis	Non-sprayed	1.00	-	-	-
	Sprayed	1.50	0.58	3.90	0.39
R. septentrionalis	Non-sprayed	1.00	-	-	-
	Sprayed	0.99	0.75	1.32	0.98
E. spilargyreius	Non-sprayed	1.00	-	-	-
	Sprayed	0.94	0.44	2.03	0.88
H. bimaculatus	Non-sprayed	1.00	-	-	-
	Sprayed	0.91	0.82	1.01	0.08
H. fasciatus	Non-sprayed	1.00	-	-	-
	Sprayed	1.04	0.90	1.20	0.60
P. normanii	Non-sprayed	1.00	-	-	-
	Sprayed	1.05	0.98	1.12	0.15

5.3.3 Predation experiments

The semifield experiments showed that both species of fish had significant impacts on the presence of all categories of anopheline and culicine larvae and pupae (Table 5.5). Average anopheline densities in the bowls before treatment were 1.01 larvae per dip. For early instar anophelines, there was a 69% reduction for *E. spilargyreius* and 96% reduction for *T. guineensis* respectively at the end of the 12-day period, whist all late stage culicines and anophelines were consumed after 24 hours.

Of the 715 pupae collected in the predation semifield experiment in year 2006, 21.7% were *An. gambiae* s.l. and the rest culicines (47.5% *Ae. vittatus* Bigot, 27.5% *Cx.*

quinquefasciatus Say, 1.3%, *Toxorhynchites spp*, and 2% other culicines). Of the *An. gambiae* s.l., 48% were identified as *An. gambiae* s.s. and 52% *An. arabiensis*.

Table 5.5. Odds ratios of presence/absence of larvae and pupae from the predation experiment. Each instar was analyzed in a separate model. Significant values in bold.

Treatment	Odds ratio	95% Wald C.I.		*P*
		Low	High	
Early anophelines				
Control	1	-	-	-
T. guineensis	0.239	0.132	0.431	**<0.001**
E. spilargyreius	0.204	0.113	0.368	**<0.001**
Late anophelines				
Control	1	-	-	-
T. guineensis	0.032	0.008	0.126	**<0.001**
E. spilargyreius	0.014	0.003	0.054	**<0.001**
Early culicines				
Control	1	-	-	-
T. guineensis	0.001	0.000	0.013	**<0.001**
E. spilargyreius	0.011	0.003	0.045	**<0.001**
Late culicines				
Control	1	-	-	-
T. guineensis	0.003	0.000	0.020	**<0.001**
E. spilargyreius	0.007	0.001	0.039	**<0.001**
Pupae				
Control	1	-	-	-
T. guineensis	0.011	0.003	0.051	**<0.001**
E. spilargyreius	<0.001	<0.001	<0.001	**<0.001**

5.3.4 Oviposition experiment

This experiment showed that ovipositing culicines detected the presence of both *E. spilargyreius* (97% reduction in mosquito larvae sampled, average density 0.05 larvae per dip) and *T. guineensis* (93% reduction, average density 0.1 larvae per dip) compared to the controls (average density 1.24 larvae per dip) and avoided ovipositing in sites where they are present. For anophelines on the other hand, the results indicate that they were poorly deterred by the presence of *E. spilargyreius* (average density 0.13 larvae per dip) and *T. guineensis* (average density 0.16 larvae per dip) in relation to the controls (average density 0.28 larvae per dip) (Fig. 5.3).

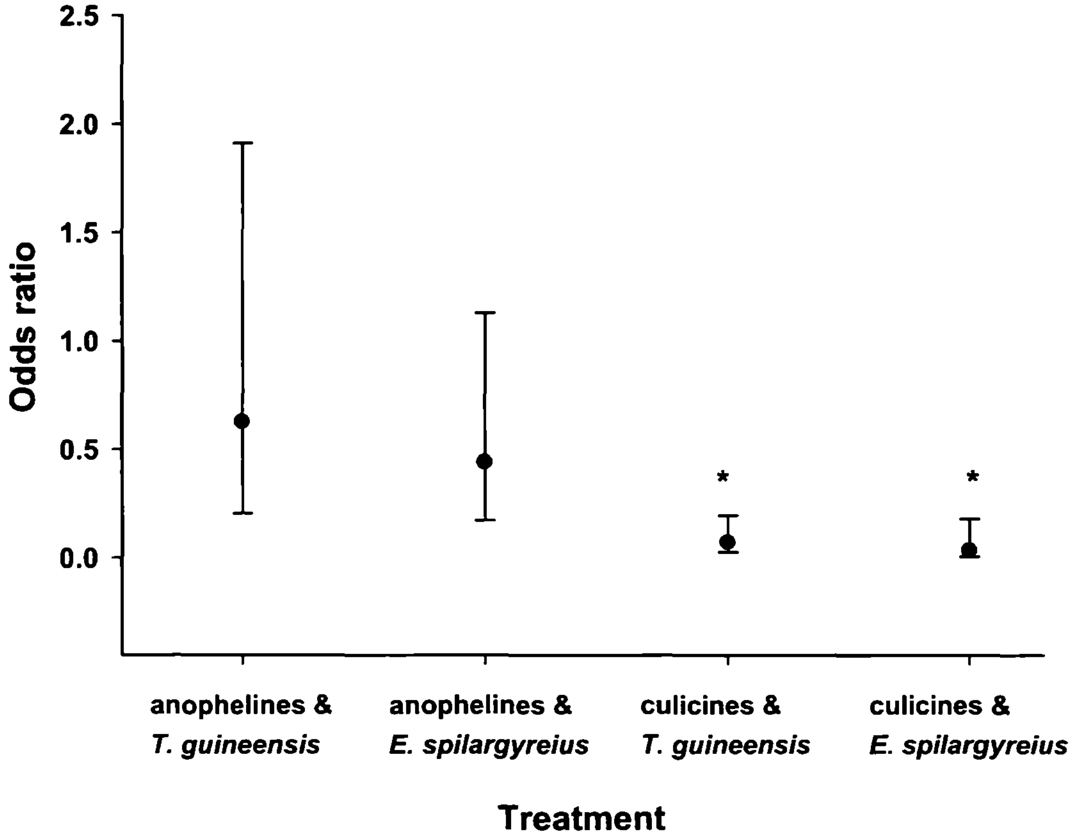


Figure 5.3 Odds ratios and 95% Wald C.I. from GEE analysis of the oviposition experiment for *T. guineensis* and *E. spilargyreius*. Experimental round was also included in the analytical model; no differences were observed between rounds for both anophelines and culicines. * denotes significant relationships.

5.3.5 Ricefield trial

The collection of data from the ricefield trial proved impossible due to the irregular rain pattern experienced in 2007 which resulted in a very late flooding of the rice paddies and subsequent drying out of some plots in less than 2 weeks after initial complete flooding.

5.4 Discussion

A comprehensive fish survey and dietary assessment of the commonest species encountered on the floodplains of the Gambia River revealed that *T. guineensis*, an illiophage, dominates the fish communities, constituting over 86% of the catches by number. Dominance of the floodplain fish community by an illiphage/detritivore is also found in other tropical floodplain systems where detritivore and herbivore species commonly dominate the fish communities (Winemiller, 1990) Five fish species were identified as being primarily insectivorous. Of these, *E. spilargyreius* was the commonest, with potentially sufficient numbers to cultivate for mosquito control.

The presence of *T. guineensis* was associated with a reduced likelihood of finding culicine larvae, but not anophelines, whereas the presence of *E. spilargyreius* showed no significant association with the distribution of mosquito larvae. Due to its high local densities it is possible that *T. guineensis* could have a direct interaction with culicines. Semifield setups have been shown to accurately predict results obtained in large scale experiments (deSzalay *et al.*, 1996) and semifield tests in this study suggest that the field observations of a negative association in local distribution between culicines and *T. guineensis* may partly be due to culicines detecting and avoiding ovipositing in habitats where *T. guineensis* is present. The fact that culicines avoided ovipositing in containers with both species of fish, suggests that the semiochemicals (chemical substances which carry a signal) detected by culicine mosquito are more general fish cues and not specific to insectivorous fish since *T. guineensis* was identified as a illiophage species.

Results from the predation semifield experiment suggest that predation by fish could also be a factor regulating mosquitoes in the field. Alternatively, it may be that in the floodplains of the Gambia River anophelines occupy different spatial niches to the *Tilapia*; with mosquitoes being concentrated close to emergent vegetation on the water's edge and the fish occupying the open areas away from the shoreline (Wellborn *et al.*, 1996; Maddrell, 1998). Moreover, it is possible that anophelines and culicines differ behaviorally and in their microhabitat preferences. The active behavior of culicines might make them more easily predated upon by visual predators, like fish, whereas anophelines often adhere to vegetation, where they lie parallel to the water surface and are relatively motionless. The general lack of mosquitoes, especially anopheline mosquito in the natural diet of fish, suggests that mosquitoes constitute a minor part in the diet of fish on the Gambia River floodplains and that fish only actively feed on them opportunistically in small aquatic habitats, such as our semifield ponds, where mosquitoes constituted a relatively large proportion of the invertebrate fauna present. This is supported by a number of studies that have shown that even for established larvivorous fish such as *G. affinis*, mosquito larvae constitute a minor proportion of their diet under natural conditions (Garcia-Berthou, 1999; Specziar, 2004; Kumar & Hwang, 2006). Despite the presence of *E. spilargyreius* prohibiting oviposition of culicines and being an active predator under semifield conditions, it did not exclude culicines from habitats in the field. This finding probably results from *E. spilargyreius* only being encountered at lower densities. By contrast the oviposition behavior of anopheline mosquitoes was not influenced by fish and as a result it seems they do not influence the distribution of anophelines on the floodplains. Moreover, this study shows that it only achieves a 69% reduction in early anophelines two days following introduction and this suggests that this species under field conditions is a less efficient predator of anophelines than *T. guineensis*. Taking into account the high abundance of *T. guineensis* on the floodplains (recorded mean catch densities of 7.59 fish/m^2; range: 0-518 fish/m^2) and their proven ability to influence oviposition in culicine mosquitoes in semifield conditions it is perhaps not surprising to see that they play a regulating role in the distribution of culicines on the floodplains.

Since culicines avoid oviposition in sites with either fish species, when effective control of both anophelines and culicines is required, it is of vital importance that all possible aquatic habitat sites should be treated, to avoid culicine mosquito selecting alternative sites for oviposition, thus minimizing the effectiveness of this mosquito control measure. Nonetheless since adult anophelines appear not to be able to detect chemical cues in the water from fish, fish may prove to be an efficient control method for reducing anopheline populations in situations where habitats are well defined and long-lived.

The results from the pilot study indicate that biological control using microbial larvicides did not affect fish species richness and abundance. However, due to the limited sample size these no-effect results should be interpreted with caution. Moreover, further semifield-level testing of the effect of mosquito larvicides on fish growth would be useful.

Tilapia guineensis, a primary animal protein source for people living along the floodplains, is a candidate for use as a mosquito control agent in West Africa as this study has shown that (1) it is by far the commonest fish in the floodplains, (2) its presence does not influence oviposition by anopheline mosquitoes and (3) it is a highly efficient predator of both early and late anophelines. Nonetheless, these results should be treated with caution as anopheline larvae did not constitute a major part of the diet of this species and therefore it might be inefficient in controlling larvae under natural conditions. With irregular rain patterns from year to year being common in West Africa (Pages & Citeau, 1990), the potential for using fish for mosquito control is limited because it can only be effectively implemented in areas with permanent water bodies. Moreover, for *T. guineensis*, the fish biomass used should be high enough (at least 26.3 g / 70L of water as used in the semifield study) to ensure that all invertebrates will be consumed and that fish will not preferentially predate on non-mosquito invertebrates. This dependence on permanent water bodies, limits the capacity in which fish can be used to control mosquitoes unless these habitats remain flooded for substantial periods for the fish to survive and have an impact in controlling mosquito. Nevertheless fish are likely to be cheaper and provide a longer-term solution to mosquito control than with larvicides. Thus fish could be used as part of an integrated control program where fish are used in more permanent sites and microbial larvicides applied to temporary ones. Potential effectiveness of the use of both fish and mosquito larvicides in the same aquatic habitats remains to be tested. Moreover, it must be emphasized that if fish are used for controlling mosquito larvae, it must be well-planned, since failures with introducing fish for mosquito control can be due to the limited attention in which these introductions take place. For example, fish might be introduced in habitats which dry up rapidly or people may harvest the fish at the end of the season, but not replace them when the habitats are flooded again. Therefore, future projects in the region planning the introduction of fish for mosquito control should take into account these potential problems and plan for a regular monitoring of the fish populations, with re-introduction of fish when needed. This study suggests that the use of fish for mosquito control in sub-Saharan Africa merits further consideration.

Chapter 6

Chemical and biological characteristics of malaria mosquito breeding sites in an urban town and surrounding area in The Gambia

Abstract

There is evidence that urban populations of *Anopheles gambiae* have adapted to highly polluted water. Yet surprisingly little is known about the chemical characteristics of these waterbodies. This and some other factors were investigated in Farafenni town and surrounding area, in The Gambia. Mosquito larvae were sampled in 178 locations in and around the town during the peak malaria transmission period in September and October 2007. Molecular analysis was used to identify *An. gambiae* s.l. and its component species among samples. The levels of reactive phosphorus, nitrates, ammonia and tannic acids were quantified spectrophotometrically. Levels of turbidity, vegetation cover and the presence of filamentous algae were also recorded.

Anopheles gambiae s.s. was most commonly found in rice fields (36% of sampled sites), whereas *An. arabiensis* was most common in urban puddles (21%). Reactive phosphorus, distance from the nearest house, turbidity, amount of vegetation cover and the presence of algae all influenced the distribution of mosquito larvae. *An. arabiensis* was found closer to houses than *An. gambiae* s.s. and the presence of algae was a strong indicator of the presence of anopheline larvae in general. Sites dominated by anophelines had higher turbidity levels compared to sites in which culicines dominated. Production of pupae was associated with high levels of reactive phosphorus concentrations. Evidence suggests that *An. arabiensis* is better adapted to urban polluted habitats, whereas for *An. gambiae* s.s., rice fields are the most important breeding habitats.

Mosquito control measures should pay particular attention to sewage treatment and removal of nutrients, especially reactive phosphorus from aquatic habitats in urban areas.

6.1 Introduction

Malaria is the most significant childhood killer in tropical countries (W.H.O., 1999; Killeen *et al.*, 2002a; Killeen *et al.*, 2002b; Hay *et al.*, 2004). Nevertheless, with the largest proportion of Africans now living in urban cities (Keiser *et al.*, 2004), evidence suggests that malaria rates in urban areas tend to be lower than those for rural environments, possibly due to the generally low extent of potential breeding sites (Robert *et al.*, 2003; Caldas de Castro *et al.*, 2004), higher standard of living and availability of anti-malaria medication (Lindsay *et al.*, 1990; Caldas de Castro *et al.*, 2004).

The conventional wisdom is that culicine mosquitoes are better adapted to breed in polluted urban environments (Frankie & Ehler, 1978; Barrera, 1996), with anopheline mosquitoes preferring clear-water habitats (Lines *et al.*, 1994; Sattler *et al.*, 2005). Nevertheless, recent evidence suggests that *An. gambiae s.s.* is adapting to breed in heavily polluted urban habitats (Awolola *et al.*, 2007), the main reasons being the attraction of anopheline mosquitoes towards the large concentrations of people living in urban environments and the general lack of aquatic predators in those urban habitats (Carlson *et al.*, 2004; Keiser *et al.*, 2004).

The availability of nitrogen and phosphorus to organisms are important drivers of the ecology of all water systems as they greatly determine the productivity of a particular aquatic system (Brönmark & Hansson, 2005). However, excessive inputs of these limiting nutrients into aquatic systems can lead to eutrophication and subsequent declines in the levels of dissolved oxygen, which can have a detrimental effect on the survival and growth of many aquatic organisms (Van der Valk, 2006). High levels of tannins, a result of plant material decomposition, in aquatic systems can have detrimental effects on plants and bacteria by inhibiting the absorption of nutrients (Cuthbert & Delgiorgio, 1992). Moreover, recent evidence suggests that tannic acids are toxic to mosquito larvae (Rey *et al.*, 1999; Rey *et al.*, 2000), and may, therefore, limit mosquito production in aquatic systems. The input of nutrients can be amplified in polluted urban environments through the improper disposal of waste (Kaye *et al.*, 2006), and in rice fields through the addition of fertilisers (Victor & Reuben, 2000; Mutero *et al.*, 2004). Aquatic habitats associated with urban agriculture in sub Saharan Africa , such as rice fields and irrigation channels, have been identified to be a major contributor of malaria vectors in urban areas in Cote d'Ivoire (Matthys *et al.*, 2006a; Matthys *et al.*, 2006b), with high levels of turbidity considered to be an important indicator of mosquito productivity in some cases (Gimnig *et al.*, 2001; Matthys *et al.*, 2006a). By contrast, clear water habitats (low turbidity) have been associated with high *Anopheles* sp. productivity in other cases within urban areas (Sattler *et al.*, 2005).

Several studies have examined the relative importance of different aquatic habitats as breeding sites for mosquitoes in rural areas in The Gambia (Bøgh *et al.*, 2003; Bøgh *et al.*, 2007; Majambere *et al.*, 2008), but little is known as to the distribution of the aquatic stages of malaria vectors and other mosquitoes in urban and peri-urban breeding sites in The Gambia. Therefore the major mosquito breeding sites in and around Farafenni town in The Gambia were identified and the distribution of mosquito species in related to environmental habitat variables was described.

6.2 Materials and methods

6.2.1 Study area

This study was carried out in and around Farafenni town (UTM coordinates: 1500200N, 435500E) in The Gambia. Rains occur from June to October and malaria transmission is largely seasonal with peak transmission between September and mid-November (Lindsay *et al.*, 1990). Sampling took place in 2007 over a short period from 11 September to 23 October to minimize any temporal variation in mosquito larval abundance and to coincide with the peak in clinical malaria cases in urban habitats in The Gambia (Lindsay *et al.*, 1990).

6.2.2 Field sampling

All aquatic habitats encountered in and around Farafenni town were sampled. Sampling sites were spread between the three main ecological zones: the urban environment within Farafenni town (zone A), the ricefield habitats surrounding Farafenni along the floodplain edge (zone B) and floodplain habitats bordering the main river channel (zone C) (Fig. 6.1). A sampling site was considered to be distinct from other adjacent sites if there was no water connection, or the sites were at least 30 m apart.

Mosquito larvae were sampled along the edges of the aquatic habitat and adjacent to any aquatic vegetation, where they are most frequently encountered (Hall, 1972) using a standard mosquito dipper (350ml capacity dipper, Clarke Mosquito Control Products, Illinois, USA). A total of 16 dips were undertaken at each site. For each dip taken, culicines and anophelines were recorded as early (first/second instar) or late (third/fourth instar) larvae or pupae. All late anopheline larvae were separated and placed individually in 3.5ml tubes containing 100% ethanol for subsequent PCR identification, as these were most likely to survive to adulthood. Seven aquatic habitat types were identified: (1) floodwater (habitats with a direct and permanent connection to the floodplains); (2) rice fields (bordering the edges of the floodplains and could be both floodwater and rain-fed); (3) floodwater puddles (puddles on the floodplains formed due to tidal movement of the floodwater or receding floodwaters); (4) urban puddles (puddles in and at the edges of Farafenni, which could be rainfed or a result of runoff from public taps or leaky pipes); (5) brick/sand pits (rain-fed, formed during the extraction of material for construction purposes); (6) road ditches (rain-fed, adjacent to main roads); (7) tyres and tin/plastic containers. At each sampling site, the GPS coordinates were recorded using a handheld Global Positioning system (GPS, Garmin GPS 12XL, Southampton, UK), and the presence and percentage cover of vegetation. A water sample was collected in a 500 ml polypropylene bottle and kept away from direct sunlight until it was taken to the laboratory for spectrophotometric analysis.

Figure 6.1 Location of the three ecological zones sampled in and around Farafenni.

6.2.3 Chemical analysis

All samples were immediately filtered through a 0.45 µm Millipore cellulose acetate membrane filter and analyzed within 3 h of collection to minimize any alteration in the levels of nutrients. All fractions were analysed spectrophotometrically. To minimise problems with contaminated reagents, pre-packaged and prepared reagents for the filterable reactive phosphorus and ammonia analysis was obtained from Hanna Ins. (HANNA, Italy).

Filterable reactive phosphorus (FRP – PO_4^{3-}) was analysed following the ascorbic acid method (Clesceri *et al.*, 1998). The phosphorus present forms a heteropoly acid-phosphomolybdic acid complex, which is reduced to form a deep blue colour. The colour is proportional to the phosphorus present and is measured spectrophotometrically (WPA spectrophotometer, Lightwave II UV/VIS Xenon sourse). These were measured against standards which were diluted from 1mg/L concentration KH_2PO_4 – P stock solution by diluting a 10 mgL^{-1} stock and further diluted to 0.2 mgL^{-1} by diluting 1 mL to 50 mL with double distilled water through a dilution series of 0.2, 0.1, 0.05, 0.25, 0.0125 mgL^{-1}, plus a zero concentration one with distilled water and reagents, using 20mm quartz cuvettes at 882 nm wavelength.

Ammonia (NH_4^+), was analysed following the Nessler method (Clesceri *et al.*, 1998). Samples were mixed with the prepared re-agents and measured using 20mm quartz cuvettes at a wavelength of 420 nm. A standard substrate curve was prepared using NH_4Cl. For the original stock solution, 0.38189 g of NH_4Cl was diluted in 1L of double distilled water (DIW, resulting concentration: 100 μgml^{-1}). This was diluted to the highest standard concentration used for the standard curve of 0.25 mgL^{-1} and then diluted to 0.125, 0.0625, 0.03105 mgL^{-1}. A blank with just DIW plus the reagents was used for the zero ammonia concentration.

For filterable reactive nitrogen (FRN – NO_3^-/NO_2^-) the Ferree method (Ferree & Shannon, 2001) was used. Absorption of untreated, filtered samples were measured using 10mm quartz cuvettes at 220 nm (UV range). For the standard curve, the blank was made from DIW and the rest (2,1,0.5 and 0.25mgL^{-1}) diluted from 1000mgL^{-1} KNO_3-N stock solution.

The concentration of tannins, was measured by taking a reading of the colour of the sample at 440 nm and then converting it to the concentration of tannins as described in Cuthbert and Delgiorgio (1992). Turbidity was measured on unfiltered samples using a turbidity meter (HANNA HI 93703, Italy).

6.2.4 PCR

Late stage anophelines larvae were identified to species for those belonging to the *An. gambiae* s.l. complex using the method of Scott *et al.* (1993) and the rest were classified as non- *gambiae* s.l. species, as described in Chapter 5.

6.2.5 Data analysis

All sampling sites were mapped using Google Earth ™ and distances between the aquatic sites and the nearest house calculated. Canonical Correspondence Analysis (CCA) (Ter Braak, 1986) using CANOCO version 4.5 (Centre of Biometry, Wageningen, the Netherlands) was used to identify the important parameters which determine the presence or absence of species/groups distributions and the amount of variance explained by these factors. In order to determine which of the variables identified by CCA analysis specifically determine the distribution of comparable mosquito categories (*An. gambiae s.s.* and *An. arabiensis*; anophelines and culicines; mosquito larvae and pupae; sites with and without mosquito), each sampling site was assigned to belong to one mosquito group depending on which one dominated the catches and Mann-Whitney tests were carried out for each variable between each mosquito group. For each comparison, sites in which no mosquitoes were collected were not accounted for in the analysis.

6.3 Results

Mosquito breeding habitats within Farafenni town comprised mostly of puddles originating from leaky pipes and taps as well rain-fed road ditches. Immediately outside Farafenni, breeding habitats were almost exclusively rice fields, together with road puddles some of which were rainfed while others were fed by floodwater from the adjacent floodplains.

Potential breeding sites further away from Farafenni were mostly floodwater habitats. Only habitat types sampled at least of six times were included in subsequent analyses and this excluded brick / sandpits, road ditches, tyres and tin/plastic containers.

Of 489 late anophelines larvae tested, 263 were positively scored by PCR (22% *An. gambiae s.s.*, 27% *An. arabiensis* and 51% non-*gambiae* s.l. anophelines).

Densities for *An. gambiae* s.s. varied significantly between habitat types (Kruskal-Wallis, n=169, P=0.05) (Fig. 6.2). This was also true for *An. arabiensis* (Kruskal-Wallis, n=169, P<0.01), non-*gambiae* anophelines (Kruskal-Wallis, n=169, P<0.01), culicines (Kruskal-Wallis, n=169, P<0.01) and pupae (Kruskal-Wallis, n=169, P<0.01).

Anopheles gambiae s.s. was present in 36% of rice fields, 19% of urban puddles, 1% of floodwater habitats and never in flood puddles. *An. arabiensis* was recorded in 3% of rice fields, 21% of urban puddles, less than 1% of floodwater habitats and never in flood puddles. Non-*gambiae* anophelines were found in rice fields (20%) and very rarely in urban puddles (<1%). Culicines were mostly common in floodwater puddles (83%), then in rice fields (76%), urban puddles (33%) and floodwater (18%). Pupae were found in 25% of urban puddles, 24% of rice fields, 17% of floodwater puddles and less than 1% of floodplain habitats.

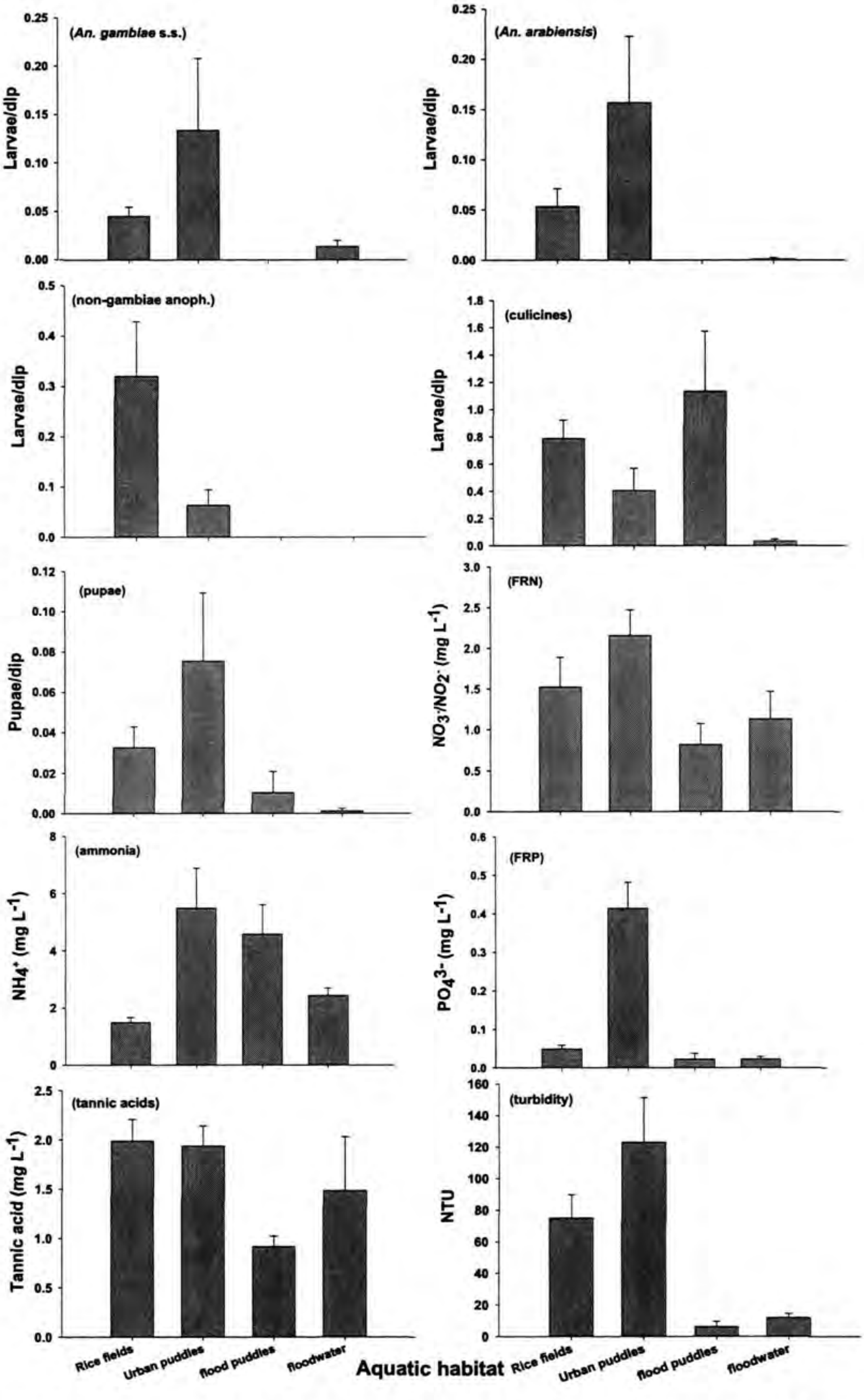


Figure 6.2. Means and standard errors of mosquito abundance and chemical factors across habitats.

Canonical Correspondence Analysis identified five factors (FRP, distance from the nearest house, % vegetation cover, turbidity and the presence of algae) which significantly influenced the distribution of mosquito larvae (Fig. 6.3). The first two axes accounted for 88.7 % of the variance (Table 6.1). Culicines were strongly associated with the presence of algae and the three anopheline groups (*An. gambiae* ss, *An. arabiensis*, and all other anophelines) with high vegetation cover and turbid habitats. Pupae were strongly associated with high levels of FRP (Fig. 6.3).

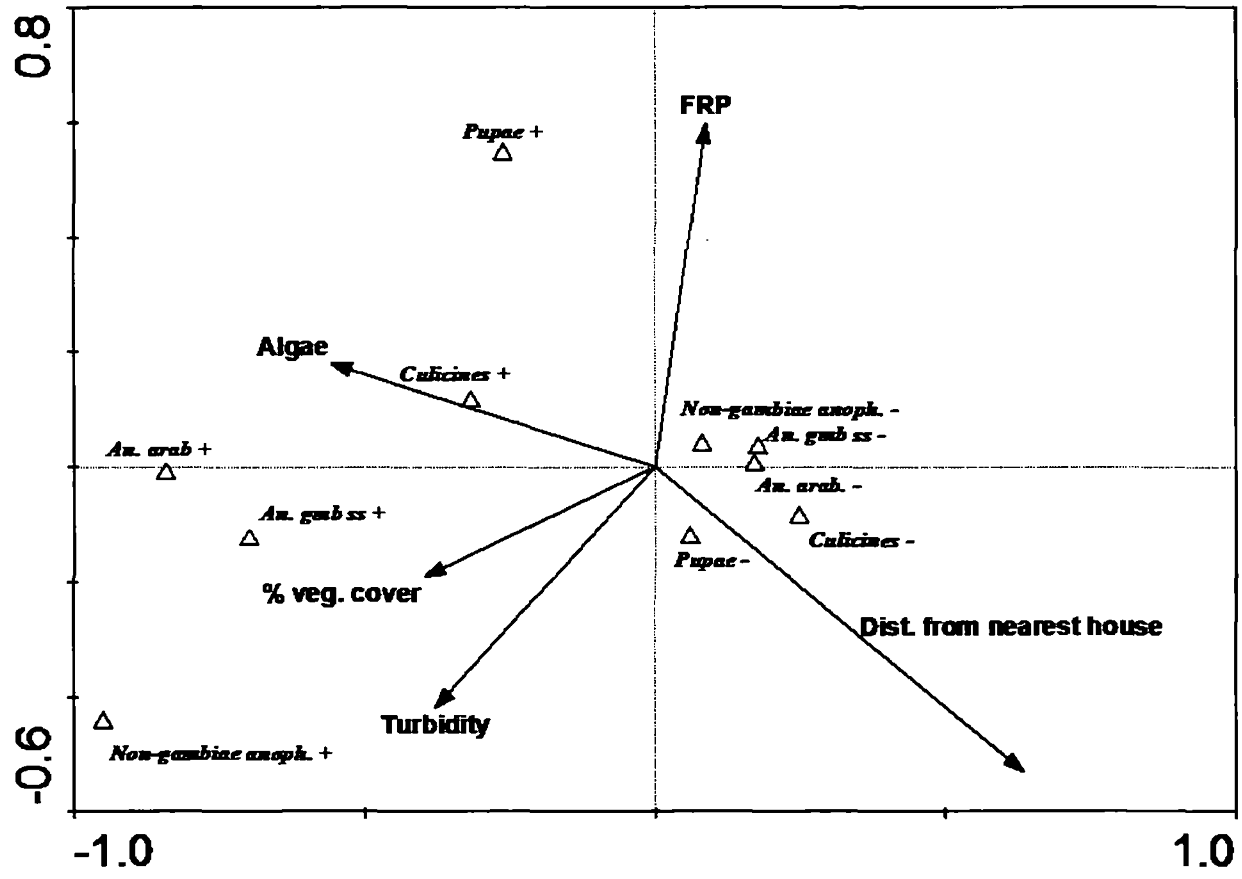


Figure 6.3 Canonical Correspondence Analysis biplot of the distribution of positive and negative sites of the mosquito/species groups sampled (Δ) and significant environmental variables (vector arrows). The position of each species centroid indicates its position in relation to the environmental conditions. Negative scores on axis 1 represent habitats with high vegetation cover and presence of algae as well as being closer to Farafenni, whereas positive scores on Axis 2 represent habitats with high concentrations of FRP and less turbid water.

Comparing specific mosquito groups, sites at which *An. arabiensis* dominated were found closer to houses (*n*, 19; median, 214 m; range, 1 to 513 m) compared to sites in which *An. gambiae* s.s. was dominant (*n*; 26; median, 286 m; range, 1 to 2094 m; Mann-Whitney U test *P*=0.05). Sites at which *An. gambiae* s.s was dominant tended to be more frequently associated with the presence of algae compared to *An. arabiensis* dominant sites, but this result only approached significance (df, 1; Pearson Chi-Square with Yate's correction; *P*=0.08). No differences were observed between sites dominated by *An. gambiae* s.l. and non-*gambiae* anophelines. Sites in which anophelines dominated were associated with higher turbidity levels, although not quite significant (*n*, 38; median, 44.84; range, 0.85 to >1000) compared to sites with culicines (*n*, 58; median, 26.26; range, 1.26 to 631; Mann-Whitney U test *P*=0.06) as well as associated with the presence of algae (df, 1; Pearson Chi-Square; *P*=0.01). Sites in which pupae dominated were associated with high FRP concentrations (*n*, 7; median, 0.485; range, 0.001 to >2.780) compared to sites in which larvae (anophelines and culicines) dominated (*n*, 93; median, 0.03; range, 0.001 to 2.036; Mann-Whitney U test *P*=0.02) and closer to houses (median [pupae], 109; range, 4 to 1012; median [larvae], 320; range, 1 to 2592; Mann-Whitney U test *P*=0.04). Sites positive with mosquitoes were associated with the presence of algae (df, 1; Pearson Chi-Square; *P*<0.001). Mosquito-positive sites also had higher concentrations of FRP (*n*, 94; median, 0.05; range, 0.001 to 0.078) compared to negative sites (*n*, 84; median, 0.017; range, 0.001 to 1.899; Mann-Whitney U test *P*=0.007), were closer to houses (median [mosquito positive], 293; range, 1 to 2592; median [mosquito negative], 955; range, 1 to 2632; Mann-Whitney U test *P*=0.002) and had higher turbidity levels (median [mosquito positive], 42.79; range, 0.85 to >1000; median [mosquito negative], 10.53; range, 0.02 to 994; Mann-Whitney U test *P*<0.001).

Table 6.1 Habitat variable loadings and ordination summary for the CCA of the presence/absence of mosquito groups in Farafenni town and surrounding area. Only the statistically significant variables (Monte Carlo significance test, 999 permutations) were included in the model and are shown here in the order added in the model; Distance from the nearest house (F-ratio: 8.60, *P*=<0.01), % vegetation cover (F-ratio: 6.67, *P*=<0.01), turbidity (F-ratio: 3.82, *P*=0.02), Presence of algae (F-ratio: 4.32, *P*=<0.01), FRP (F-ratio: 2.42, *P*=0.05).

	Axis 1	Axis 2
Canonical coefficients for environmental variables		
FRP	0.09	0.60
turbidity	-0.38	-0.42
% vegetation cover	-0.40	-0.19
Algae	-0.56	0.18
Distance from nearest house	0.63	-0.53
Correlation of environmental variables with species axis		
FRP	0.04	0.20
turbidity	-0.17	-0.14
% vegetation cover	-0.18	-0.07
Algae	-0.26	0.06
Distance from nearest house	0.29	-0.18
Summary statistics for ordination axis		
Eigenvalues	0.10	0.02
Species-environment correlations	0.46	0.34
Cumulative % variance		
species	9.80	12.00
Species - environment	72.4	88.7
Sum of all eigenvalues	1.00	
Sum of all canonical eigenvalues	0.14	

6.4 Discussion

Recent evidence suggests that anopheline mosquitoes have adapted to heavily polluted urban habitats (Awolola *et al.*, 2007), and this study shows that urban habitats can be very important as breeding sites for anophelines. Interestingly, in this study *An. arabiensis* was more commonly encountered in urban puddles than rice fields and dominated breeding habitats closer to houses, compared to *An. gambiae* s.s. This comes as a surprise as *An. gambiae* s.s. is considered to be more closely associated with humans and highly specialised on feeding on humans (Pates *et al.*, 2001), compared to *An. arabiensis* which readily feeds on cattle and other animals (Mahande *et al.*, 2007). However some studies have suggested that both species have similar feeding preferences (Diatta *et al.*, 1998; Duchemin *et al.*, 2001). A possible explanation for the observed distribution in this study is that *An. arabiensis* is better adapted to breed and survive in polluted urban habitats. It is already established that *An. arabiensis* can tolerate more extreme thermal environments than *An. gambiae* s.s. (Kirby & Lindsay, 2004). This pattern of distribution is also reported elsewhere, Colluzzi (1984) and Kristan *et al.* (2003) showed that *An. arabiensis* occurs more frequently in urban habitats such as polluted water pools and road ditches in Nigeria and Ghana, compared to *An. gambiae* s.s. that was more common in rural clear-water habitats.

An. gambiae s.s. is considered the most important malaria vector in Africa because of its highly anthrophilic behaviour. Larvae of this species were most commonly found in rice fields. Taking into account the extensive expanses of rice fields, it is expected that rice fields contribute a large proportion to the total productivity of *An. gambiae* s.s. mosquito in The Gambia. Moreover, with the world prices in rice increasing, coupled with the ever increasing demand in rice, the abundance of rice fields is likely to increase in the future and therefore their importance in the production of anophelines will increase.

Gimnig *et al.* (2001) identified the presence of filamentous algae as the single most important indicator for the presence of anopheline mosquitoes in western Kenya and this was also the case for this study. They also identified *An. gambiae* s.s. to be associated with algae more frequently than *An. arabiensis*. This tended also to be the case in the current study, but the difference was not significant. Algae can provide important structure in the habitat, but might also be an indicator of the presence of single-celled algae in the same habitat that can be an important food source for the larvae (Bern & Dahl, 1999; Mokany, 2007). Moreover, algae can be an indicator of older, more mature aquatic habitats and therefore more likely to have been found and colonised by mosquitoes. More importantly, pupae were strongly associated with habitats with high levels of FTP. This is a strong indication that the availability of phosphates plays an important role in mosquito productive habitats in which a large proportion of the larvae reach the pupal stage, perhaps due to the elevated levels of potential microbial food sources. On the other hand, levels of tannic acids are high in productive mosquito habitats and do not seem to restrict growth in mosquitoes, as demonstrated by the high densities of pupae in urban puddles (Fig. 6.2).

This study demonstrates that the most important anopheline breeding sites in an urban/semi-urban town in The Gambia are distributed in close proximity to where people live. From a mosquito perspective, breeding in aquatic habitats close to where they have taken bloodmeals minimises the amount of energy that has to be allocated to flying to more distant, but clearer aquatic habitats, perhaps enabling energy to be invested in producing more eggs or reducing mortality risk before reproducing. The relatively polluted and turbid aquatic urban habitats will impose a strong selection pressure on the larvae and it is possible that *An. arabiensis*, already better adapted to warmer habitats with reduced availability of water, is better adapted for these conditions.

The overall close proximity of anopheline breeding sites to areas of human habitation and the lack of anopheline mosquitoes in natural floodplain habitats further away from the built environment is an important consideration from an operational perspective in malaria control. It should be possible to restrict mosquito control measures to areas within and adjacent to the towns and achieve similar success in controlling malaria vectors while minimising the overall costs.

Chapter 7

General discussion

The importance of floodplains and wetlands in riverine ecosystem functioning has become increasingly clear in recent years (Moore et al., 1989; Van der Valk, 2006), in particular in terms of fisheries productivity (Welcomme, 1979; Marchand, 1987) and disease transmission (Bøgh et al., 2007). Nevertheless, the ecology of, African floodplains, has been poorly studied, with the bulk of studies on vast floodplain systems such as the Congo dating back to colonial times (Campbell, 2005). This thesis provides a comprehensive study of the lower River Gambia floodplains in relation to the ecology of fish and larval mosquitoes, focusing on the possible interactions between the two groups.

7.1 Fish communities and the environment

This study has investigated which environmental variables play a role in determining the structure of the Gambia River floodplain fish communities (Section 1.5) and has shown that fish are well adapted to the seasonal changes in physical conditions encountered on the floodplains. Variations in the levels of a number of water parameters (pH, conductivity, DO, depth and water temperature) determine the structure of the floodplain fish communities during the different stages of the rainy season. These habitat variables vary seasonally in response to the river hydrology and direct rainfall. Extreme variability in these variables, such as the very high conductivities encountered at the end of the dry season and very low pH values during the peak of the rainy season, restrict which species can tolerate those conditions and which of the different aquatic habitat types they utilise. Furthermore, fluctuations in these variables may play a role in triggering fish to emigrate onto the floodplains as fish species richness in bolongs was highly correlated with elevated DO levels and low temperatures and pH levels. Emigration of fish into newly flooded habitats is also determined by the starting densities of fish in remnant pools prior to the start of the rains. This density-dependent emigration is possibly more pronounced in fish species with more complicated social interactions (territories, dominance hierarchies, etc.). In these cases, emigration can be a characteristic of either a strong fitness benefit, in which case the more dominant individuals would be the first ones to emigrate, or a characteristic of weak fitness, in which case subordinate individuals would be the first to emigrate.

7.2 Mosquitoes, the environment and interactions with fish

The distribution of mosquitoes is influenced strongly by the distance to the nearest house, as that determines the flying distance, and thus the energy expenditure, that the gravid female mosquito will have to allocate in finding a suitable breeding habitat (Chapter 6). Furthermore, the presence of algae and high levels of phosphorus are also strong indicators of productive mosquito habitats. High levels of these variables is probably a strong indication of more mature and productive habitats, which provide the mosquito larvae with the food and cover required to reach the late developmental stages and to eclode. The presence of cover is expected to be even more important in those habitats in which mosquito larvae are likely to be exposed to aquatic predators, most importantly fish. This study has shown that the presence of fish does potentially play a significant role in inhibiting the presence of mosquito larvae. In particular, fish reduce culicine abundance. Culicines were shown, under semi-field conditions, to actively avoid breeding in habitats where fish are present, and were heavily predated upon by fish. These results arising from semi-field experiments are further supported by field data which have shown a negative association between culicine larvae and the presence of the most dominant floodplain fish, *T. guineensis*.

7.3 The River Gambia and environmental change

The Gambia River is located at a very sensitive location at the border between the dry Sahel, which dominates to the north of the river, and the wetter equatorial rainforests of Central Africa and the Guinean coast to the south. The Sahel region has experienced a period of drought since the 1950s with already reported severe impacts on the Saloum and Casamance estuaries in Senegal (Pages & Citeau, 1990; Thomson et al., 2004). This long-term climate change is attributed to increased aerosol loading and greenhouse gases, which also play a major role in global climate change (Held et al., 2005; Williams et al., 2007). This long-term drought has already led to significant declines in water flow in other major West African rivers (Ndiaye, 2000; Mikhailov & Isupova, 2008) leading to issues related to water management, as well as, amplifying already existing socio-economic problems (Magistro & Lo, 2001; Varis & Fraboulet-Jussila, 2002). Long-term droughts are known to increase the acidity in acid-sulphate floodplain soils in Australia (Lin et al., 1995), and with acid-sulphate soils being common in The Gambia (Giglioli & Thornton, 1965), similar problems are expected with detrimental effects to swamp rice agriculture (Webb, 1992) and the fish communities (Chapter 2).

The importance of climate change in altering malaria transmission in the region is still unclear. Recent models suggest that global warming will lead to an altitudinal increase in malaria distribution (Tanser et al., 2003), whereas other models predict little or no change (Rogers & Randolph, 2000); therefore, no general consensus on the impact of climate change on malaria transmission exists (Zell, 2004). More likely, climate change will influence the distribution of the different malaria vectors with consequences on malaria transmission. *An. arabiensis* is considered to be better adapted to warmer habitats that are more prone to desiccation (Lindsay et al., 1998; Kirby & Lindsay, 2004; Gray & Bradley, 2005) and is therefore expected to become more predominant in the warmer and more unpredictable environments predicted under future climate change.

7.4 Damming the Gambia River

The vast majority of the world's major rivers are impacted through the construction of impoundments such as dams and weirs, but the Gambia River remains as the last major river in West Africa and one of the last eight in Africa not to have been impounded (W.W.F., 2006). Nevertheless, a major hydroelectric dam project is already underway on the Gambia River and it is due to be completed in 2011 (McNeil, 2006). This in conjunction with the ongoing drought in the region is expected to influence both the floodplain and the main river channel fish communities. Major changes in the fish communities following the construction of dams has been reported elsewhere, both upstream and downstream of the dam sites (Läe, 1992; 1995; Simier et al., 2004).

The reduced year-round water flow, which is expected to lead to important changes in the aquatic habitat availability and characteristics is expected to severely impact the floodplain fish communities downstream of the dam flooding site (chapter 2). The reduced flooding, and consequently the decreased availability of downstream mosquito breeding habitats might decrease the malaria transmission. Moreover, the increased salinity downstream will favour the production of *An. melas*, a more salt-tolerant species (Giglioli, 1964), but also of minimal importance in malaria transmission (Jawara et al., 2008), compared to *An. gambiae* s.l. and further contribute to a decrease in the transmission of malaria in the downstream reaches of the river.

Damming will possibly also alter the mosquito ecology on the floodplains upstream of the flooding site and possibly change the pattern of malaria transmission. The construction of the dam will alter the flooding pattern of the river and may create permanently flooded areas upstream of the dam even in the dry season, probably changing malaria transmission from primarily seasonal to year-round. Moreover, the increase in irrigated agriculture which will follow the dam construction will further create favourable breeding habitats for mosquitoes as rice-fields in particular have been shown to provide major anopheline breeding habitats (Ijumba & Lindsay, 2001; Ijumba et al., 2002; Bøgh et al., 2003; Majambere et al., 2008).

DeGeorges & Reilly (2007) suggested that the proposed construction of a barrage in the lower reaches of the Gambia River would result in the replacement of *An. melas* by *An. funestus*, a more efficient malaria vector and may therefore intensify the malaria transmission in that region. This pattern was observed in Madagascar where the construction of a hydroelectric dam and the subsequent intensification of irrigated agriculture led to increases in the densities of *An. funestus* with a subsequent increase in malaria transmission (Marrama et al., 2004). Increased malaria incidence in close proximity to dam sites has also been reported in Ethiopia (Ghebreyesus et al., 1999). Similar cases are also reported in Asia (Kusumawathie et al., 2006b). Other important diseases are also expected to intensify. In Senegal the construction of a dam has led to increased schistosomiasis problems (Southgate, 1997; Sow et al., 2002), with similar patters also reported earlier following the construction of the Aswan Dam in Egypt (Abdel-Wahab et al., 1979). On the other hand the more permanent pooling upstream of the construction site, will create floodplain mosquito breeding habitats in which fish can possibly be used more effectively when taking into account the limitations in using fish in habitats with unpredictable flooding/drying phases (Chapter 5).

The likely negative impact of the dam on fish productivity within the floodplains, the expected increase in disease burden due to climate change, and decreases in agricultural (mainly rice) productivity on the floodplains due to the increased salt-intrusion and increasing acidity of the acid-sulphate soils, are expected to intensify the poverty experienced by West African people, a region already considered some of the poorest in the world (Cour, 2001; Thomson et al., 2004). Careful water management will have to take place in order to alleviate possible negative impacts on the environment, account for changes in disease transmission, and meet the region's water demands.

7.5 Future research

This study provides baseline information on the ecology of fish and larval mosquitoes utilising the River Gambia, one of the very few unimpacted large river-floodplain systems in Africa (Fig. 1.4). Using the knowledge acquired during this study, it should be possible to develop models predicting how the construction of the dam, coupled with the ongoing climatic changes will affect floodplain fish communities of the Gambia River. This would provide useful information on how water management after dam construction could be optimised to alleviate these impacts on the fish communities. Possible changes in the distribution of the different *Anopheles* species could also be predicted and this will have a direct influence of malaria transmission.

Results from this study have raised important questions that should be addressed in future research. This study has shown that seasonal variations in pH, DO and water depth influence fish catch biomass and species richness in the bolons (Chapter 2). Since bolons provide ways for fish access onto floodplains, it is possible that variations in these variables play a role in triggering fish to emigrate. Controlled experiments, such as the one described in Chapter 4, can be modified to assess whether changes in pH and DO play a role in triggering fish to emigrate. In particular, it is possible that fish respond to changes in water depth, such as swelling of the main river channel at the beginning of the wet season or receding waters during the dry season, by moving on and off the floodplains. Moreover, the role of dominance hierarchies at different maturity stages on emigration behaviour should also be investigated further, so that the specific mechanisms that drive emigration could be more clearly understood.

The role of pH and DO in floodplain fish emigration, as well as, the importance of conductivity in the structuring of the fish communities on the Gambia River floodplains, should be tested in other similar floodplain – estuary boundary systems with similar climatic regimes (ex. Rio de la Plata, Argentina; Hawkesbury River and Murray-Darling River, Australia). Extending the range of habitats studied will improve our understanding of the generality with which fish communities respond to environmental variation.

Which fish species inhabit which floodplain habitats depends not only on emigration timings and triggers, but also on the physiological responses and the ability of the particular species to tolerate the specific habitat conditions. The Gambia floodplains offer some harsh habitats in terms of extreme levels of some of the habitat variables measured (DO: 0.11-15.13 mg L^{-1}, conductivity: 0.044 – 33.7 mS cm^{-1}, pH: 3.1 – 9.5, Fig. 2.4). Those habitats experiencing very acidic, and in other cases deoxygenated conditions, limit the species that can use them (Chapter 2). Hence experiments testing the tolerances of the different fish species, especially the more dominant ones, to extreme variations in those variables, will provide a clearer understanding as to the specific mechanisms structuring fish communities in space and time. Furthermore, this information will provide valuable information in the case of species of potential interest to aquaculture, such as *T. guineensis*, as the specific tolerances of this species will determine its potential suitability for aquaculture.

Results showing mosquito control by fish under semi-field conditions (Chapter 5), offer only limited information on the true potential of the tested species under natural conditions, due to the fact the they do not take into consideration issues regarding alternative prey availability or control efficiency in habitats with high levels of vegetation cover. Moreover, the lack of high numbers of mosquito larvae, especially anophelines, in the natural diet of fish, seems to suggest that the presence of alternative prey can be an important limiting factor under natural conditions. Therefore, it is important that the ability of *T. guineensis* and *E. spilargyreius* under conditions with alternative prey and vegetation tested. Fish proved unsuitable for controlling larvae in habitats with unstable/unpredictable flooding pattern (Chapter 5). It is therefore of great importance that their predatory capacity is tested at a larger scale in more permanently flooded habitats before use for mosquito control in an intervention trial.

The relative distribution of *An. gambiae* s.s. and *An. arabiensis* in peri-urban settings (Chapter 6) suggests that *An. arabiensis* is probably more tolerant to organic pollution encountered in breeding habitats close to houses. The relative ability of these two species to survive under different levels of organic pollution should be tested under controlled laboratory conditions. Differences in the ability of the two species to survive in heavily polluted habitats can have important repercussions for urban malaria transmission, especially now with large proportions of people living in urban habitats.

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Freshwater Biology (2009) **54**, 254–271 doi:10.1111/j.1365-2427.2008.02105.x

Fish community characteristics of the lower Gambia River floodplains: a study in the last major undisturbed West African river

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SUMMARY

1. The Gambia River is the last major West African river that has not been impounded. However, a hydroelectric dam is being constructed and substantial changes to the hydrology and ecology of the system are expected.
2. Little information is available on the impact of water impoundments in semi-arid regions on downstream floodplain fish communities, due to the scarcity of pre-intervention data. Because profound impacts on physical habitat, salinity and nutrient transport can occur downstream of such impoundments, a knowledge of the species-habitat associations of biota such as fishes is necessary for understanding likely changes and how to limit them.
3. Fish were sampled using cast and hand nets along two transects on the floodplain, and with fyke nets in two 'bolongs' (creeks) from May to November 2005 and 2006 in the lower reaches of the Gambia River, close to the salt water front where ecological changes due to the construction of the dam are likely to be pronounced.
4. Greatest fish species richness was associated with low conductivity, low pH and deep water. Bolongs held greater species richness compared with other floodplain habitats, probably because they acted as conduits for fish moving on and off the floodplain. Species richness and catch biomass increased rapidly following the first rains and then declined.
5. Using a multivariate analysis, three main species groups were identified on the floodplain; one associated with deeper water, one with less brackish water and one with shallow, open water. *Tilapia guineensis* was the commonest species on the floodplains.
6. The floodplains provide nursery habitats as many fish captured were immature, particularly for species where adults are mainly encountered in the main channel. Several small-sized floodplain specialists were also represented by a high proportion of mature individuals.
7. Impoundment is expected to reduce seasonal flooding of the floodplain in the lower Gambia River, downstream of the impoundment, resulting in reduced occurrence of aquatic habitats, especially bolongs, together with lower dissolved oxygen and increased salinity, leading to alteration of the floodplain fish communities, benefiting salt-tolerant species, reducing overall species richness and probably reducing floodplain fish production.

Keywords: dams, habitat associations, lateral migration, tropical rivers, water impoundments

Introduction

Rivers and estuaries are biologically diverse and complex systems (Sala *et al.*, 2000; Darwall & Vie,

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2005) that provide important goods and services, such as food and transport, to human populations (Balmford *et al.*, 2002). Today, relatively few of these environments remain undamaged (Dynesius & Nilsson, 1994; Welcomme, 1995; Richter *et al.*, 1997b; Malmqvist & Rundle, 2002), although innovative approaches are being taken to improve protection of freshwater landscapes (Thieme *et al.*, 2007; Roux *et al.*, 2008). Among the most common modifications to large rivers are the construction of dams and levees. The direct impacts of such impoundments on migratory fish species are well documented in both tropical and temperate rivers (Baxter, 1977; Halls, Hoggarth & Debnath, 1999; Kingsford, 2000; Lucas & Baras, 2001; Anderson, Pringle & Rojas, 2006; Fukushima *et al.*, 2007). However, disruption of the natural hydrological regime, by construction of dams and other flow regulation devices, has far more pervasive effects on catchment function and ecological integrity and it is this that is considered to be the most detrimental human impact to river systems (Ward & Stanford, 1989; Poff *et al.*, 1997; Richter *et al.*, 1997a; Amoros & Bornette, 2002; Lasne, Lek & Laffaille, 2007).

The effects of dams on fish species that inhabit floodplains have sometimes been documented in Africa. On the Niger River in Mali, dam construction reduced the abundance of five fish species (*Gymnarchus niloticus* Cuvier, *Polypterus senegalus* Cuvier, *Gnathonemus niger* Günther, *Citharinus citharus* Geoffroy Saint-Hilaire and *Clarotes laticeps* Rüppell), which use the floodplain for feeding and reproduction (Läe, 1995). Further downstream, in Nigeria, the construction of another dam lead to the disappearance of zooplanktivorous fish species from the floodplains (Nwadiaro, 1989). For most other African river systems, however, the direct and indirect effects of dams and barrages on floodplain species are poorly understood, mainly due to the lack of pre-impoundment data. The original composition of the fish communities was not well known for the Bia Basin in Cote d'Ivoire (Gourene *et al.*, 1999), the Zambezi River in Zambia (Karenge & Kolding, 1995) and the Kafue River, Zambia (Dudley & Scully, 1980).

Commonly, studies examining the impacts of dams on ecological communities have concentrated on the effects upstream of impoundments. However, in semi-arid regions some of the most profound impacts can occur a long distance downstream from the impoundment through, (i) altered flow and high evapotranspiration leading to increased salinity, (ii) alterations to physical habitat and (iii) reduced silt and nutrient transport (Baxter, 1977; Saad & Abbas, 1985a,b; Stromberg *et al.*, 2007). Despite the ecological importance of such changes, little consideration has been given to determining the relationships between the assemblages of species and habitat characteristics in rivers of semi-arid regions, in zones sensitive to changes in hydrology. Such knowledge is fundamental for the provision of advice as to the likely impacts of upstream impoundments and how to ameliorate such effects.

The Gambia River is one of the last eight major (river length > 1000 km) river systems in Africa to remain free flowing and the only one in West Africa (W.W.F., 2006). The last 500 km of the river has only a 1 m drop (Webb, 1992) and contiguous floodplains, seasonally inundated by floodwater (Lesack, 1986). This low gradient results in an extensive estuary and brackish water penetrates as far as 200 km from the river mouth. However, because of the strong seasonality of freshwater flow, the estuary is characterized by great seasonal fluctuations in salinity (0–33 practical salinity units (PSU) at 96 km from the estuary mouth), resulting in a dynamic mix of marine, estuarine and freshwater fish species in the main channel (Albaret *et al.*, 2004). The Gambia estuary is also the last in West Africa that is free from extensive human disturbances and retains a normal salinity gradient, unlike neighbouring estuaries (Albaret *et al.*, 2004). However, this is about to change as a hydroelectric power project funded by the African Development Bank is underway at Sambangalou on the Gambia River in Senegal with the flooding of the dam scheduled for 2011 (McNeil, 2006). This will be the first major impoundment project on the river and, as is the case for other West African rivers such as the Sine-Saloum and Casamance, it is expected to alter severely the hydrology of the river, affecting local fish populations and the wider ecological characteristics.

Although several studies have examined fish communities from the main channel of the Gambia River (Lesack, 1986; Albaret *et al.*, 2004; Vidy, Darboe & Mbye, 2004; Ecoutin, Albaret & Trape, 2005), very little is known about those species inhabiting the floodplain. The only two studies to have described the fish fauna of the floodplains were based on expeditions to the lower river in 1931 (Svensson, 1933) and 1950 (Johnels, 1954). As has been the case with other major West African rivers (Barusseau, Diop & Saos, 1985; Panfili *et al.*, 2006), it is likely that the effects of damming the Gambia River will include a reduction of floodplain inundation downstream and an increase in salt-water intrusion up-river. In order to understand probable impacts on the fish assemblages of the lower Gambia River floodplains, our aim was to describe seasonal variation in the pre-impoundment fish community and its relationship to physical parameters (conductivity, turbidity, dissolved oxygen, pH and temperature) and habitat (ricefields, mud flats, bolongs) at floodplain sites near the upper limit of the salt front. This in the area downstream of the future dam that we regard as likely to be most sensitive to the impoundment. Given the paucity of knowledge of fish in the lower reaches of many rivers in semi-arid regions, we discuss how our approach of concentrating research resources at one or a few sensitive sites can be a valuable tool for provision of pre-impoundment data and, through determination of species – habitat associations, for predicting likely fish community responses to changes in hydrology. We also discuss how this type of information could be used by national environment protection and development agencies to alleviate likely impacts.

Methods

Study area

The Gambia River is 1130 km long, has a catchment area of 78 000 km^2 and flows from Guinea, through Senegal and bisects The Gambia. The single rainy season lasts from June to October, with the highest long-term rainfall recorded in August. Peak river discharge occurs in September, with a rapid rise and fall in flow decreasing almost to zero by December to early July (Lesack, Hecky & Melack, 1984).

In contrast to the Sine-Saloum to its north and Casamance to its south, the Gambia River is considered a 'normal' estuary, with a decreasing salinity gradient from the mouth towards the head of the river (Barusseau *et al.*, 1985). The salt front moves seasonally along the river due to the distinct 'dry' and 'wet' seasons. It reaches 200 km upriver at the end of the dry season and moves downstream in the rainy season (Cooper, 1927; Sylla *et al.*, 1995). Tidal influences are noticeable throughout the length of The Gambia to the Senegal border (Johnels, 1954), a distance along the channel of 460 km. Lesack et al. (1984) recorded a unimodal flood curve for the Gambia River with a very short duration of just 2–3 months and a very steep decline (i.e. rapidity of change) (Welcomme & Halls, 2001) following the end of the rains. Floodplain borders the river channel along the lower 670 km, with the last 200 km being fringed by mangrove forest. The Gambia River floodplains lie in an area of open Sudan savanna, where the river floods for just 4 to 5 months of the year, before drying out almost completely, apart from various bolongs (creeks) which connect to the river and tidal floodwater adjacent to the bolongs.

A total of 93 species of fish have been recorded from the Gambia River. The fish fauna is described as Nilo-Sudanian, with the upper river colonized mainly by Guinean species, but has a relatively low species diversity compared to the Senegal and Niger basins (Leveque, Paugy & Teugels, 1991). The lower reaches contain many estuarine and marine species that migrate upriver seasonally (Baran, 2000).

Sampling

This study was conducted along two transects and two adjacent bolongs on the floodplains east of Farafenni town in Gambia (13° 34′N, 15° 35′W), approximately 193 km and 209 km upstream of the estuary mouth (Fig. 1). This area approximates the upper limit of brackish water during the dry season. No commercial fishing takes place in the two 100 km^2 zones of floodplain in which our study sites were

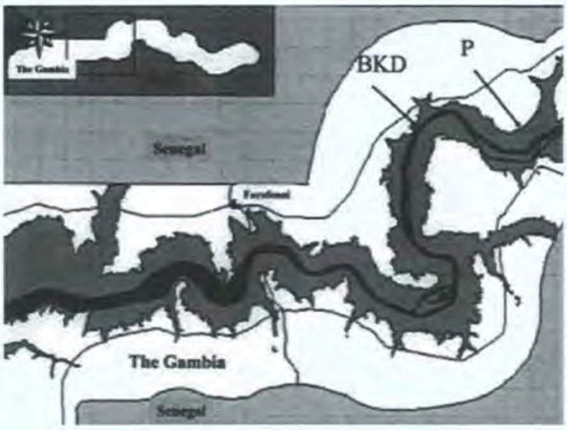

Fig. 1 Location of the Gambia River and the study sites; Balanghar-Ker Derry [BKD] and Palaka [P].

based and there were just three artisanal fishermen catching food for local consumption. Therefore we expect this limited fishing pressure to have had little influence on the species composition, relative abundance and size range of the fish community. The floodplains in this area are characterized by a stretch of mangroves along the main river channel and some of the larger connecting bolongs. Landward of the mangroves are continuous areas of bare mudflats (Bøgh *et al.*, 2007), where there is prolonged desiccation during the dry season and a high salt content, mainly chlorides and sulphates (Giglioli & King, 1966). Ricefields are encountered sporadically on the floodplains, from the edge of the main river channel to the edge of the floodplain, depending on the relative access to the site by the local people (V. Louca, personal observation). Swamp rice is cultivated between 110–290 km from the river mouth, where the river is still tidal (Webb, 1992). The rice is grown first in rainfed nurseries away from the floodplains, and at the peak of the rainy season transplanted in to ricefields on the floodplains. No pesticides are used in the areas we studied. The farmers do not stock the ricefields with fish, and their colonization is through natural dispersal. Neither do farmers normally harvest fish from these fields. Mudflats that receive periodic flooding in the dry season from the spring tides support the perennial *Sesuvium portulacastrum* L., as well as seasonal *Heleocharis* spp and beds of *Paspalum* spp (Giglioli & Thornton, 1965; Bøgh *et al.*, 2007). The area is therefore characterized by the presence of some saltmarsh vegetation, but also retains characteristic freshwater flora such as water lilies (*Nymphaea* spp.) in some habitats such as semi-permanent pools.

The two transects (Balanghar-Ker Derry [BKD], 13°39′N, 15°23′W, Palaka [P] 13°40′N, 15°13′W) were sampled monthly in 2005 and 2006 from May to November, starting 1 month prior to the rainy season and continuing up to 1 month after the end of the rains, covering the period from minimum flooding, through maximum flooding and part-way through the period of decreasing inundation. Each transect started from the beginning of the floodwater to the main river channel or, as in the case of the Palaka transect, to the point where it was impossible to continue due to dense vegetation. Sampling took place with a cast net (diameter: 230 cm, mesh size: 10 mm) and a hand net (25 × 17 cm, mesh: 2 mm) every 150 m along each transect during the first 5 h of daytime. Prior to the start of the project, a number of sampling techniques (electric-fishing, minnow-traps and a seine-net) were tested, but all were ineffective, as relatively few fish were caught. The cast net, a popular fishing technique in The Gambia, proved an effective method of catching a wide variety of fish in open floodwater, channels or gaps in vegetation. The hand net was used to sample smaller fish species and juvenile fish in the shallower vegetated areas (<30 cm). At each sampling point a cast-net was thrown at three different locations within 20 m of either side of the transect point. Five cumulative minutes of sweeping were also undertaken with the hand-net within the same sampling area. Together, these methods provided effort-standardized sampling throughout the study period along floodplain transects.

Choice of sample size at each sampling location was determined by the relationship between the number of species caught and sample size, the ability to sample undisturbed areas within each habitat patch (typically 200–300 m^2) at transect points, and time constraints. For the cast-net samples a doubling of sampling effort, from three to six cast net throws, resulted in a 15% increase in the number of species caught in mudflats and ricefields, and a 23% increase in the bolongs. Analysis of the sampling efficiency of the hand nets revealed that 5 min pushnetting caught 100% of species in 10 min in bolongs, 86% in mudflats and 66% in ricefields.

The vegetation present at an aquatic site can influence the type and amount of food available for fish, as well as provide vital cover (Hickley & Bailey, 1987; Welcomme, 2002), and changes in vegetation cover due to the construction of the dam could therefore influence fish abundance and species composition. Seven vegetation types were defined; barren (areas with no vegetation), grass (*Paspalum* sp, *Sporobolus* spp), sedge (*Eleocharis* sp.), tall reeds (*Phragmites karka* Retz., *Cyperus papyrus* L.), sea purslane (*Sesuvium* spp.), cultivated rice (*Oryza sativa* L.) and water lilies (*Nymphaea* spp.). The dominant vegetation type was determined based on the emergent and/or submerged macrophytes which were most abundant within 20 m each side of each transect sampling point. In addition, the total percentage vegetation cover and number of vegetation types present at each point were also recorded. Mangrove habitats (*Rhizophora* spp, *Avicennia* spp.) were only encountered as a thin strip at the edge of the main river channel and were not sampled as they were part of the main river channel and outside the scope of this study.

Each sample location on the transect was categorized as one of five aquatic habitat types: mudflats, rice fields, bolongs, pools (semi-permanent; rainfed and mostly not connected with the rest of the inundated floodplain except during short periods during heavy rainfall), and puddles (natural or man-made depressions less than 20 m in diameter, rainfed or filled with floodwater during high tides and lasting only a few days before completely drying out). Each water body was assessed as to whether it had a permanent connection to the rest of the floodwater or not. At each location water quality parameters (conductivity, pH, temperature, dissolved oxygen) were measured in the field with a multiparameter probe (WTW Multi 350i, Weilheim, Germany). Water samples were collected and taken to the laboratory for turbidity determination using a turbidity meter (HANNA HI 93703; HANNA Instruments, Padua, Italy). Water depth was measured to the nearest cm with a metre rule at three different locations within the sampling area, and then averaged.

Two bolongs, each in close proximity to but not part of a transect, were additionally sampled over a two-day period in the week after each transect sampling, because they provide important connections between main river and floodplain habitats. Doubling of sampling effort from one to two 24-h periods, resulted in an 18% increase in species richness for the fyke net catches, suggesting a two-day period to be a reasonable descriptor of community composition susceptible to capture by this method. The sampling locations for bolongs BKD and P were 1330 m and 970 m, respectively, from the main river channel. A two-way fyke net (mesh 10 mm) was placed in each bolong, connected with a 5 mm mesh leader net as described in Vidy *et al.* (2004). Nets were placed to obstruct and sample the entire width (BKD: 8 m; P: 5 m) of each bolong. However, on several occasions, during exceptionally high water flows, the bolong overflowed, so that some fish may have bypassed the net. Fykes were checked early in the morning (06:30–07:30) and evening (18:30–19:30). On all sampling occasions, the water depth was recorded to the nearest cm at three locations, in front of each fyke net and at the middle of the leader, and averaged. Water temperature, pH, turbidity and conductivity were all measured as described above. The study transects were located in the middle of two approximately 100 km^2 zones where detailed mapping of mosquito breeding sites has taken place (Majambere *et al.*, 2008). Detailed data on the percentage of flooded habitats for each month during 2005 and 2006 were collected as a measure of the extent of floodplain inundation.

Processing of samples

Fish were preserved in 4% formalin and taken to the laboratory for subsequent identification, sexing and gonad analysis. Fish were identified to species using Paugy, Leveque & Teugels (2003). Species were assigned to the bioecological categories of Albaret *et al.* (2004), which group West African fishes in terms of their marine and freshwater evolutionary origins and their reliance on freshwater, estuarine and marine habitats for part/all of their lifecycles. Bioecological categories, or environmental guilds, have been proposed as a way of assessing the ecological condition of rivers and as a reliable way of determining the impacts of river impoundments on biodiversity and fisheries management (Welcomme, Winemiller and Cowx, 2006).

Each fish was sexed and the reproductive status and maturity assessed by macroscopic observation using the classification stages of Panfili *et al.* (2006). The percentage of immature fish in catches was calculated to assess the use of the floodplains as a nursery habitat for juvenile fish, with species that comprised over 50% immature fish suggesting a high utilization of floodplains as nursery habitats. This was expressed as the number of female fish of smaller standard length than the size at sexual maturity.

Statistical analysis

Repeated Measures ANOVA (SPSS version 15; SPSS Inc., Chicago, IL, U.S.A.) was used to analyse differences in environmental variables between the aquatic habitat types. Transect catches from each sampling point and occasion were converted to Catch Per Unit Effort (CPUE) for each of the sampling methods for each species. Cast net data for each sample site and occasion were converted to the average number of fish (or biomass) of each species per cast throw, and hand-net data to number (or biomass) of fish for each species per minute of sweeping. The two CPUE values were added to provide a combined value for each sampling point, date and species, providing standardized CPUE data for comparison.

General Estimating Equations (GEE) were used to analyse the relationship between species richness and total catch biomass with abiotic variables, using SPSS version 15. This analysis extends generalized linear models (GLMs) to account for repeated measures and clustering of samples as well as allowing for linear and nonlinear models (Horton & Lipsitz, 1999). Separate models were tested for species richness and catch biomass with environmental parameters in the bolongs and floodplains. Puddles and pools, water body types which were encountered on less than six sampling occasions, were excluded from the statistical analysis. A Gamma distribution model with a log-link was used to test the catch biomass. This non-symmetric function is appropriate for measures related to dimensions, including biomass. The Poisson distribution model is appropriate for counts of animal/plant units and therefore for testing species richness (Ter Braak & Smilauer, 2002).

Canonical Correspondence Analysis (CCA) (Ter Braak, 1986) was used to investigate the influence of environmental variables on species distribution from transect samples using CANOCO version 4.5 (Centre of Biometry, Wageningen, the Netherlands). A partial CCA was undertaken with year, transect and transect points controlled for as covariables, so that repeated sampling effects were accounted for. To remove possible collinearity effects, only environmental variables explaining a significant additional proportion of the variance independent of other variables were used in the model. Forward selection was used to identify significant variables for inclusion and each was tested using a Monte Carlo permutation test with 999 runs. Data were log-transformed to prevent a few values from dominating a variable's contribution. Only species which were caught on more than three sampling occasions were used in the analysis to avoid undue influence of very rare species.

Results

Physical variables

Peak rainfall occurred in July in 2005 and August–September in 2006. The peak inundation of the floodplain occurred in July–August and the pattern of floodplain inundation suggests that flooding is a result of both increased local rainfall and increased flooding from the main river channel (Fig. 2). Dissolved oxygen (DO) values ranged from 0.11–15.13 mg L^{-1}, conductivity 0.044–33.7 mS cm^{-1} (*c.* 0–21.5 PSU), temperature 20.5–39 °C, pH 3.1–9.5, turbidity 0.4–1000 NTU and water depth 2–79 cm. The high conductivity values encountered on the floodplains principally reflect increased salinity, associated with tidal influences, low rainfall and low discharge. Temperature, DO, conductivity and turbidity, but not pH, differed significantly between aquatic habitats. Only waterbodies that were sampled on more than six occasions were used in the analysis, which thus excluded puddles and pools. Mean conductivity (ANOVA, d.f. = 2 and 239, $P < 0.001$) and DO (ANOVA, d.f. = 2 and 239, $P = 0.008$) were significantly lower in rice fields, temperature was significantly lower in bolongs (ANOVA, d.f. = 2 and 239, $P = 0.005$), turbidity was significantly higher in rice fields (ANOVA, d.f. = 2 and 239, $P < 0.001$) and bolongs were significantly deeper than other aquatic habitats (ANOVA, d.f. = 2 and 239, $P < 0.001$).

Physical variables changed markedly during the rainy season (Fig. 3). Bolongs and mudflat aquatic habitats were warmest at the end of the rainy season in September–October, whereas for rice fields this occurred immediately before the first rains in May. Turbidity peaked at the end of the rainy season for mudflats and bolongs. In ricefields, peak turbidity was experienced in the middle of rainy season, coinciding with rice transplantation. At the start of the rains pH declined, with a minimum in August in all three habitat types. In floodwater and bolongs pH rose progressively, reaching pre-rainy season values by the end of the season. Conductivity declined through the rainy season, whereas DO dropped following the first rains and then remained stable through the rainy season. Water depth showed no clear temporal pattern for the three aquatic habitat types, possibly reflecting greater tidal rather than seasonal influence on water depth.

Floodplain fish community composition – transect samples

Thirty-two species of fish belonging to 15 families were collected from the floodplain transects in 2005 and 2006 (Table 1). One species, *Tilapia guineensis*, made up 72% of the catch by number. Similar proportions of species of estuarine/marine origin

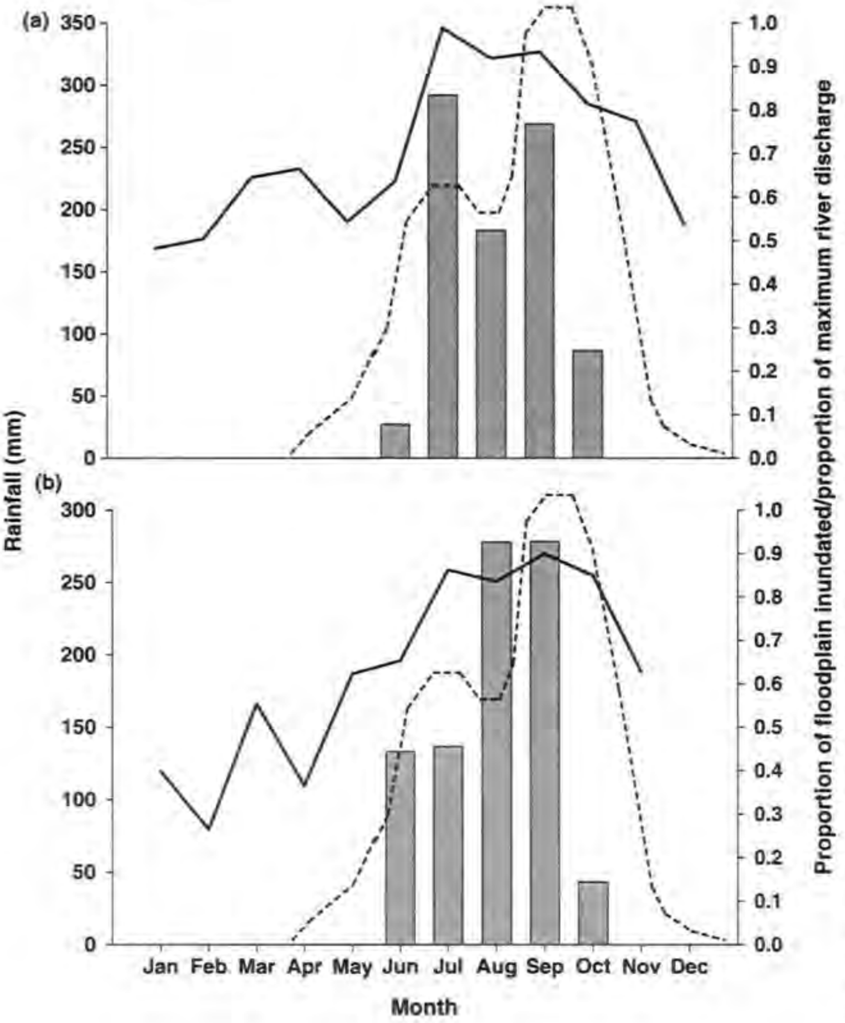

Fig. 2 Seasonal changes in total monthly rainfall (bars), proportion of floodplain inundated (solid line) and schematic of river discharge curve expressed as proportion of the maximum (dotted line) for (a) 2005 and (b) 2006. The seasonal river discharge curve is based on Lesack *et al.* (1984), and was measured 500 km from the river mouth.

(ecological categories Ec, Em, Es, ME, see Table 1) occurred on the floodplain transects (65%) and in the bolongs sampled along the transects (62%, Table 1).

Fish species richness increased with lower conductivity (Table 2) and increasing water depth. When monthly catches were compared to the dry season (May) catches, species richness did not vary significantly, suggesting that it changed little with the progression of the rainy season and with inundation, although the species composition did change (see Temporal changes in species abundance). Barren mudflats, which dominated the floodplains, were chosen as a reference 'vegetation' type for comparison with fish catches associated with other vegetation types. Four dominant vegetation types exhibited significantly higher fish species richness compared to barren mudflats; sedge (59% higher), rice (36% higher), reeds (36% higher) and water lilies (67% higher). Mudflats were the commonest habitat on the floodplain transects and were chosen as a reference group for statistical comparisons (Table 2). Bolongs exhibited significantly higher catch biomass (29% more) and species richness (15% more) than mudflats, whereas rice fields had 21% less catch biomass (borderline significance). Catch biomass and species richness increased with increasing water depth, whereas richness increased with decreasing conductivity. Waterbodies with a permanent connection to floodwater had 335% higher average catch biomass compared to ones with no permanent connection.

Catch per unit effort of the ten commonest species in the three main aquatic habitat types along transects, separated by sampling method are presented in Table 3. *Tilapia guineensis* was the commonest species in all habitats. The killifishes *Poropanchax normani* and *Epiplatys spilargyreius* were more commonly caught in

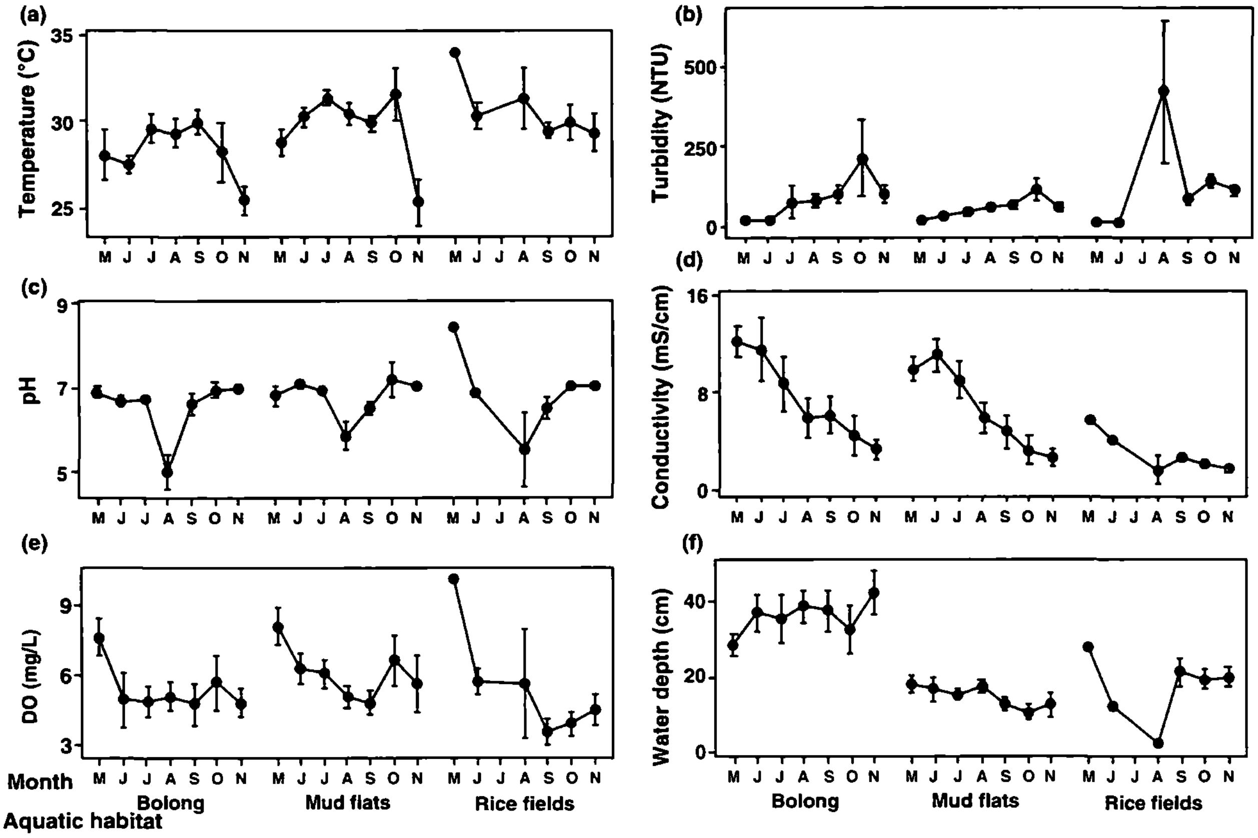

Fig. 3 Temporal changes in means and 95% CI's of (a) water temperature, (b) turbidity, (c) pH, (d) electrical conductivity, (e) dissolved oxygen and (f) water depth for the three commonest aquatic habitats sampled on the Gambia River floodplains (data combined for 2005 and 2006).

hand nets; *P. normani* was encountered mainly in bolongs, and *E. spilargyreius* in rice fields. The characin *Rhambdalestes septentionalis* was mostly caught by cast nets in the bolongs.

Habitat associations

Monte Carlo tests performed using CCA showed a significant contribution of four variables (conductivity, % vegetation cover, water depth and pH) to explaining fish species distributions (Table 4). Figure 4 summarizes the relationship between the abundance of fish species caught on the floodplains in 2005 and 2006 and the factors included in the model, of which the first two axes accounted for 77.1% of the variance. A cluster of species, principally *Elops lacerta, Monodactylus sebae, Brycinus nurse, Rhambdalestes septentrionalis* and *P. normani*, was associated with deeper water habitats. *Periophthalmus barbarus* was associated with habitats with higher conductivity ranges, whereas *Synodontis shall, Chrysichthys nigrodigitatus, Liza falcipinnis, Tylochromis jentinki, Hepsetus odoe, Porogobius schlegelli* and *Pellonulla leonensis* were associated with lower conductivities. *Barbus macrops* and *Liza grandisquamis* were associated with habitats with sparse vegetation cover and *E. spilargyreius* and *Epiplatys bifasciatus* with dense vegetation cover. These species clusters were confirmed using cluster analysis. Using CCA, no clear pattern of habitat associations of the different bioecological categories identified above was observed.

Of the 21 species for which sufficient samples were taken on the floodplain by all sampling methods, more than 50% of females comprised reproductively immature fish in 13 species (Table 1). This group included one characin (*B. nurse*) and eight catfishes, with the rest being of estuarine/marine origin demonstrating the use of floodplains as nursery habitats for these species.

Table 1 Relative abundances and species abbreviations used in the CCA plot (Fig. 3) of all the fishes sampled in the Gambia River floodplain in 2005 and 2006. The percentage numbers of non-mature female fish are provided for those species with a sufficient sample size ($n > 20$)

					2005				2006			
					Transect		Bolong		Transect		Bolong	
Family	Species	Abbr.	Cat	% juv.	BKD %	*P* %	BKD %	*P* %	BKD %	*P* %	BKD %	*P* %
Elopidae	*Elops lacerta* Valenciennes	ELAC	ME	100	3	0	0	<1	1	<1	0	1
Clupeidae	*Pellonula leonensis* Boulenger	PLEO	Ec	21	1	<1	5	11	0	0	77	25
	Sardinella maderensis Lowe	SMAD	ME	-	1	0	0	0	0	0	0	0
	Ethmalosa fimbriata Bowdich	EFIM	Em	-	1	0	0	0	0	0	0	0
Hepsetidae	*Hepsetus odoe* Bloch	HODO	Co	-	<1	0	0	0	<1	0	0	0
Characidae	*Rhambdalestes septentrionalis* Boulenger	RSEP	Co	8	1	1	0	1	3	1	<1	3
	Brycinus nurse Rüppell	BNUR	Co	100	<1	1	1	4	<1	0	0	<1
	Alestes dentex L.	ADEN	Co	-	0	0	0	<1	0	0	0	1
Cyprinidae	*Barbus macrops* Boulenger	BMAC	Co	25	0	<1	0	1	0	<1	0	3
Bagridae	*Chrysichthys nigrodigitatus* Lacepède	CNIG	Ec	82	2	<1	41	54	1	<1	8	50
	Chrysichthys johnelsi Daget	CJON	Ce	100	0	0	2	2	<1	<1	<1	4
Schilbeidae	*Schilbe intermedius* Rüppell	SINT	Co	79	0	0	12	3	0	0	<1	1
Clariidae	*Clarias anguillaris* L.	CANG	Co	-	0	<1	0	1	0	0	<1	0
Mochokidae	*Synodontis schall* Bloch & Schneider	SSCH	Co	100	0	<1	10	12	0	<1	1	1
	Synodontis batensoda Rüppell	SBAT	Co	50	0	<1	7	1	0	0	<1	<1
Cyprinodontidae	*Poropanchax normani* Ahl	PNOR	Co	20	15	1	0	0	12	<1	0	<1
	Epiplatys spilargyreius Duméril	ESPI	Co	30	1	3	0	0	3	4	0	<1
	Epiplatys bifasciatus Steindachner	EBIF	Co	-	0	0	0	0	1	<1	0	0
	Aplocheilichthys spilauchen Duméril	ASPI	Es	-	0	0	0	0	0	<1	0	0
Gerreidae	*Eucinostomus melanopterus* Bleeker	EMEL	ME	-	0	0	0	0	0	0	<1	0
Sciaenidae	*Pseudotolithus senegalensis* Valenciennes	PSEN	ME	-	0	0	1	1	0	0	0	0
Monodactylidae	*Monodactylus sebae* Cuvier	MSEB	Es	100	<1	0	1	3	0	<1	2	2
Cichlidae	*Tilapia guineensis* Bleeker	TGUN	Es	57	56	90	6	2	72	91	2	<1
	Tylochromis jentinki Steindachner	TJEN	Es	100	4	0	4	0	2	0	3	<1
	Tylochromis intermedius Boulenger	TINT	Es	-	0	0	0	0	<1	0	0	0
	Oreochromis niloticus L.	ONIL	Es	-	0	0	0	0	0	<1	0	0
	Tilapia zilli Gervais	TZIL	Es	-	0	0	0	0	0	<1	0	0
	Hemichromis bimaculatus Gill	HBIM	Es	35	1	2	1	0	0	1	0	<1
	Hemichromis fasciatus Peters	HFAS	Ec	9	2	2	1	<1	3	1	1	1
Mugilidae	*Liza grandisquamis* Valenciennes	LGRA	Em	100	5	0	1	1	1	<1	0	3
	Liza falcipinnis Valenciennes	LFAL	Em	100	3	<1	0	0	<1	<1	0	<1
	Mugil cephalus L.	MCEP	ME	-	0	0	0	0	<1	0	0	0
Polynemidae	*Polydactylus quadrifilis* Cuvier	PQAD	ME	-	0	0	1	1	0	0	1	1
Gobiidae	*Gobionellus occidentalis* Boulenger	GOCC	Es	-	0	0	0	0	<1	0	<1	0
	Nematogobius maindroni Sauvage	NMAN	Es	100	2	<1	3	0	<1	<1	0	0
	Porogobius schlegelii Günther	PSCH	Es	25	1	<1	4	2	0	1	5	<1
	Periophthalmus barbarus L.	PBAR	Es	-	0	0	0	0	<1	0	0	<1
Anabantidae	*Ctenopoma kingsleyae* Günther	CKIN	Co	-	0	0	0	0	<1	0	0	0
Cynoglossidae	*Cynoglossus senegalensis* Kaup	CSEN	Em	-	0	<1	1	<1	0	0	0	0
Total number					488	2850	209	355	923	3285	471	451

Bioecological categories follow Albaret *et al.* (2004).: Co, continental species, occasional in estuaries; Ce, continental species from estuarine origin; Ec, estuarine species from continental origin; Es, strictly estuarine species; Em, estuarine species from marine origin; ME, marine-estuarine species, using estuaries as nurseries.

Table 2 General Estimating Equations output for species richness and catch biomass with abiotic factors in the Gambia River floodplains (transect samples) and bolongs (fyke catches). OR refers to Odds Ratio, the relative importance of the measured variable in relation to the reference group for the nominal variables and the relative change in relation to 1 unit of change in the independent variable

	Floodplains				Bolongs			
	Richness		Catch biomass		Richness		Catch biomass	
	OR	*P*	OR	*P*	OR	*P*	OR	*P*
Temperature	0.994	0.671	0.986	0.215	**0.925**	**<0.001**	0.992	0.770
pH	0.966	0.343	0.995	0.871	**0.943**	**0.012**	**0.983**	**<0.001**
Conductivity	**0.982**	**0.001**	1.004	0.650	1.010	0.483	0.993	0.464
Oxygen	1.006	0.565	1.010	0.265	**1.050**	**0.027**	**1.065**	**0.039**
Water depth	**1.008**	**0.002**	1.004	0.083	**1.005**	**0.001**	**1.009**	**<0.001**
Turbidity	0.999	0.265	1.002	0.122	1.000	0.701	0.998	0.588
No. of veg types	1.036	0.239	0.994	0.803	N/A	N/A	N/A	N/A
% veg cover	**0.996**	**0.006**	0.997	0.136	N/A	N/A	N/A	N/A
Catches:								
Day	N/A		N/A		**0.619**	**0.001**	**0.585**	**<0.001**
Night:	N/A		N/A		1		1	
Year:								
2005	0.889	0.223	0.847	0.094	1.060	0.794	0.923	0.405
2006	1		1		1		1	
Site:								
BKD	**0.823**	**0.014**	**0.706**	**0.001**	**0.858**	**<0.001**	**0.585**	**<0.001**
P	1		1		1		1	
Vegetation type:								
Barren	1		1		N/A	N/A	N/A	N/A
Grass	1.264	0.120	1.052	0.670	N/A	N/A	N/A	N/A
Sedge	**1.588**	**0.001**	1.064	0.649	N/A	N/A	N/A	N/A
Rice	**1.360**	**0.050**	1.239	0.171	N/A	N/A	N/A	N/A
Tall reeds	**1.362**	**0.043**	0.980	0.895	N/A	N/A	N/A	N/A
Water lilies	**1.674**	**0.004**	1.076	0.635	N/A	N/A	N/A	N/A
Aquatic habitat								
Floodwater	1		1		N/A	N/A	N/A	N/A
Rice fields	1.149	0.253	0.787	0.057	N/A	N/A	N/A	N/A
Bolongs	**1.287**	**0.003**	**1.148**	**0.047**	N/A	N/A	N/A	N/A
Month:								
May	1		1		1		1	
June	1.024	0.834	1.077	0.458	**1.277**	**<0.001**	**1.556**	**0.001**
July	1.050	0.687	1.110	0.269	**0.747**	**<0.001**	0.897	0.579
August	0.850	0.138	0.982	0.844	1.154	0.223	1.113	0.247
September	0.849	0.060	1.025	0.792	0.744	0.423	0.738	0.118
October	0.935	0.581	0.880	0.343	1.148	0.677	0.968	0.781
November	0.850	0.178	**0.730**	**0.043**	**0.690**	**<0.001**	**0.608**	**<0.001**
Connectivity:								
Yes	1.308	0.189	**3.351**	**0.012**	N/A	N/A	N/A	N/A
No	1		1		N/A	N/A	N/A	N/A

Significant values are given in bold.

Bolongs – fyke net samples

In total, 29 species of fish belonging to 16 families were captured in fyke nets in the bolongs (Table 1). Two species, *P. leonensis* (a clupeid) and *C. nigrodigitatus* (a bagrid catfish), made up 64% of the total catch. Five species occurred mostly in night catches. These were four catfishes: *C. nigrodigitatus, Chrysichthys johnelsi, Synodontis schall, Synodontis batensoda* and the threadfin *Polydactylus quadrifilis*. Fish richness and biomass were tested against continuous variables using GEE analysis. Categorical variables (day/night catches, sampling bolong, year and month) were also incorporated into the model, with bolong accounted

Table 3 Catch per unit effort (cast net: number of fish per cast net throw; hand net: number of fish per minute of sweeping) of the 10 commonest species compared between the Gambia River floodplain habitats sampled along the transects of mudflats, rice fields and bolongs for the two sampling methods, cast net and hand net over the whole study period

	Mudflats		Rice fields		Bolongs	
Species	Cast net (mean ± SE)	Hand net (mean ± SE)	Cast net (mean ± SE)	Hand net (mean ± SE)	Cast net (mean ± SE)	Hand net (mean ± SE)
Rhambdalestes septentrionalis	0.04 ± 0.01	0.00 ± 0.00	0.13 ± 0.05	0.00 ± 0.00	0.42 ± 0.16	0.00 ± 0.00
Chrysichthys nigrodigitatus	0.06 ± 0.02	0.00 ± 0.00	0.03 ± 0.02	0.00 ± 0.00	0.07 ± 0.03	0.00 ± 0.00
Poropanchax normani	0.04 ± 0.02	0.21 ± 0.06	0.03 ± 0.02	0.17± 0.06	0.06 ± 0.03	0.59 ± 0.14
Epiplatys spilargyreius	0.01 ± 0.01	0.30 ± 0.03	0.00 ± 0.00	0.35 ± 0.06	0.00 ± 0.00	0.17 ± 0.03
Tilapia guineensis	14.36 ± 3.2	0.18 ±0.02	9.99 ± 1.32	0.19 ± 0.04	4.91 ± 0.74	0.11 ± 0.02
Tylochromis jentinki	0.05 ± 0.01	0.00 ± 0.00	0.02 ± 0.02	0.00 ± 0.00	0.09 ± 0.03	0.00 ± 0.00
Hemichromis bimaculatus	0.16 ±0.03	0.04 ± 0.01	0.11 ± 0.03	0.02 ± 0.01	0.01 ± 0.01	0.04 ± 0.01
Hemichromis fasciatus	0.16 ± 0.03	0.01 ± 0.00	0.21 ± 0.05	0.02 ± 0.01	0.11 ± 0.03	0.01 ± 0.00
Liza grandisquamis	0.01 ± 0.00	0.00 ± 0.00	0.20 ± 0.09	0.00 ± 0.00	0.11 ± 0.04	0.00 ± 0.00
Liza falcipinnis	0.05 ± 0.03	0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.00	0.08 ± 0.03	0.00 ± 0.00

Table 4 Habitat variable loadings and ordination summary for the canonical correspondence analysis of the fish assemblages in the Gambia River floodplain for Axis 1 and Axis 2

	Axis 1	Axis 2
Canonical coefficients for environmental variables		
Water depth	0.90	−0.03
% vegetation cover	0.50	0.53
Conductivity	−0.24	0.75
pH	0.00	0.20
Correlation of environmental variables with species axis		
Water depth	0.53	−0.01
% vegetation cover	0.29	0.18
Conductivity	−0.14	0.25
pH	0.00	0.07
Summary statistics for ordination axis		
Eigenvalues	0.12	0.04
Species-environment correlations	0.58	0.34
Cumulative % variance:		
species:	2.60	3.40
species-environment:	58.8	77.1
Sum of all eigenvalues:	4.69	
Sum of all canonical eigenvalues:	0.20	

Only the statistically significant (Monte Carlo significance test, 999 permutations) habitat variables were included in the model and are shown here; Water depth (*F*-ratio: 7.71, *P* = 0.001), % vegetation cover (*F*-ratio: 1.98, *P* = 0.010, Conductivity (*F*-ratio: 7.71, *P* = 0.015), pH (*F*-ratio: 7.71, *P* = 0.025).

for as a repeated measure variable (Table 2). Fish catch biomass and species richness increased with decreasing pH, increasing DO and water depth, suggesting increased standing stocks in the bolongs through the main period of high river flow, but perhaps also due to high tide levels. Fish species

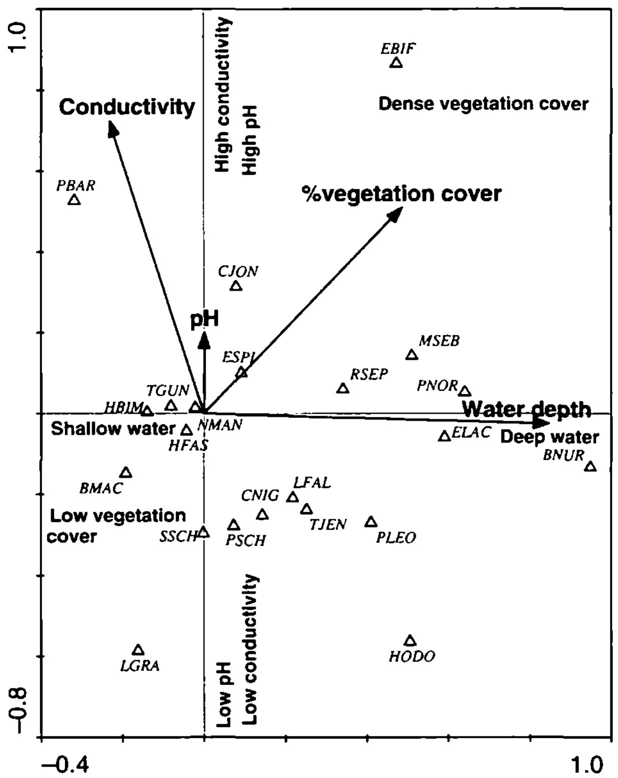

Fig. 4 Canonical correspondence analysis biplot of the distribution of the 22 commonest fish species (Δ) and significant environmental variables (vector arrows) sampled on transects of the floodplain. The position of each species centroid indicates its association with the environmental conditions. The corresponding species name for the species acronyms are given in Table 1. Positive scores on axis 1 represent mainly deeper and more permanent water habitats with denser vegetation cover. Positive scores on axis 2 represent habitats associated with higher conductivity and pH.

richness in the bolongs was significantly higher in June than in dry season reference conditions in May and subsequently lower in July and November, suggesting that bolongs were mostly inhabited by fish following the first rains and that this use subsequently declined.

Temporal changes in species abundance

While species richness in the bolongs and the floodplain (combined data from all methods over 2005 and 2006) did not differ significantly between months, the catches of individual species showed marked changes during the rainy season (Fig. 5). Catches of four species, *L. qrandisquamis*, *R. septentrionalis*, *T. guineensis* and *Hemichromis bimaculatus* peaked immediately before the rainy season; catches of three species (*C. nigrodigitatus*, *P. leonensis*, *S. schall*) peaked in the first 2 months following the onset of the rains, whereas catches of *Schilbe intermediatus*, *T. jentinki*, *P. normanii* and *E. spilargyreuius* were highest in the middle and latter part of the rainy season. Catches of other species such as *H. fasciatus* varied little throughout the rainy season.

Discussion

This is the most comprehensive study of fishes in the floodplains of the Gambia River, the last major river in West Africa without any impoundments, and provides baseline information on the structure of fish community and floodplain habitat in the lower reaches before impoundment of the river by a hydroelectric dam. A lack of pre-intervention data is one of the common problems in determining the impacts of changes to aquatic environments, especially in equatorial regions, and this study will enable future impacts to be assessed. The study also demonstrates

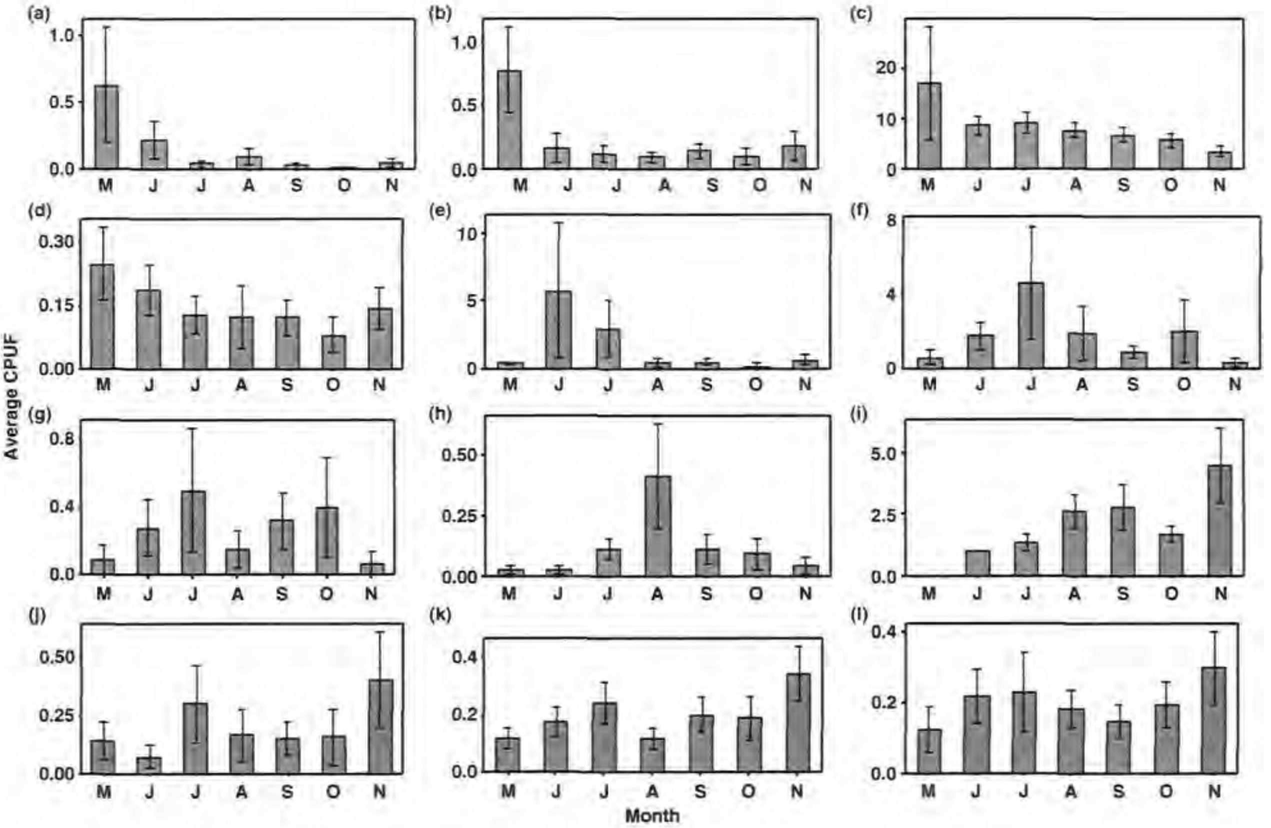

Fig. 5 Temporal changes and SE in the total catches of some of the commonest species caught in the floodplains and bolongs for 2005 and 2006; sampling effort was consistent between months: (a) *Liza grandisquamis*, (b) *Rhambdalestes septentrionalis*, (c) *Tilapia guineensis* (d) *Hemichromis bimaculatus* (e) *Pellonula leonensis* (f) *Chrysichthys nigrodigitatus*, (g) *Synodontis schall*, (h) *Tylochromis jentinki*, (i) *Schilbe intermedius* (j) *Poropanchax normani* (k) *Epiplatys spilargyreius* (l) *Hemichromis fasciatus*.

clear structuring of the fish assemblages by environmental factors that are predicted to change markedly downstream of the dam following impoundment (Mcneil, 2006), suggesting that significant changes to the wetlands and their fish communities are likely. The effects of construction of the hydroelectric dam on downstream hydrology of the river, subsequent changes in environmental variables and impacts on the fish communities of the lower Gambia floodplains are summarized in a conceptual model (Fig. 6).

In total, 19 families and 39 species of fishes occurred on the lower floodplains, compared to 26 families and 95 species described for the whole of the Gambia River (Leveque *et al.*, 1991). This indicates that a substantial part of the river's fish fauna utilizes the floodplains in the lower river. Six of the eight ecological categories sampled by Albaret *et al.* (2004) were present on the floodplains, with the two categories not encountered being marine ecotypes. This reflects the location of the sampling sites at the current upper limit of salt penetration, restricting the occurrence of strongly marine affiliated species in the locality. Twenty-six out of 39 species caught on the floodplains and bolongs are of estuarine/marine origin, indicating a strong influence of estuarine species on the fish communities of the floodplains. However, 12 strictly freshwater species also occurred, reflecting the current suitability of habitats for this ecological group, especially during the wet season flooding phase. No clear pattern of habitat associations of the different bioecological categories identified above was observed in our study. This is probably because these bioecological categories were defined on the basis of the evolutionary origins and resultant salinity tolerance of each species (Albaret *et al.*, 2004). Even though these categories would be expected to be related to particular conductivity ranges, this was not always the case in our study. For example, species of freshwater evolutionary origin (e.g. *H. odoe*) and some species of marine origin (e.g. *L. falcipinnis*) were both associated with low conductivities.

Our results indicate that the fish communities of the floodplains in our study are not random associations of species, but are governed primarily by four environmental factors (conductivity, pH, water depth and

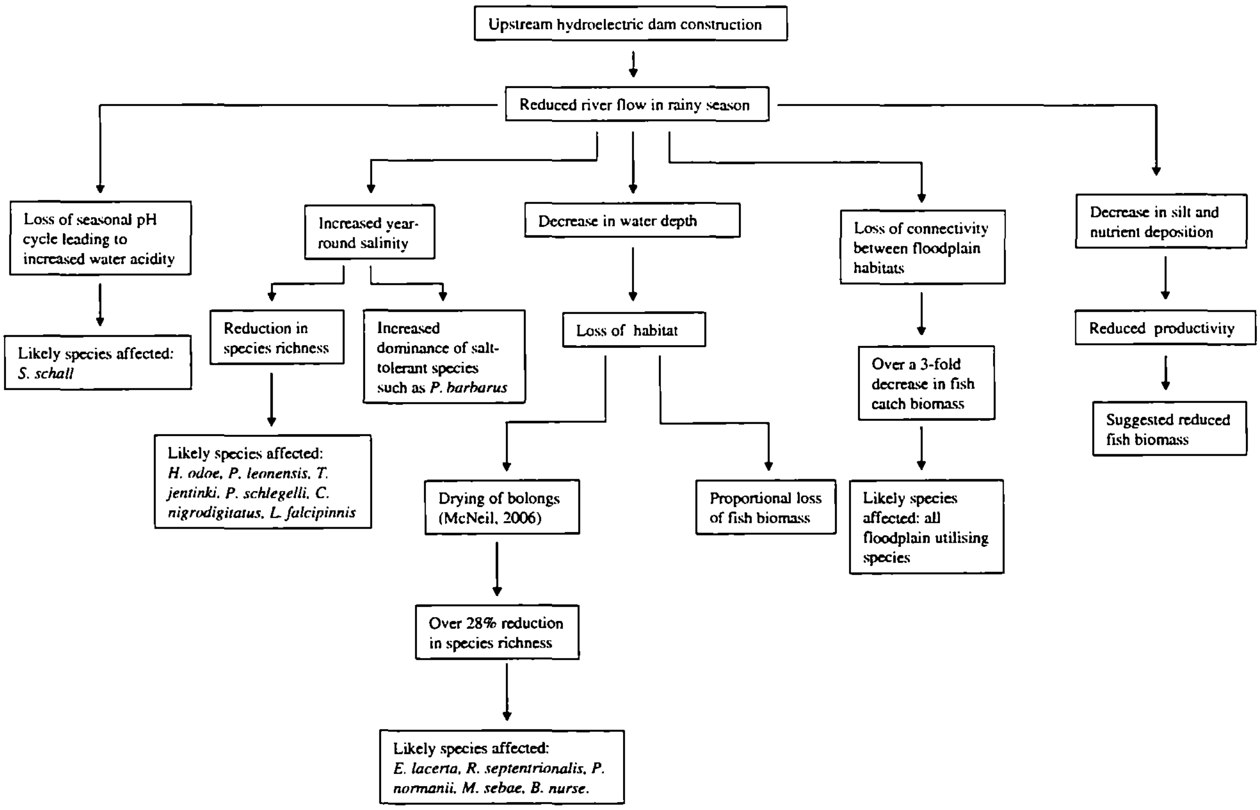

Fig. 6 Conceptual model of the proposed effects of the hydroelectric dam on the fish communities of the Gambia River floodplains.

vegetation cover) all of which are expected to be affected after the completion of the hydroelectric dam. Reduced water flow downstream of the impoundment will result in a dramatic alteration of the flood curve of the river from the one described by Lesack (1984), with an expected decrease in both the amplitude and the duration of the flood leading to lower water levels, increased conductivities caused by higher salt intrusion and alterations in vegetation cover and plant species composition (Fig. 6). Moreover, decreased connectivity between floodplain pools and the rest of the floodplain will restrict access and decrease both the number of fish species and fish biomass found in them (Fig. 6) as we have shown that connectivity is a key factor affecting these attributes. Previous plans to dam the Gambia River in the late 1970s were rejected, mainly due to the anticipated changes in salinity and pH that would have severely impacted rice cultivation along the middle and lower reaches of the river (Webb, 1992). Plans for an anti-salinity barrage to block the saline intrusion were rejected, as this would have led to increased sediment acidity levels upstream of the barrage. High concentrations of iron sulphates in the mangrove soils reduce local sediment and water pH, but tidal currents limit the accumulation of this acidity. The reduced tidal environment upstream of a barrage would increase retention of acidic materials and severely impact rice productivity. Our results indicate that pH plays a significant role in controlling the structure of fish communities on the floodplains (Fig. 6), as well as possibly triggering the migration of species through the bolongs. The three commonest aquatic habitats show a clear seasonal variation pattern in pH, with lower values at the peak of the rainy season, indicating that pH is not only influenced by tidal fluctuations as suggested previously (Webb, 1992). Furthermore, higher DO values, deeper water and lower water temperature all seem to cause an increase in the number of species using the bolongs, with all of these parameters probably associated with higher water flows which result in increased water depth, greater oxygenation of the water, lower temperature and the washing off of iron sulphates from the soils to the water, resulting in lower pH.

These results concur with other studies from the region demonstrating the importance of water temperature and conductivity (Benech & Niare, 1998), and water level (Welcomme, 1979, 1985; Lowe-Mcconnell, 1987), as key drivers of fish migration in floodplain river habitats. The lower Gambia floodplains provide nursery or potential nursery habitats for many species and this is demonstrated by the high number of species comprising mostly immature individuals, including some of those for which adults occur mostly in the main channel rather than the floodplain (Albaret *et al.*, 2004; Ecoutin *et al.*, 2005). A fuller answer as to the importance of the lower Gambia River floodplains as nursery habitats requires analysis of the relative sources of juvenile recruitment to the adult populations, particularly for those species where the adults commonly inhabit the main channel. Species with a large proportion of mature fish tended to be small-sized (*P. leonensis, R. septentrionalis, B macrops, P. normani, E. spilargyreius, H. fasciatus, H. bimaculatus, P. schlegelli*), as these are more likely to benefit from the reduced predation pressure on the floodplains compared to the main river channel (Welcomme, 1979). Artisanal fishing in the area is not expected to be the reason for the large proportion of small-sized fish caught on the floodplains, as no commercial or large scale fishing takes place on the floodplains and in the main river channel in the area. This is also supported by Lesack (1986), who suggests that variations in fish catches in the Gambia River are due to changes in environmental variables influencing emigration and immigration, rather than fishing pressure.

The environmental impact assessment report on the hydroelectric dam project (McNeil, 2006) predicts that dam construction will result in many Gambian bolongs drying due to the reduced flows. We expect this to have a severe impact on the fish species that use the floodplain, since we have shown that the bolongs hold the highest species richness and biomass indicating and that they are a vital aquatic habitat on the floodplains (Fig. 6). Moreover, drying of the bolongs will restrict access of the fish onto the floodplain, decreasing further the number of species using other aquatic floodplain habitats, such as mud flats and ricefields (Fig. 6).

Tilapia guineensis was the commonest species encountered on the floodplains, comprising 72% of transect catches by number and was mainly encountered in mudflat and ricefield habitats (Table 3). It is a very important food source for people in rural areas adjacent to floodplains. Peak abundance of this species occurs in the first 2 months following the onset of the rains and then progressively declines. This is the start of the 'hungry season', when adults carry out hard manual labour in their fields waiting for the harvest at the end of the rains (Ceesay *et al.*, 1997). Consequently, reduced flows following the construction of the dam are expected to have a major impact on tilapia biomass and therefore restrict a major protein supply for the local people at a particularly critical time of year.

Previous studies have shown that dam construction alters the frequency and degree of inundation of floodplains downstream of impoundments (Dumont, 1992), leading to less flooding, large increases in water salinity and decreases in DO, particularly within the tropics (Adams & Hughes, 1986). This, together with existing information (Webb, 1992; McNeil, 2006), suggests that the construction of the dam on the Gambia River could have a marked effect on the distribution and migration of the fishes in the lower Gambia floodplains since water depth, conductivity, oxygen and pH were found to be factors affecting distribution and seasonal changes in CPUE. It is anticipated that species associated with lower conductivities will disappear from the floodplains and overall decreases in DO will alter the timing of species migrations (Fig. 6). Salt water inundation is also likely to depress severely the cultivation of the swamp rice that is grown in large areas of the floodplains during the rainy season. Since rice is a staple diet of most Gambians, increased salinity is likely to have serious consequences for food production in the lower reaches of the river.

The construction of the dam is also likely to have a widespread impact on the ecology of the downstream area. Reduced flooding is expected to decrease the heterogeneity of the floodplains, reduce nutrient input and increase salt retention. West Africa forms part of the Palaearctic flyway and the Gambia River floodplains provide vital habitats for migrating and resident birds (Bos, Grigoras & Ndiaye, 2006). Anticipated changes in wetland vegetation and associated changes in invertebrates and fish production are expected to alter food availability for the different bird species, with possible long-term declines in avian biodiversity in the region.

Management of the dam after its construction will have to address these issues to minimize the impacts on the downstream habitats, fish and wider ecology, as well as other activities such as rice-growing. Maintaining high water flow during the rainy season in a manner that follows the natural flood regime of the river will slow down salt intrusion at the lower reaches of the river and ensure that at least some of the bolongs will stay connected with the main channel, thus allowing fish access. Moreover, periodic flushing with high water flow, ideally at the peak of the rainy season in August–September (as this coincides with the natural fluctuation in pH recorded in our study) should limit the accumulation of sulphates in the mangrove soils. Yet these activities are unlikely to be supported by a policy of maximizing profitability from hydropower income generation, nor do they assist retention of water in the reservoir to support electricity generation during the dry season. Maintenance of catchment integrity and function across national boundaries can only be achieved by sensitive international cooperation and this will undoubtedly be needed in the case of the lower Gambia River.

This study identifies important factors influencing the structure of floodplain fish communities of an unimpacted, semi-arid, floodplain river system and demonstrates the sensitivity of fish communities to seasonal and spatial variations in environmental conditions. The sensitivity of species to anticipated changes in environmental conditions should always be taken into account in assessments addressing the potential impacts of impoundments on fishes and other biota. However, within semi-arid regions in particular, governments and development agencies need to take greater account of the potential impacts downstream of proposed dams, as some of the most profound environmental changes can occur a long distance from the site of intervention.

Acknowledgments

This work was supported by a studentship to Vasilis Louca from the National Institutes of Health (grant number: 1 VO1 AI058250-01) and by award of the Freshwater Biological Association Hugh Cary Gilson Memorial Award in 2005. We are grateful to the Medical Research Council's Laboratories in The Gambia for provision of facilities and support at Farafenni Field Station and the Gambian Fisheries Department for their cooperation. Many thanks to Pierre Gomez for the provision of the rainfall data and to two anonymous reviewers who provided valuable comments on the manuscript.

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(Manuscript accepted 6 August 2008)

Ecology of Freshwater Fish 2009: 18: 60–64
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Factors triggering floodplain fish emigration: importance of fish density and food availability

Louca V, Lindsay SW, Lucas MC. Factors triggering floodplain fish emigration: importance of fish density and food availability.
Ecology of Freshwater Fish 2009: 18: 60–64. © 2008 The Authors.
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Abstract – Emigration is a widespread phenomenon among fish species in seasonal habitats, but little is known about the factors which trigger individuals to emigrate to new habitats. In controlled experiments using *Tilapia guineensis*, a species widely occurring in the seasonal floodplains of West Africa, density of fish played a significant role in triggering fish migration, whereas a lack of food available caused an increase in exploratory behaviour but with no impact on successful emigration. The impact of fish density and subsequently interactions between individuals on emigration suggests that this may be an important causal factor of emigration in fish species exhibiting social interactions.

Key words: emigration; *Tilapia guineensis;* seasonal movement; floodplains; food availability; density

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Accepted for publication June 9, 2008

Introduction

Migration is one of the commonest behavioural adaptations of animals living in seasonal environments and occurs in a variety of taxa including mammals, insects, birds and fish (Kennedy 1951; Wolff 1994; Lucas & Baras 2001; Makrakis et al. 2007; Castello 2008), but surprisingly, little is known about the factors which trigger individuals to emigrate to new habitats (Taylor & Norris 2007). Emigration is defined as a one-way movement from the home area (Lidicker & Stenseth 1992; Dingle & Drake 2007) and suggested cues that trigger this exploratory behaviour include unfavourable environmental conditions, lack of resources, predation pressure and intra- and inter-specific competition (Bell 1991).

The relative strength of the different factors which trigger emigration may vary between species and particular environments. The proximate food limitation hypothesis assumes that territories are only important as a mechanism of capturing food (Marschall & Crowder 1995), suggesting that only food availability truly determines the individual's decision to migrate. By contrast, other studies suggest that a wider range of factors such as water temperature, flow and cover availability can trigger fish emigration (McMahon & Hartman 1989; Keeley 2001). Under controlled conditions McMahon & Tash (1988) recorded increased emigration rates of the desert pupfish, *Cyprinodon macularius*, in response to a doubling in densities and a consequent halving of available food and cover. Keeley (2001) found both food and density, rather than either exclusively, to be important components of demographic changes (emigration and mortality) in steelhead trout, *Oncorhynchus mykiss*. It is important to tease apart individual factors that influence fish migratory behaviour so that their relative influence can be assessed. As a result of difficulties in isolating causal factors for emigration in the field, it has been suggested that only well-controlled laboratory studies can identify the true significant factors (McMahon & Tash 1988; Matter et al. 1989; McMahon & Matter 2006). Yet, these same experiments, on fish and non-fish taxa, have been mostly carried out on species which do not exhibit well-defined seasonal migration patterns (McMahon & Tash 1988; Matter et al. 1989; McMahon & Matter 2006). Emigration behaviour is considered to be at least partly genetically determined (Dingle 1980; Lidicker & Stenseth 1992) and, therefore, experiment testing factors that influence emigration had to consider species adapted to seasonal environments.

Floodplain habitats are highly seasonal and provide dynamic conditions, some of which may present threats to fish and in other cases, advantages. Whilst

doi: 10.1111/j.1600-0633.2008.00323.x

fish may become concentrated into isolated pools or channels as water levels recede, floodwater also provides access to new habitat, which can be important for reproduction and/or feeding. Exploitation of seasonal floodplains by fishes may, therefore, be triggered by specific environmental conditions. The Guinea tilapia, *Tilapia guineensis*, is widely distributed on West African floodplains (Campbell 1987). It is the commonest fish species encountered on the highly seasonal Gambia River floodplains, and readily colonises new habitats which become available during the rainy season (V. Louca, unpublished data). Although most cichlids have very limited migratory habits (Hert 1992; Lucas & Baras 2001), this is not the case in cichlids living in seasonal floodplains habitat (Benech & Penaz 1995). While average Guinea tilapia densities in inundated floodplain have been recorded as 11 fish·m^{-2}, densities of 40–70 fish·m^{-2} are not uncommon and in floodplain pools densities of 500 fish·m^{-2} can occur (V. Louca, unpublished data). In this species, the strongest territorial behaviour is exhibited by adult reproductive individuals which defend small areas from conspecifics (Campbell 1987), and this is consistent with cichlid behaviour in general in which social interactions between siblings of juvenile cichlids start as simple physical encounters and avoidance and progress to elaborate lateral posturing and finally to strong sexual and dominance interactions (Valerio & Barlow 1986; Keenleyside 1991).

This study examined, under controlled conditions, the role of food availability and fish density in emigratory behaviour of the tropical floodplain fish, the Guinea tilapia. We hypothesised that exploratory behaviour leading to emigration would increase with elevated density and reduced food, because of increased competition for space and food resources.

Methodology

Study site and test fish

The study was carried out at the Medical Research Council's field station at Farafenni town (UTM coordinates: 1500200N, 435500E), The Gambia, located in the southern Sahel region and characterised by a single rainy season from June to October. It lies in an open flat Sudan savannah dominated by the Gambia River and the highly seasonal floodplains which border it (Svensson 1933; Pages & Citeau 1990).

Juvenile Guinea tilapia were collected from local floodplains using cast nets in 2007. Specimens were kept in large holding tanks for a minimum of 2 weeks to acclimatise the fish and accustom them to being fed on aquarium dried flake food (Tetramin, fed *ad libutum*). The total length of the fish collected varied from 5 to 7 cm, a range which represents nonbreeding individuals (V. Louca, unpublished data). Young Guinea tilapia do not show any sexual dimorphism (Paugy et al. 2003), so sexes were not differentiated in the study.

Emigration experiments

Six cement tanks were constructed under a shed with open sides so that the tanks would be exposed to the natural day/night variations in shade temperature and light, but prevent any changes in the water level of the tanks because of rainfall. Each tank was divided into two parts, each 1.0-m long and 1.0-m wide, with a water depth of 0.75 m, and a connecting ramp in the middle (Fig. 1). Fish were placed on one side of the tank (A) and a clear tube (length 7 cm, diameter 3 cm) connected to the narrowing ramp (length 15 cm) (Fig. 1), prevented return of fish which moved to the opposite side of the tank. Following introduction of fish into the holding tank, the water level was raised using a hose pipe and kept constant at 0.5 cm at the ramp (about one-third of fish body depth), so as to make fish movement across the ramp challenging, so that only those individuals with sufficiently strong motivation to emigrate would do so (McMahon & Matter 2006). Preliminary observations showed that tilapia readily approached and accessed the ramp and those which successfully traversed it did not return to the holding tank (cumulative increase in numbers in receiving compartment B and recorded no incidences of fish accessing the ramp via the tube). The effect of fish density on emigration was tested with high (40 fish·m^{-2}), medium (25 fish·m^{-2}) and low (10 fish·m^{-2}) density treatments, densities naturally encountered in the wild, all of which were fed standard aquarium flake at a ration of 5% of fish biomass/day (Legendre & Ecoutin 1989). Experiments lasted for 7 days and comprised 12 tank replicates per treatment. For the food treatment, 25 fish per tank were used for

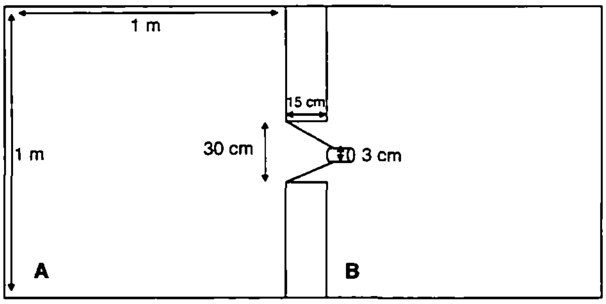

Fig. 1. Experimental setup of the emigration test tanks. Fish were introduced on side A (75 cm deep), and emigrating individuals moved across the ramp (water depth at the ramp, 0.5 cm) to side B. The clear tube at the end of the ramp stopped fish from moving back to side A.

treatment and control groups. Food (standard aquarium flake, 5% of average fish biomass/day) was provided for the control group and no food was given to the treated group for the whole 7-day duration of each experimental round. There were 12 tank replicates each for the food and control treatments.

Preliminary observations showed that fish approached and traversed the ramp throughout the day, but the lack of light prevented night-time observations. Behavioural observations were therefore carried out daily between 14:00 and 17:00, for 90 min in one randomly selected tank per treatment and the exploratory behaviour of the fish in that tank was assessed by counting the number of times fish moved onto the ramp (an individual fish exposing its whole body on the ramp). As the ramp was the area of the tank that became newly available at the start of the experiment, we consider an individual fish's effort to move onto the ramp as a good indicator of increased exploratory behaviour. The total number of fish that crossed into the emigration section over 24 h was recorded daily at 17:00 from counts of fish in the emigration section of each tank. No mortality or loss of fish was recorded during the study. Individual fish were used only once to avoid problems related to learned behaviour.

Statistical analysis

The impacts of the density and food treatments on the number of fish which migrated and the number of attempted crossings were analysed using General Estimating Equations. This analysis extends generalised linear models to account for repeated measures and clustering of samples as well as allowing for linear and nonlinear models (Horton & Lipsitz 1999). As tanks were repeatedly sampled daily, it was important to select a method which accounts for repeated measures. Tank number was incorporated into the model as a repeated measures variable assuming an exchangeable correlations matrix. Data were fitted to a negative binomial distribution with a negative binomial link function as untransformed data followed a negative binomial distribution. All analysis was performed in SPSS version 15.

Results

The starting fish density in the holding tank had a highly significant effect on the proportion of fish which migrated ($P < 0.01$, Table 1) with the highest emigration rate observed with an initial density of 40 fish·m^{-2}, with a relative odd's ratio (O.R., the proportional change relative to the reference group of 20 fish·m^{-2}) of 1.48, whereas there was no significant difference between medium and low densities (Table 1). By contrast, food availability had no impact on the proportion of fish emigrating (Table 1). Both food availability (O.R. = 1.22) and the highest fish density (40 fish·m^{-2}; O.R. = 1.13) caused a significant increase in the relative level of exploratory behaviour (Table 1). Relative levels of exploratory behaviour per fish, both for fish kept with and without food did not vary significantly over time (Table 1), but there was a significant decrease in the daily proportion of fish migrating for the medium (25 fish·m^{-2}) fish density.

Discussion

For animals exhibiting social interactions, recent models based on emigration behaviour argue against

Table 1. Comparisons of the proportion of Guinea tilapia that successfully migrated across the ramp and relative frequency of exploratory movements onto the ramp per fish in relation to fish density and food availability.

			Range			95% Wald C.I.		
Factors		Median	Min.	Max.	Odds' ratio	Low	High	*P*
Emigration (proportion of fish over 7-day experimental period)	High density	0.54	0.02	0.92	1.48	1.24	1.75	**<0.01**
	Med. density	0.02	0.00	0.76	1.23	0.97	1.55	0.09
	Low density	0.00	0.00	0.20	1.00	–	–	–
	No food	0.20	0.00	0.92	1.04	0.84	1.31	0.70
	Food supplied	0.02	0.00	0.76	1.00	–	–	–
Change in emigration over time (days)	High density	0.03	0.00	0.63	0.99	0.99	1.00	0.11
	Med. Density	0.00	0.00	0.62	0.98	0.97	0.99	**0.04**
	Low density	0.00	0.00	0.20	0.99	0.98	1.01	0.15
Ramp explorations(during 90-min observation period)	High density	0.09	0.00	2.60	1.13	1.00	1.28	**0.05**
	Med. density	0.00	0.00	0.29	0.95	0.79	1.19	0.60
	Low density	0.00	0.00	0.60	1.00	–	–	–
	No food	0.15	0.00	5.50	1.22	1.05	1.41	**0.01**
	Food supplied	0.00	0.00	0.29	1.00	–	–	–
Change in ramp explorations over time (days)	No food	0.15	0.00	5.50	0.99	0.99	0.98	0.21
	Food supplied	0.00	0.00	0.29	0.98	0.94	1.02	0.34

C.I. is 95% confidence interval. Significant values are given in bold.

resource availability as a driving force for emigration, but suggest social interaction to be a far more important factor (Wolff 1994). However, others argue that resource availability, habitat use and social interactions and their effects on emigration are closely intertwined (McMahon & Matter 2006). Cichlid fish are known to exhibit complex behavioural patterns with a variety of different interactions between individuals including juveniles (Keenleyside 1991). In this study, high fish density was shown to be a primary factor triggering emigration. During the dry season, the floodplains of the Gambia River are reduced to small water bodies with high densities of fish taking refuge in them (Svensson 1933; V. Louca, unpublished data). Interactions between tilapias with established territories within those shrinking habitats and other individuals that find refuge in them during the dry season is likely to be a major factor driving fish out on to newly flooded areas at the beginning of the rainy season.

These results show that a lack of food induces increased exploration (Table 1), probably to find food, but there is no indication in our experimental set-up that it triggers them to make the extra effort needed to negotiate a shallow-water conduit and emigrate to a new habitat (Table 1). This finding is also in accordance with Mesick (1988) who concluded that food is not a strong trigger of emigration in stream-dwelling trout. These processes may be considered in the context of a mechanistic model whereby the availability of resources (e.g., food, cover, territorial space) affects the exploratory behaviour of individuals, such that elevated motivation of individuals and increased exploratory behaviour will lead eventually to emigration (Sale 1969; McMahon & Matter 2006). In this study, the exploratory behaviour for fish with and without food did not vary over time suggesting that food availability is a relatively weak motivation for fish to emigrate. Emigration patterns in fish which occupy more permanent habitats, for example salmonids in streams and tropical fish in coral reefs are mostly well-understood. Dominant fish hold territories and subordinate individuals exhibit increased exploratory behaviour and emigration, with subsequent high costs for the emigrating individuals, which often move to areas of poor quality habitat where energy gain may be low and predation risk high (Clarke 1970; Larson 1980; Marschall & Crowder 1995; Keeley 2001). However, if local resource availability is low, substantial costs can also be involved for fish that do not emigrate (McMahon & Tash 1988), so there is a potential trade-off of fitness costs and benefits to emigration. In the case of species such as the Guinea tilapia, which utilise seasonally flooded areas, emigrating into newly flooded, high-quality habitat unoccupied by other fish and with few aquatic predators can be expected to increase their survival chances (Welcomme 1979; Lowe-McConnell 1987; Lucas & Baras 2001). In these habitats, emigration may, therefore be a characteristic of strong fitness benefit.

Acknowledgements

This work was supported by the National Institutes of Health (grant number: 1 VO1 AI058250-01) and by an award of the Freshwater Biological Association Hugh Cary Gilson Memorial Award to V. Louca in 2005. We are grateful to the Medical Research Council's Laboratories in The Gambia for provision of facilities and support at Farafenni Field Station and the Gambian Fisheries Department for their cooperation.

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VECTOR CONTROL, PEST MANAGEMENT, RESISTANCE, REPELLENTS

Role of Fish as Predators of Mosquito Larvae on the Floodplain of the Gambia River

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J. Med. Entomol. 46(3): 000–000 (2009)

AQ: 1

ABSTRACT We examined the potential of using native fish species in regulating mosquitoes in the floodplain of the Gambia River, the major source of mosquitoes in rural parts of The Gambia. Fishes and mosquito larvae were sampled along two 2.3-km-long transects, from the landward edge of the floodplain to the river from May to November 2005 to 2007. A semifield trial was used to test the predatory capacity of fish on mosquito larvae and the influence of fish chemical cues on oviposition. In the field, there was less chance of finding culicine larvae where *Tilapia guineensis*, the most common floodplain fish, were present; however, the presence of anophelines was not related to the presence or absence of any fish species. In semifield trials, both *T. guineensis* and *Epiplatys spilargyreius* were effective predators, removing all late-stage culicine and anopheline larvae within 1 d. Fewer culicines oviposited in sites with fish, suggesting that ovipositing culicine females avoid water with fish. In contrast, oviposition by anophelines was unaffected by fish. Our studies show that *T. guineensis* is a potential candidate for controlling mosquitoes in The Gambia.

KEY WORDS *Anopheles gambiae*, fish, mosquitoes, predation, oviposition

The use of fish for controlling mosquitoes was an important tool in the pre-DDT era (Floore 2006, Walker and Lynch 2007). Typically fish were introduced into all potential mosquito breeding habitats, including ricefields, marshes, dams, canals, and ponds (Hadjinicolaou and Betzios 1973, Motabar 1978). However, the introduction of DDT in the mid-1940s led to a significant decrease in the use of biological control (Gabaldon 1969). Nevertheless, after concerns regarding the harmful effects of chemicals on nontarget species and the development of insecticide resistance by mosquitoes (Milam et al. 2000), interest in the biological control of malaria vectors has been rekindled (Killeen et al. 2002, Killeen 2003).

Fish have been used successfully for controlling both culicine and anopheline mosquitoes (Tabibzadeh et al. 1970, Victor et al. 1994) but are used relatively infrequently in sub-Saharan Africa (Walker and Lynch 2007). Mosquito control using fish has focused on a limited number of species, primarily *Gambusia affinnis* Baird and Girard and *Poecilia reticulata* Peters, that have traditionally been used for controlling mosquito larvae (Sitaraman et al. 1975, Gall et al. 1980, Cech and Linden 1987, Homsky et al. 1987, Blaustein 1992, Valero et al. 2006, Walton 2007). One of the most important concerns when introducing exotic fish for mosquito control is their impact on native species (Benigno 2001, Hoddle 2004). In Greece, the introduction of *G. affinis* led to a decline of the endemic fish species *Valencia letourneuxi* Sauvage (Economidis 1995), with similar findings reported elsewhere (United States, Spain, Australia) (Motabar 1978, Arthington 1991, Garcia-Berthou 1999, Leyse et al. 2004). The problems with introducing exotic species have spurred interest in the use of native species for controlling mosquitoes (Romand 1985; Mancini and Romi 1988; Fletcher et al. 1992, 1993; Frenkel and Goren 1999; Lee 2000; Kusumawathie et al. 2006; Marti et al. 2006; Yildirim and Karacuha 2007).

Using fish for mosquito control can be unpredictable, with several failures reported in the literature (Bence 1988, Blaustein 1992). However, the number of failures may be larger caused by publication bias, over-representing successful trials. The importance of mosquito larvae in the natural diet of fish, exclusions of mosquitoes from aquatic habitats caused by predation, or avoidance by ovipositing female mosquitoes has rarely been studied, with studies often reporting contradictory results. In Colombia, larvae of *Anopheles albimanus* Wiedemann were found to be negatively associated with fish and predatory invertebrates, such as dragonfly and mayfly nymphs (Marten et al. 1996). This phenomenon is thought to be far more widespread in nature, with predatory fish influencing the distribution of many species of aquatic invertebrates (Wellborn et al. 1996, Maddrell 1998). In contrast, in Pakistan, larvae of *Anopheles subpictus* Grassi were positively related with the presence of aquatic pred-

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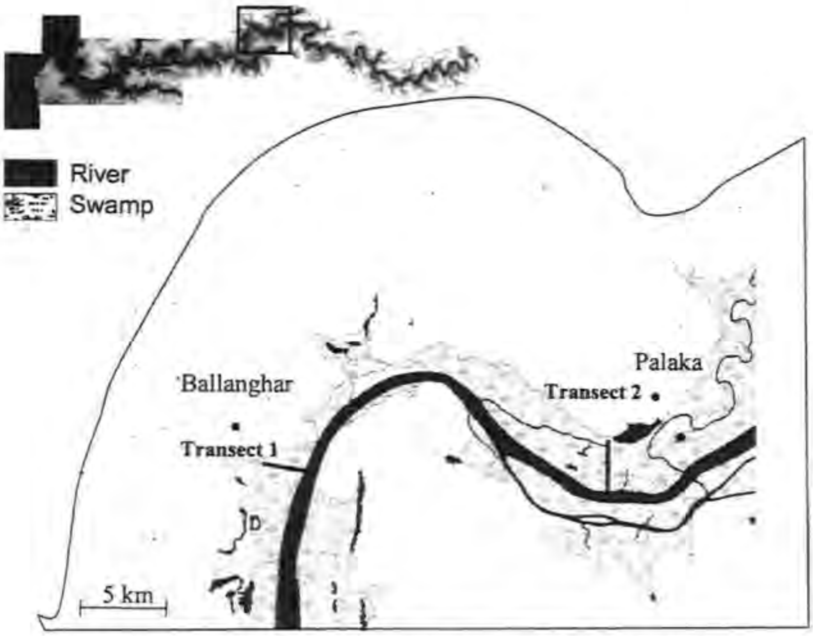

Fig. 1. Location of the study sites on the Gambia River floodplain.

ators including fish, although the authors were unable to provide an explanation for this (Herrel et al. 2001).

Several aquatic invertebrate taxa have evolved avoidance behaviors to minimize predation risk (Kerfoot and Sih 1987, Tjossem 1990, Resetarits 2001, Abjornsson et al. 2002). This behavior has also been reported in mosquito species, mainly culicines, in response to both invertebrate and vertebrate (mainly fish) predators (Spencer et al. 2002, Kiflawi et al. 2003, Angelon and Petranka 2004, Blaustein et al. 2004, Bond et al. 2005, Munga et al. 2006). Identifying whether mosquitoes detect and avoid ovipositing in habitats containing fish is important because it affects the efficacy of fish to control mosquitoes because gravid female mosquitoes may select alternative breeding sites. Considering the importance of African anopheline mosquitoes in the transmission of malaria and the renewed interest in using fish for mosquito control, it is surprising that no studies have been carried out to determine whether *Anopheles gambiae* s.l. Giles, the principal vector of malaria in Africa, avoids fish. Although several studies have examined the potential of native fish species to control African malaria vectors, the importance of these species in the ecology of the mosquito has been overlooked (Kumar and Hwang 2006). We therefore set out to test the hypothesis that native fish species can be used for mosquito larval control in West Africa. The following predictions were tested: (1) the absence of aquatic stages of mosquitoes will be associated with the presence of certain floodplain fish species under natural conditions, (2) the diet of these fish species will include mosquitoes, (3) the presence of insectivorous fish will reduce oviposition by female mosquitoes under semifield conditions, and (4) insectivorous fish will be efficient predators of mosquitoes under semifield conditions. The study was carried out in the floodplain of the Gambia River, the major source of anopheline mosquitoes in rural parts of The Gambia (Bøgh et al. 2007, Majambere et al. 2008). This study formed part of a larger project investigating the use of microbial larvicides for controlling malaria vectors and, taking into account the lack of published information on the indirect effects of microbial larvicides on fish communities in lentic systems, allowed us to investigate at a pilot study scale whether this activity affected fish populations in the floodplain.

Materials and Methods

Study Area. This study was conducted along two transects (Balanghar-Ker Derry village [transect 1], 13°39′ N, 15°23′ W, Palaka village [transect 2] 13°40′ N, 15°13′ W), each ≈2.3 km long, on the floodplain east of Farafenni town (UTM coordinates: 1500200N, 435500E), The Gambia, 193 and 209 km upstream of the estuary mouth, respectively, and approximately at the upper limit of brackish water during the dry season (Fig. 1). The transects were chosen to cross all vegetation zones typical of the floodplains. Rains occur from June to October, with the highest long-term rainfall recorded in August. Baseline data were collected in 2005 when no sites were treated with larvicide. In 2006, transect 1 was treated weekly with *Bacillus thuringiensis* Berliner variety *israelensis*, followed by transect 2 in 2007 (Majambere et al., unpublished data).

Each transect was located at the center of a zone ≈100 km^2 in area, where all aquatic sites were treated at weekly intervals from May to November. In 2006

≈2,200 kg of Bti WDG and 1,200 kg Bti CG were applied in spray zone 1, with 3,200 kg Bti WDG and 3,700 kg Bti CG in 2007 in zone 2. The floodplain in this area was characterized by a stretch of mangroves along the main river channel and some of the larger connecting creeks. Behind the mangroves were continuous areas of mudflats that were often entirely barren because of the prolonged desiccation during the dry season and high content of soluble salts, mainly chlorides and sulfates (Giglioli and King 1966). Rice fields occurred in two belts on the floodplain: one along the landward edge of the floodplain and the other closer to the river. Mudflats that receive periodic flooding in the dry season from the spring tides support the perennial *Sesuvium portulacastrum*, as well as seasonal *Heleocharis* spp. and beds of *Paspalum* spp. (Giglioli and Thornton 1965, Bøgh et al. 2007). The area was therefore characterized by the presence of some salt marsh vegetation but also retains characteristic freshwater flora such as water lilies (*Nymphaea* spp.) in some habitats, such as semipermanent pools.

Field Mosquito and Fish Sampling. Two transects were sampled monthly from May to November in 2005, 2006, and 2007, beginning ~1 mo before the rains and ending 1 mo after the rains. Each transect started from the beginning of the floodwater and ended at the main river channel in the case of transect 1 and in the thick forest fringing the river in the case of transect 2. Mosquito larvae were sampled by taking 10 dips with a standard mosquito dipper (350 ml capacity dipper; AQ: 2 Clarke Mosquito Control Products, IL) every 150 m along each transect between 0700 and 1300 hours. Dips were made within 20 m either side of the transect point. The presence or absence of anophelines and culicine larvae at each sampling site was recorded. Late anopheline larvae were transferred to plastic containers with water from the sampling site and transported to the laboratory and allowed to emerge for subsequent identification.

Fish sampling took place along the transects within 20 m of the mosquito-sampling locations using a cast net (diameter: 230 cm, mesh size: 10 mm) and a hand net (25 by 17 cm in area, mesh size: 2 mm). The cast net was used for sampling in open water and areas of sparse vegetation, and the hand net was used to sample smaller fish species and juvenile fish in the shallower vegetated areas (<30 cm). Five cumulative minutes of sweeping were undertaken with the hand-net and three cast net throws were taken within the sampling area. Together, these methods provided effort-standardized sampling throughout the study period along floodplain transects. Fish were preserved in 4% formalin and taken to the laboratory for subsequent identification. Fish were identified to species using Paugy et al. (2003). Each sampling location on the transect was categorised as one of four aquatic habitat types according to the classification scheme of Majambere et al. (2008): floodwater habitats, rice fields, creeks, or pools. Pools were defined as semipermanent, rain fed, and not connected with the rest of the inundated floodplain except during short periods during heavy rainfall.

Diet Analysis. The modified Costello method (Costello 1990) of Amundsen et al. (1996) was used to describe the feeding habits of the different fish species and to identify the insectivores, the feeding guild most likely to prey on mosquito larvae. For each prey item in each fish species, the percentage occurrence ($\%F_i$) and the prey-specific abundance (P_i) were calculated as follows:

$$\%F_i = (N_i/N) \times 100$$

$$P_i = (\Sigma S_i/\Sigma St_i) \times 100$$

where N_i is the number of fish with prey i in their stomach, N is the total number of fish with stomach contents, S_i is the stomach contents wet weight comprised of prey i, and ΣSt_i is the total stomach content weight in only those fish with prey i in their stomach.

Prey abundance values for every prey item were obtained by the product of the percentage occurrence ($\%F_i$) and prey-specific abundance (P_i), which is also represented by the area enclosed by the coordinates of the two axes on a $\%F_i$ versus P_i graph. In assigning species to trophic guilds, prey items (starting from the most common one) that totaled 50% of the total prey abundance were used to define the trophic guild of the species. The following trophic guilds were used: (1) omnivores, fish that included both animal and plant material in the items that contributed the first 50% of the prey abundance values; (2) insectivores, this group included both aquatic and terrestrial insect prey items; (3) detritivores, fish that fed primarily on organic detritus that may include mineral material; (4) piscivores, prey items that included other fish; (5) planktivores, this category included zooplankton, mainly cladocerans and crustacean larvae; (6) molluscivores, diet comprising mainly gastropods and bivalves; and (7) herbivores, fish that fed primarily on plant material. Only fish species with a minimum of 20 individuals caught with usable stomach contents (not empty or fully digested) were used in the analysis.

Semifield: Predation Experiment. This experiment was based on a setup that had been used previously for testing the efficacy of microbial larvicides in the field (Fillinger et al. 2003, Majambere et al. 2007). Twenty-five plastic bowls with an upper diameter of 53 cm, a lower one of 40 cm, and a height of 40 cm (70-liter volume) were sunk into an open sunlit area on the MRC field station in Farafenni with the lip protruding 5 cm above the soil. Bowls were set out in a grid 2 m apart, with five rows of five bowls. Overflow holes were created in each bowl, 35 cm from the bottom, to allow excess water to run-off during heavy rains. These holes were 1 cm in diameter and were covered with untreated nylon mosquito netting (mesh: 0.2 mm) to prevent larvae and fish from escaping. A collar of netting (inner diameter: 25 cm, mesh: 1 mm) was placed around the rim of each bowl, directed inward and upward at a 45° angle, to prevent any fish present from jumping out of the bowls.

Each bowl was filled with soil to a depth of 5 and 30 cm of unchlorinated tap water. The soil was thoroughly mixed beforehand to prevent variations in the soil conditions between bowls. Bowls were allowed to be colonized by mosquitoes for 8 d and for late instar larvae to develop. Subsequently, the 25 bowls were ranked in terms of their anopheline larval densities at the end of the 8-d period. The 18 bowls with the highest densities were kept and the rest were emptied. Subsequently, these bowls were separated into six groups of three each with similar anopheline densities. The two treatments, addition of six *Epiplatys spilargyreius* Duméril (average biomass: 0.45 g/70 liters) or six *Tilapia guineensis* Bleeker (average biomass: 26.3 g/70 liters) per bowl, and controls, with no fish, were assigned randomly within each one of these six groups.

Epiplatys spilargyreius was selected for this experiment because this species was most frequently found with mosquito larvae in its stomach and was also the most common insectivore species and a surface feeder, whereas *T. guineensis* was selected because it was the most abundant fish in the floodplain, was a bottom feeder, and is known to readily emigrate and colonize newly available floodplain habitats (Louca et al. 2008a, b). More than 200 individuals of both species were collected from the floodplain. Each fish species was kept in separate stock containers and fed on standard aquarium flake food (Tetramin, fed ad libitum) AQ: 3 before use in the experiments. Individual fish were used only once during the experiment to avoid the influence of learned behavior on mosquito predation. Fish of similar sizes were used to avoid variations within, but not between, species in the predatory capacity because of size differences. The size range for *E. spilargyreius* was 3–5 cm total length (TL: tip of snout to margin of caudal fin), which is the size range for adult fish (Paugy et al. 2003), and for *T. guineensis*, the range was 5–7 cm TL. This represents the most appropriate sizes that can survive adequately in the experimental bowls used for this project but also includes the size at which these fish are commonly found in floodplain habitat.

The experiment was run for a further 12 d. Mosquito sampling took take place daily between 1700 and 1900 hours. Five dips were taken from each bowl using a standard dipper: four from the sides and one from the center. The presence or absence of anopheline and culicine larvae was noted and recorded as early (first and second instar), late (third and fourth instar), or pupae. All larvae were replaced, whereas pupae were removed for subsequent species identifications as described below. Any dead fish were replaced with fish kept in the holding bowl.

Semifield: Oviposition Cues. Nine bowls were placed 4 m apart in a grid arrangement in the same location as described above for the predation experiment. The greater distance between bowls than in the predation experiment was used to reduce the possibility of mosquitoes confusing chemical cues between bowls. Each bowl, including controls had a 20 by 20 by 20-cm netting cage (mesh size: 0.2 mm) suspended in the middle of the bowl, ≈1 cm below the water surface. Three randomly chosen bowls contained six *E. spilargyreius* placed within the cage, three had six caged *T. guineensis*, and three without fish served as controls. Dipping for mosquito larvae was carried out as described above for 7 d after first colonization, while the bowls were left open and oviposition continued. Three separate trials were carried out. New bowls were used between trials and experiments to avoid cross-contamination of fish chemical cues.

Mosquito Identification. All pupae were collected from the semifield experiments and late anopheline larvae from the field study were placed in separate individual mosquito cages and allowed to eclode. Adult anophelines were identified morphologically using Gilles and DeMeillon (1968). Culicine mosquitoes were identified as *Culex quinquefasciatus* Say, *Toxorhynchites* spp., *Aedes vittatus* Bigot, and other culicines. Sibling species of the *An. gambiae* complex were subsequently identified by amplification of ribosomal DNA using polymerase chain reaction (PCR) (Scott et al. 1993).

Statistical Analysis. Data were entered using Epi-Info version. Because of the large number of sites AQ: 4 sampled for which zero counts of mosquito larvae were obtained, mosquito data were transformed to presence or absence of larvae. Canonical correspondence analysis (CCA) (Ter Braak 1986) was used to analyze the influence of environmental variables (habitat type, treated/untreated with larvicides, transect, year, distance from the floodplain edge, percentage vegetation cover, sampling month, and presence/absence of each of the four most common insectivore fish species, as well as the commonest fish species, *T. guineensis*), on the presence/absence of anophelines and culicine larvae. A partial CCA was undertaken with sampling point controlled for as a covariable to account for repeated measures. Only environmental variables explaining a significant additional proportion of variance were used to avoid possible collinearity effects. Forward selection was used to identify significant variables and each variable was tested using Monte Carlo permutation test (999 runs). The CCA multivariate method is a descriptive approach that does not quantify the impact of each of the variables on the mosquitoes individually. Therefore, the impact of each of the variables identified using CCA on the presence/absence of anophelines and culicines was tested using general estimating equations (GEEs) using SPSS version 15. This analysis AQ: 5 extends generalized linear models (GLMs) to account for repeated measures and clustering of samples as well as allowing for linear and nonlinear models (Horton and Lipsitz 1999). A binomial distribution with a logit link function was used to test the effect of those variables identified by CCA as having a significant impact determining the distribution of positive and negative anophelines and culicine sites on each of those mosquito groups separate. All *P* values were adjusted to account for the number of comparisons carried out.

For those fish species that significantly influenced the distribution of mosquitoes in the field, separate analyses were carried out using only the hand-net samples, because these were collected from the edges of aquatic habitats where mosquitoes were also sam-

Table 1. Diet guilds (both sexes together) are provided for fish species with sufficient sample size ($n > 20$) sampled in 2005–2006

Fish species	Diet (n)	Fish	Molluscs	Terr. arthropods	Aq. invert.	Zoopl-ankton	Fish/invert. eggs	Fish remains (scavenging)	Detritus	Macrophytes	Plant seeds	Diet guild
Elops lacerta	29	**78.28**	21.72	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	P
Rhambdalestes septentrionalis	60	0.00	0.00	**41.85**	**31.87**	21.81	1.89	0.67	1.92	0.00	0.00	I
Chrysichthys nigrodigitatus	31	4.87	7.31	0.19	**81.62**	0.02	0.00	5.98	0.00	0.00	0.00	I
Poropanchax normanii	353	1.95	0.85	3.54	14.83	5.30	0.63	0.26	**69.51**	2.82	0.29	D
Epiplatys spilargyreius	108	0.00	0.00	**36.46**	**39.44**	7.16	0.00	0.00	16.94	0.00	0.00	I
Epiplatys bifasciatus	26	11.11	0.00	**66.66**	11.12	11.11	0.00	0.00	0.00	0.00	0.00	I
Tilapia guineensis	1,431	0.00	0.38	0.78	3.78	1.72	0.29	2.36	**86.91**	3.60	0.19	D
Hemichromis bimaculatus	39	0.00	4.06	4.07	**79.68**	0.00	4.06	0.00	4.06	0.00	4.09	I
Hemichromis fasciatus	29	**66.67**	0.00	0.00	33.33	0.00	0.00	0.00	0.00	0.00	0.00	P
Liza grandisquamis	32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**97.18**	2.82	0.00	D
Liza falcipinnis	26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**100.00**	0.00	0.00	D
Porogobius schlegelli	39	0.00	**75.00**	0.00	25.00	0.00	0.00	0.00	0.00	0.00	0.00	M

Percentage abundance of each prey item is provided ($\%F_i \times Pi$). The prey item/items that add up to a minimum of 50% of prey abundance and therefore determine the diet guild in which a species belongs are highlighted in bold.

D, detritivores; I, insectivores; P, piscivores; M, molluscivores.

pled, reflecting a better representation of possible interactions between fish and mosquito.

Semifield data were incorporated untransformed in a mathematical model and analyzed using GEE analysis. Bowl identity was accounted for as a repeated-measures variable assuming an exchangeable correlations matrix. For the predation semifield experiment, the presence of anopheline and culicine mosquito was tested against the two fish treatments using a binomial distribution with a logit link function to test the predatory capacity of the two fish species.

In the oviposition experiment, larval densities (number of larvae per dip) were tested against the two fish treatments using a normal distribution and a log link function because a better goodness-of-fit was achieved with this distribution model compared with using a binomial model and testing presence/absence of mosquito. Comparisons between treatments were made only when at least one bowl was colonized by mosquitoes. The percentage reduction in larval mosquito densities was calculated using the formula of Mulla et al. (1971): $\% \text{ reduction} = 100 - (C_1/T_1 \times T_2/C_2) \times 100$, where C_1 and C_2 describe the average number of larvae in the control tanks pre- and post-treatment, and T_1 and T_2 describe the average number of larvae in the treated with fish tanks pre- and post-treatment.

A Poisson probability distribution with a log link function was used to test the impact of spraying with microbial larvicides on the fish species richness (number of fish species caught). The Poisson distribution model is appropriate for counts of animal/plant units and is therefore appropriate for testing species richness (Ter Braak and Smilauer 2002). Catches of the most common six fish species followed a negative binomial distribution; therefore, a negative binomial distribution model, with a negative binomial link, was used to test the impact of microbial larvicide spraying on the abundances of these species.

Ethics. Durham University Ethics Advisory, Gambia Government/Medical Research Council Joint Ethics Committee, and Gambian Fisheries Department granted ethical approval. All fish were handled according to the ethical animal treatment rules (Anon 2003).

Results

Mosquitoes and Fish Feeding Habits. A total of 11,013 fish were caught along the transects between 2005 and 2007 (see species list in Louca et al. 2008b). *T. guineensis* was the dominant species, comprising >86% of the combined catch with an average density of 7.59 fish/m^2 (range: 0–518 fish/m^2) and an average catch biomass of 296 g/m^2 (range: 0–1959 g/m^2). Because most species were rare, with only a few individuals caught, reliable diet data could only be obtained for 12 species. For *E. spilargyreius*, the second species tested under semifield conditions, the average density was 0.1 fish/m^2 (range: 0–1 fish/m^2) and average biomass of 0.02 g/m^2 (range: 0–0.1 g/m^2). Fish belonging to several feeding guilds were identified (Table 1), but only three species were collected with T1
mosquitoes in their stomachs as adult mosquitoes were observed in stomachs of *Rhambdalestes septentrionalis* Boulenger and anopheline larvae in *Ctenopoma kingsleyae* Günther, while culicine larvae occurred in *E. spilargyreius* and *R. septentrionalis*. The insectivores mostly consumed aquatic Hemiptera, adult stages of terrestrial insects (Diptera, Coleoptera), larval/pupal AQ: 6

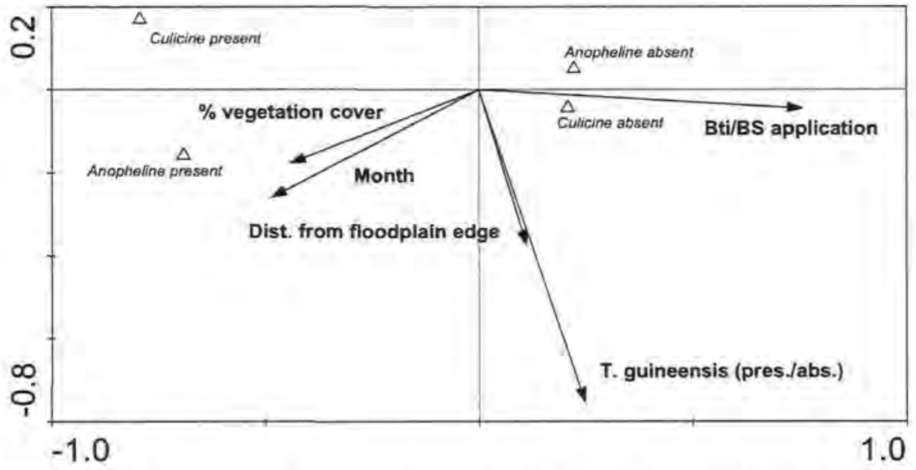

Fig. 2. CCA biplot of the distribution of positive and negative sites for anophelines and cilucine larvae (Δ) and significant environmental variables (vector arrows) at $P \leq 0.05$. The position of each centroid indicates its association with environmental variables.

stages of non-mosquito Diptera, and Odonata nymphs (Table 1).

CCA identified five significant variables (percentage vegetation cover, sampling month, distance from floodplain edge, the presence or absence of *T. guineensis*, and larvicide application) that determined the distribution of sites with or without anophelines or culicines (Fig. 2). The impact of these variables on the presence or absence of anopheline and culicine larvae was further tested using GEE analysis. Larviciding significantly decreased anophelines by 68% and culicines by 74% (Table 2). The presence of *T. guineensis* was associated with a 38% decrease in culicine mosquito (Table 2). Moreover, anophelines were associated with habitats with higher vegetation cover (Fig. 2; Table 2). Mosquito control using microbial larvicide did not have a significant impact on the fish species richness on the floodplain, and no impact was determined in terms of the abundances of the most common fish species encountered on the floodplain (Table 3).

A subsample (n = 173) of late-instar anopheline larvae collected along the transects were brought back to the laboratory to dentify them after emergence of the adults. Of these, 41.6% were *An. coustani* s.l. Laveran, 31.8% were *An. gambiae* s.l., 11.6% were *An. funestus* Giles, 9.8% were *An. pharoensis* Theobald, and 5.2% were *An. squamosus* Theobald. Those mosquitoes identified as *An. gambiae* s.l. (n = 55) were further identified to species by PCR analysis, and 76% were identified as *An. gambiae* s.s., 12% as *An. arabiensis* Patton, and 12% as *An. melas* Theobald.

Predation Experiments. The semifield experiments showed that both species of fish had significant impacts on the presence of all categories of anopheline and culicine larvae and pupae (Table 4). Average anopheline densities in the bowls before treatment were 1.01 larvae per dip. For early-instar anophelines, there was a 69% reduction for *E. spilargyreius* and 96% reduction for *T. guineensis* at the end of the 12-d period, whereas all late stage culicines and anophelines were consumed within 24 h.

Of the 715 pupae collected in the predation semifield experiment in 2006, 21.7% were *An. gambiae* s.l. and the rest were culicines (47.5% *Ae. vittatus* Bigot, 27.5% *Cx. quinquefasciatus* Say, 1.3%, *Toxorhynchites* spp., and 2% other culicines). Of the *An. gambiae* s.l., 48% were identified as *An. gambiae* s.s. and 52% as *An. arabiensis*.

Oviposition Experiment. This experiment has shown that ovipositing culicines detected the pres-

Table 2. Factors associated with the presence and absence of anopheline and culicine larvae during the 2005, 2006, and 2007 rainy seasons

Factors	Odds ratio	95% Wald CI		P
		Low	High	
Anophelines				
Intervention				
Nonsprayed	1.00	—	—	—
Sprayed	0.38	0.24	0.59	**<0.001**
T. guineensis				
Absent	1.00	—	—	—
Present	1.12	0.87	1.44	0.36
Percent vegetation cover	1.01	1.01	1.02	**<0.001**
Sampling month	0.96	0.92	1.00	0.05
Distance from floodplain edge	1.00	1.00	1.00	0.85
Culicines				
Intervention				
Nonsprayed	1.00	—	—	—
Sprayed	0.26	0.17	0.38	**<0.001**
T. guineensis				
Absent	1.00	—	—	—
Present	0.62	0.45	0.84	**0.002**
% vegetation cover	1.01	1.00	1.02	0.03
Sampling month	1.01	0.98	1.04	0.43
Distance from floodplain edge	1.00	1.00	1.00	0.95

Only those variables identified as significant by the CCA were included in the model. Significant values following Bonferonni correction in bold (Bonferonni significance level, $P \leq 0.025$).

CI, confidence interval.

Table 3. Influence of application of microbial larvicides on fish species richness (no. species) and abundance of the most common fish species

Factors	Odds ratio	95% Wald CI		P
		Low	High	
Fish species richness				
Nonsprayed	1.00	—	—	—
Sprayed	0.81	0.64	1.03	0.09
Year				
2005	1.00	—	—	—
2006	0.96	0.75	1.21	0.72
2007	0.57	0.42	0.78	**<0.001**
Transect				
1	1.00	—	—	—
2	1.01	0.67	1.53	0.94
T. guineensis				
Nonsprayed	1.00	—	—	—
Sprayed	1.50	0.58	3.90	0.39
R. septentrionalis				
Nonsprayed	1.00	—	—	—
Sprayed	0.99	0.75	1.32	0.98
E. spilargyreius				
Nonsprayed	1.00	—	—	—
Sprayed	0.94	0.44	2.03	0.88
H. bimaculatus				
Nonsprayed	1.00	—	—	—
Sprayed	0.91	0.82	1.01	0.08
H. fasciatus				
Nonsprayed	1.00	—	—	—
Sprayed	1.04	0.90	1.20	0.60
P. normanii				
Nonsprayed	1.00	—	—	—
Sprayed	1.05	0.98	1.12	0.15

Bonferroni-corrected significant values in bold (Bonferroni significance level, $P \leq 0.007$).

CI, confidence interval.

Table 4. Odds ratios of presence/absence of larvae and pupae from the predation experiment

Treatment	Odds ratio	95% Wald CI		P
		Low	High	
Early anophelines				
Control	1	—	—	—
T. guineensis	0.239	0.132	0.431	**<0.001**
E. spilargyreius	0.204	0.113	0.368	**<0.001**
Late anophelines				
Control	1	—	—	—
T. guineensis	0.032	0.008	0.126	**<0.001**
E. spilargyreius	0.014	0.003	0.054	**<0.001**
Early culicines				
Control	1	—	—	—
T. guineensis	0.001	0.000	0.013	**<0.001**
E. spilargyreius	0.011	0.003	0.045	**<0.001**
Late culicines				
Control	1	—	—	—
T. guineensis	0.003	0.000	0.020	**<0.001**
E. spilargyreius	0.007	0.001	0.039	**<0.001**
Pupae				
Control	1	—	—	—
T. guineensis	0.011	0.003	0.051	**<0.001**
E. spilargyreius	<0.001	<0.001	<0.001	**<0.001**

Each instar was analyzed in a separate model. We adjusted for experimental trial (number of trials: 4) in the model. Bonferroni-corrected significant values in bold (Bonferroni significance level, $P \leq 0.01$).

CI, confidence interval.

ence of both *E. spilargyreius* (97% reduction in mosquito larvae sampled, average density 0.05 larvae per dip) and *T. guineensis* (93% reduction, average density 0.1 larvae per dip) compared with the controls (average density 1.24 larvae per dip) and avoided ovipositing in sites where they are present. For anophelines, however, our results indicate that they were poorly deterred by the presence of *E. spilargyreius* (average density 0.13 larvae per dip) and *T. guineensis* (average density 0.16 larvae per dip) in relation to the controls (average density 0.28 larvae per dip; Fig. 3).

F3

Discussion

A comprehensive fish survey and dietary assessment of the most common species encountered on the floodplain of the Gambia River showed that *T. guineensis*, a detritivore, dominates the fish communities, constituting >86% of the catches by number. The Gambia River floodplain exhibits low fish diversity compared with other tropical floodplain systems (Welcomme 1979, Cotner et al. 2006, Winemiller et al. 2006). This is partly because of the fact that the Gambia River has an impoverished fish fauna compared with other West African river systems (Leveque et al. 1991) but may also result from the low concentrations of nutrients found in the floodplains (V. Louca, unpublished data). Dominance of the Gambia floodplain fish community by a detritivore is also found in other tropical floodplain systems where detritivore and herbivore species commonly dominate the fish communities (Winemiller 1990). Five fish species were identified as being primarily insectivorous. Of these, *E. spilargyreius* was the most common, with potentially sufficient numbers to cultivate for mosquito control.

Our analysis showed that the presence of *T. guineensis* was associated with a reduced likelihood of finding culicine larvae, but not anophelines, whereas the presence of *E. spilargyreius* showed no significant association with the distribution of mosquito larvae. Because of ts high local densities, it is possible that *T. guineensis* could have a direct interaction with culicines. Semifield setups have been shown to accurately predict results obtained in large-scale experiments (deSzalay et al. 1996), and our semifield tests suggest that the field observations of a negative association in local distribution between culicines and *T. guineensis* may partly be caused by culicines detecting and avoiding ovipositing in habitats where *T. guineensis* is present. The fact that culicines avoided ovipositing in containers with both species of fish suggests that the semiochemicals detected by culicine mosquito are more general fish cues and not specific to insectivorous fish, because *T. guineensis* was identified as a detritivore species.

Results from the predation semifield experiment suggested that predation by fish could also be a factor regulating mosquitoes in the field. Alternatively, it may be that, in the floodplain of the Gambia River, anophelines occupy different spatial niches to the *Tilapia*, with mosquitoes being concentrated close to emergent vegetation on the water's edge and the fish

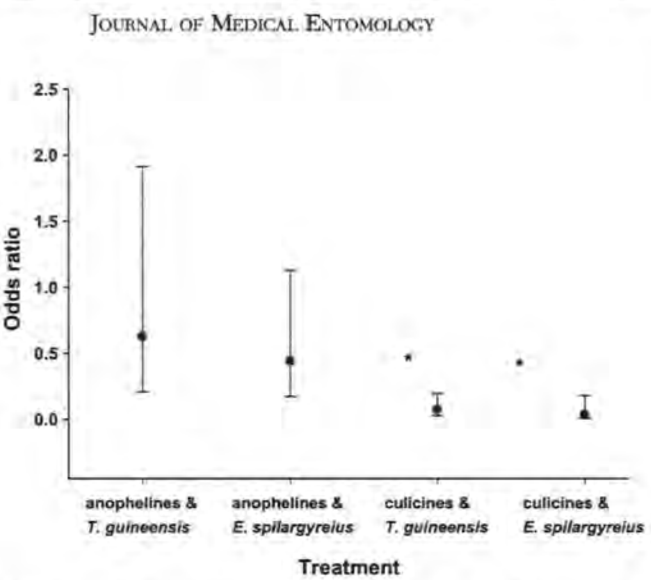

Fig. 3. Odds ratios of the oviposition experiment for *T. guineensis* and *E. spilargyreius*. Experimental round was also included in the analytical model: no differences were observed between rounds for both anophelines and culicines. *Bonferonni corrected significant values in bold: Bonferonni significance level, $P \leq 0.025$.

occupying the open areas away from the shoreline (Wellborn et al. 1996, Maddrell 1998). Moreover, it is possible that anophelines and culicines differ behaviorally and in their microhabitat preferences. The active behavior of culicines might make them more vulnerable to predation by visual predators, like fish, whereas anophelines often reside in vegetation, where they are relatively motionless and parallel to the water surface. The general lack of mosquitoes, especially anopheline mosquitoes in the natural diet of fish, suggests that mosquitoes constitute a minor part in the diet of fish on the Gambia River floodplain and that fish only actively feed on them opportunistically in small aquatic habitats, such as our semifield ponds, where mosquitoes constituted a relatively large proportion of the invertebrate fauna present. This is supported by a number of studies that have shown that, even for established larvivorous fish such as *G. affinis*, mosquito larvae constitute a minor proportion of their diet under natural conditions (Garcia-Berthou 1999, Specziar 2004, Kumar and Hwang 2006). Despite the presence of *E. spilargyreius* inhibiting oviposition of culicines and being an active predator under semifield conditions, it did not exclude culicines from habitats in the field. This finding probably results from *E. spilargyreius* only being encountered at lower densities. In contrast, the oviposition behavior of anopheline mosquitoes was not influenced by fish, and as a result, it seems they do not influence the distribution of anophelines on the floodplain. Moreover, we showed that it only achieves a 69% reduction in early anophelines 2 d after introduction, and this suggests that this species under field conditions is a less efficient predator of anophelines than *T. guineensis*. Taking into account the high abundance of *T. guineensis* on the floodplain (recorded mean catch densities of 7.59 fish/m^2; range: 0–518 fish/m^2) and their proven ability to influence oviposition in culicine mosquitoes, it is perhaps not surprising to see that they play a regulating role in the distribution of culicines on the floodplain.

Because culicines avoid oviposition in sites with either fish species, when effective control of both anophelines and culicines is needed, it is of vital importance that all possible aquatic habitat sites should be treated to avoid culicine mosquito selecting alternative sites for oviposition, thus minimizing the effectiveness of this mosquito control measure. Nonetheless because adult anophelines do not seem to be able to detect chemical cues in the water from fish, fish may prove to be an efficient control method for reducing anopheline populations in situations where habitats are well defined and long living.

These nonsignificant results from the pilot study indicate that biological control using microbial larvicides did not affect fish species richness and abundance. However, because of the limited sample size, these no-effect results should be interpreted with caution. Moreover, further semifield level testing of the effect of mosquito larvicides on fish growth would be useful.

Tilapia guineensis, a primary animal protein source for people living along the floodplain, is a candidate for use as a mosquito control agent in West Africa because we have shown that (1) it is by far the most common fish in the floodplain, (2) its presence does not influence oviposition by anopheline mosquitoes, and (3) it is a highly efficient predator of both early and late anophelines. Nontheless, these results should be treated with caution because anopheline larvae did not constitute a major part of the diet of this species and therefore they might be inefficient in controlling larvae under natural conditions. With irregular rain patterns from year to year being common in West Africa (Pages and Citeau 1990), the potential for using fish for mosquito control is limited because it can only be effectively implemented in areas with permanent water bodies. Moreover, for *T. guineensis*, the fish biomass used should be high enough (at least 26.3 g/70 liters of water as used in the semifield study) to ensure that all invertebrates will be consumed and that fish will not preferentially prey on non-mosquito invertebrates. This dependence on permanent water bodies limits the capacity in which fish can be used to control mosquitoes unless these habitats remain flooded for substantial periods for the fish to survive and have an impact in controlling mosquitoes. Nevertheless, fish are likely to be cheaper and provide a more long-term solution to mosquito control compared with larvicides. Thus, fish could be used as part of an integrated control program where fish are used in more permanent sites and microbial larvicides applied to temporary ones. Potential effectiveness of the use of both fish and mosquito larvicides in the same aquatic habitats remains to be tested. Moreover, it must be emphasized that if fish are used for controlling mosquito larvae, it must be well planned because failures with introducing fish for mosquito control can be caused by the limited attention in which these introductions take place. For example, fish might be introduced in habitats that dry up rapidly or people may harvest the fish at the end of the season but not replace them when the habitats are flooded again. Therefore, future projects planning the introduction of fish should take into account these potential problems and plan for a regular monitoring of the fish populations, with reintroduction of fish when needed. Our study suggests that the use of fish for mosquito control in sub-Saharan Africa merits further consideration.

Acknowledgments

We thank the local communities in and around our study areas for help and cooperation throughout the study. This work was supported by the National Institutes of Health (Grant 1 VOI AI058250-01) and an award of the Freshwater Biological Association Hugh Cary Gilson Memorial Award in 2005. We are grateful to the Medical Research Council's Laboratories in The Gambia for provision of facilities and support at Farafenni Field Station and the Gambian Fisheries Department for cooperation. We also thank M. Drammeh and B. Salleh for help in the field and two anonymous referees for valuable comments.

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Received 14 July 2008; accepted 13 January 2009.