Movement, home range, and ecological divergence in the commercially fished Nile perch in Lake Nabugabo, Uganda.

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Abstract

The large piscivorous Nile perch (*Lates niloticus)* was introduced to the Lake Victoria basin in the 1950s and 1960s and eventually became one of the most valuable commercial species of East Africa's inland fisheries. Intense fishing-induced mortality may be contributing to dramatic ecological change in this species (reductions in body size and biomass; shifts in distribution and diet), and reinforcing patterns of ecological divergence in some lakes in the region. In this thesis I use an evolutionary ecology approach to explore habitat associated ecological divergence in the Nile perch in Lake Nabugabo, Uganda. I describe home range, movement, and habitat selection of Nile perch, and quantify divergence in phenotypic traits between major habitat types and across Nile perch ontogeny. Using radio telemetry I tracked 14 Nile perch for 5 months and used ArcGIS 9.3 to quantify movement patterns throughout Lake Nabugabo. I used movement data in combination with detailed ecological information to quantify habitat selection in the heavily fished inshore zones of the lake. Geometric morphometric and colour analyses were used to quantify divergence in body shape and skin colour across different size classes of Nile perch from ecologically distinct wetland and forest edge habitats. Nile perch exhibited low levels of daily movement and relatively small home ranges; and they preferred regions of the lake characterized by low temperature and high dissolved oxygen. Geometric morphometric and colour analyses revealed habitat-associated phenotypic divergence in both skin colour and body shape, although not all trends were consistent across size classes. The source of phenotypic divergence (genetic vs. plastic) remains unknown; however the level of site tenacity exhibited by Nile perch suggests that ecological isolation between forest edge and wetland fish may be higher than expected. These results have important implications for development of territorial

jurisdiction by Beach Management Units, the decentralized structure of fisheries management in the region. Knowing that Nile perch, one of the most important commercial catches in the Lake Victoria basin, have definable home ranges provides a biologically relevant rationale for the insertion of territorial boundaries for BMUs. Clearly defined resource-use boundaries may provide additional incentives for members to follow fishery rules and may prove to be instrumental in improving BMU efficacy.

Résumé

La grande perche du Nile piscivore (*Lates Niloticus*) a été introduite dans le bassin du lac Victoria dans les années cinquantes et soixantes pour devenir une des espèces les plus précieuses pour l'économie de la pêche en intérieure de l'Afrique de l'est. Un taux de mortalité très élevé relié à la pêche contribuerait à des changements écologiques dramatiques pour l'espèce (réduction de la taille du corps et de la biomasse; changements dans la distribution et le régime alimentaire), et renforcerait les conventions de divergence écologique dans certains lacs de la région. Dans cette thèse, j'utilise une approche écologique évolutive pour explorer l'écosystème associé à la divergence écologique de la perche du Nile dans le lac Nabugabo en Uganda. J'identifie le domaine vital, les schémas de mouvement et l'utilisation de l'habitat de la perche du Nile, et quantifie ainsi la divergence des phénotypes dans les différents habitats et toute l'ontogenèse de la perche du Nile. En utilisant la technique de la radiotélémesure, j'ai traqué 14 perches du Nile pendant 5 mois et avec l'ArcGIS 9.3, j'ai quantifié les schémas de mouvements dans le lac Nabugabo. J'ai associé les données des schémas de mouvement avec des données écologiques détaillées pour quantifier l'utilisation de l'habitat dans les zones de pêche intense du lac. La géométrie morphométrique et les analyses de couleur ont été utilisées pour quantifier les divergences dans la taille, forme et couleur des différentes classes de perche du Nile dans les habitats distincts de bord de forêts et de marécages. La perche du Nile a démontré des niveaux de mouvements journaliers peu élevés pour un domaine vital plutôt restreint; Elle préférait les régions du lac de basse température à oxygène hautement dissous. La géométrie morphométrique et les analyses de couleur ont révélé des divergences phénotypiques associées à l'écosystème dans la forme et la couleur de la perche, bien que ces

tendances n'aient pas été constantes à travers toutes les classes de tailles. La source de la divergence phénotypique (génétique contre plastique) demeure inconnue; par contre, le niveau de ténacité au choix du site manifesté par la perche du Nile suggère que l'isolation écologique entre le bord de forêt et les marécages serait plus élevé que prévu. Ces résultats ont des implications importantes pour le développement d'une juridiction territoriale dans les Unités de Gestion des Plages (UPG), la structure décentralisée qui gère la pêche dans la région. Sachant que la perche du Nile, une des plus espèces les plus importantes pour la pêche commerciale dans le bassin du lac Victoria, démontre des domaines vitaux définissables fournit une raison biologique pour favoriser des délimitations territoriales de pêche par les UGP. Ces délimitations de ressources clairement définies pourraient motiver les membres des UPG à suivre le règlement des consignes de pêche et devenir essentiel pour améliorer l'efficacité des UGP.

Contribution of Authors

This Masters thesis was completed under the supervision of Dr. Lauren J. Chapman in the Department of Biology at McGill University. There are 2 chapters in this thesis, both of which are co-authored by Dr. Chapman who was integral in developing core ideas, building research design, implementing methods of data collection, and providing recommendations on analyses. Dr. Chapman also provided logistic support in Montreal and Uganda, and useful feedback while writing both manuscripts.

The guidance of Dr. Chapman was essential for the successful completion of this thesis, however both chapters are primarily the result of my independent research. For both chapters I carried out the literature review, field research, statistical analyses, and manuscript preparation. For chapter 1, I was responsible for implementing a radio telemetry Nile perch movement monitoring program. I was also instrumental in the creation of a detailed ethno-geographic map of Lake Nabugabo that indicates the distribution of shoreline vegetation, provides depth contours and shows the placement of fish landings, shoreline developments and important fishing locations. This map was created in collaboration with Dr. Lauren Chapman, Dr. Colin Chapman, Dr. Ismael Vaccarro, Andrew Beyekweso, Dr. Dennis Twinomugisha, Johanna Bleecker and fishers at Lake Nabugabo. For Chapter 2, I was responsible for photographing fish, applying standard geometric morphometric techniques, and developing a protocol for analysis of brown pigments in fish scales.

The two chapters of this thesis were prepared for submission to peer-reviewed scientific journals. The first chapter was formatted for Fisheries Research (in revision) and the second for Evolutionary Ecology (in prep).

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General Introduction

Inland waters represent some of the most seriously threatened ecosystems on our planet because of intense anthropogenic influences that have centered around waterways for millennia (Welcomme et al. 2010, Cooke et al. 2011). Inland waters supply valuable resources including fertile ground for agriculture, irrigation, drinking water, transportation, and fish stocks that provide food and economic support for local communities. Anthropogenic activities can dramatically alter environmental conditions experienced by natural populations, and organisms inhabiting these areas must adapt rapidly, or face local extinction given sustained levels of human-induced directional selection. Recent studies have shown that anthropogenic activities can hasten adaptive phenotypic change in natural populations (Palumbi 2001, Stockwell et al. 2003, Hendry et al. 2008) altering their trophic position and behavioral interactions with biotic and abiotic components of the environment. As human population density continues to rise the importance of focusing research on conservation and resource management grows.

Fresh waters are especially important to developing nations where inland aquatic resources play a central role in the socio-economic well being of local communities (Welcomme et al. 2010). Food fishes, in particular, are extremely important and highly exploited resources in aquatic ecosystems, and provide a critical source of livelihoods in many developing nations. In 2009, it was estimated that over 56 million people in the developing world relied on inland fisheries for employment, income and food security (BNP 2009). Furthermore, FAO’s most recent report estimates inland fishery production at 11.2 million tonnes/year accounting for ~13% percent of total global capture fisheries and aquaculture production (FAO 2010). Although this seems low when compared to marine capture fisheries and aquaculture, it is important to consider that inland waters cover less than 1% of the earth's surface. Given the high population growth rates in many tropical developing countries and accelerating pressure on freshwater resources, it is critical that we understand effects of fishing on the ecology and evolution of stocks. My thesis explores ecological divergence in the stock of an non-indigenous predatory fish in a tropical inland fishery that has experienced intense fishing pressure.

There is a growing body of evidence that size selective mortality, such as that produced by fishing, can lead to changes in life history traits of harvested species (Law 2000, Stokes and Law 2000, Heino and Godø 2002, Cooke et al. 2009) and can bring about ecological change and divergence among populations (Conover and Munch 2002, Grift et al. 2003, Hutchings 2005, Reznick and Ghalambor 2005, Conover et al. 2006). Fisheries can lead to directional selection through a process known as 'fishing down' whereby large individuals in a population or community are lost in favor of smaller, shorter-lived fishes that are less-fit and not as effective at maintaining stocks (Pauly et al. 1998, Conover and Munch 2002, Hsieh et al. 2010). For example, over-exploitation of North Atlantic cod stocks coincided with a 2-year decline in age at maturity between 1960 and 2000 (Hutchings 2005). Fishing-induced mortality can also have a number of indirect effects on ecological interactions between target species and other elements of their environment. Changes in temperature preference, avoidance of fishing gears, modifications in habitat use, and dietary shifts have been documented in association with fishing pressure (Ona and Godø 1992, Heino and Godø 2002, Askey et al. 2006, Kerwath et al. 2007). Heterogeneous exploitation centered in optimal habitat zones of target species can fundamentally alter distribution and movement patterns of stocks leading fish to use sub-optimal habitats (Heino and Godø 2002). This has the potential of precipitating patchy intra-region divergence in ecological traits of harvested species.

Depending on movement patterns, site tenacity, and home range sizes, this ecological divergence could be transient, ontogenetic, or lead to distinct phenotypes within the population (Law 2000). Relative to temperate marine systems, effects of exploitation on fishes in tropical inland waters have received little attention and much uncertainty remains as to the rapidity and extremity of such processes in these systems. This thesis investigates ecological divergence coincident with intense fishing pressure in the exotic Nile perch (*Lates niloticus* L.), a predatory fish in the Lake Victoria basin of East Africa that has fueled extremely important fisheries, but at the cost of catastrophic loss of native fish biodiversity.

History of Nile perch in the Lake Victoria basin

Lake Victoria in equatorial East Africa is the largest tropical lake in the world, and represents one of the world's most important inland fisheries (Matsuishi et al. 2006, Balirwa 2007, Chapman et al. 2008). For many decades Lake Victoria supported a productive multi-species fishery, but the 20th century brought massive ecological change to this region as human population density increased and demands on aquatic resources intensified. By the 1950's many large-bodied native fishes had been overexploited (Balirwa et al. 2003, Chapman et al. 2008, Goudswaard et al. 2008), and non-native species were introduced to the lake influencing faunal composition and balance. The most infamous introduction is that of the Nile perch, which was released into Lake Victoria and other lakes in the region such as Nabugabo and Kyoga in the 1950s and 1960s (Balirwa et al. 2003, Pringle 2005, Goudswaard et al. 2008). In Lake Victoria, Nile perch population abundance increased dramatically in the 1980s, and this non-indigenous fish became an important part of the fishery yield (Ogutu-Ohwayo 1994, Goudswaard et al. 2008, Paterson and Chapman 2009). The upsurge in Nile perch coincided with a further decline of native species and the disappearance of an estimated 40% of the unique flock of endemic haplochromine cichlids (Witte et al. 1992, Seehausen et al. 1997, Balirwa 2007). This loss of ecological diversity is thought to be partly responsible for a shift in food web structure, a change in the lake's status from meso- to eutrophic, and for the development of hypolimnetic anoxia (Hecky et al. 1994, Hecky et al. 2010).

The upsurge of Nile perch created a huge export market for Uganda, Kenya, and Tanzania, and a rapid expansion of the fish freezing industry (Balirwa et al. 2003). The export market fueled intense fishing pressure leading to an increase in the numbers of fishers and fishing boats, a decline in catch rates per fisher, and an apparent decline in the biomass of Nile perch in some heavily fished regions of the lake (Balirwa et al. 2003, Matsuishi et al. 2006, Mkumbo et al. 2007). Coincident with intense fishing pressure on Nile perch in lakes Victoria, Kyoga, and Nabugabo, and presumably a decrease in predator pressure, there has been a resurgence of some fishes, most notably an increase in the biomass of haplochromine cichlids (Chapman et al. 2003, Chapman et al. 2008). The dynamics of the Nile perch and its potential prey species are very complex and driven, at least in part, by fishing pressure that has steadily increased. There is a growing body of evidence that dynamics among fishers, Nile perch, and perch prey have contributed to ecological and phenotypic change in the Nile perch including shifts in life-history traits, diet, habitat use, and morphology (Schofield and Chapman 1999, Paterson and Chapman 2009, Paterson et al. 2010). The temporal and spatial scale of these changes may reflect the spatial structure of fishing pressure, but also the movement patterns of Nile perch, which are not well understood. In this thesis, I integrate spatial ecology of Nile perch with patterns of phenotypic divergence. I focus on the introduction of Nile perch in Lake Nabugabo, Uganda.

Nile perch in Lake Nabugabo

Lake Nabugabo is a satellite of Lake Victoria that, like Lake Victoria has also experienced Nile perch introduction, intense fishing, and dramatic ecological change. Several studies in this lake have focused on the ecology of Nile perch in two major shoreline habitats: wetland ecotones and forest edge (exposed). Nile perch in exposed habitats have undergone a reduction in body size, decline in total catch, and reduced catch per unit effort (CPUE) (Balirwa et al. 2003, Chapman et al. 2003, Paterson and Chapman 2009). A larger percentage of Nile perch are now found near wetland ecotones than in the mid 1990s, Nile perch from wetland ecotones are proportionately larger than fish captured in exposed waters, and diet of Nile perch differs dramatically between the two habitat types (Paterson and Chapman 2009). It is likely that the change in size and distribution of Nile perch reflects, at least in part, intense harvest in their preferred open water habitat (Schofield and Chapman 1999, Paterson and Chapman 2009). There is also evidence for habitat-associated morphological divergence in juvenile Nile perch with individuals from hypoxic wetlands having larger gills than those captured in well-oxygenated waters (Paterson et al. 2010). Taken together, these findings point towards the possibility that cascading effects of heterogeneous fishing pressure may further reinforce or drive divergence in Nile perch diet, morphology, and other phenotypic traits between wetland and forest edge habitats. This divergence may be transient if Nile perch move across habitats, ontogenetic if juveniles are more site tenacious than adults, or lead to distinct adult phenotypes if Nile perch movement is limited across all life-history stages.

The goal of this thesis is to investigate habitat-associated ecological divergence in Lake Nabugabo's Nile perch population and provide insights into sustainable management of Nile perch stocks in the Lake Victoria basin. To achieve this goal I conducted two studies represented by Chapters 1 and 2 of this thesis. In the first chapter, I quantified movement patterns of Nile perch to determine the degree to which fish from different habitats can be seen as ecologically distinct units. I used radio telemetry to track Nile perch movement patterns, characterize home range size, and quantify habitat selection in the inshore waters of Lake Nabugabo. The aim of this study was to enhance our knowledge of the ecological interactions of Nile perch with its environment and to inform our understanding of habitat-associated trait divergence. I hope that this work will also lead to further development of Nabugabo's Beach Management Unit (BMU) by defining home range characteristics of the Nile perch and providing a biological rationale for the insertion of territorial boundaries in this newly-implemented, decentralized system of fishery management. In the second chapter I quantified aspects of habitat-associated phenotypic divergence in Nile perch across size classes. I used geometric morphometric and colour analyses to quantify patterns of divergence between wetland and forest edge components of the population. I also compared eco-morphological relationships across Nile perch size classes to determine if trends are consistent across a size range of Nile perch that encompasses strong ontogenetic dietary shifts. In both chapters, I emphasize the need for increased knowledge of Nile perch ecology including a broader knowledge of Nile perch movement behaviour, habitat choice, and life history traits, and an improved understanding of the nature of observed trends of phenotypic divergence. I also suggest avenues for future research in this field to build upon the groundwork established by this thesis.

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Movement and home range of introduced Nile perch (*Lates niloticus*) in Lake Nabugabo, Uganda: Implications for ecological divergence and fisheries management

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ABSTRACT

Nile perch (*Lates niloticus)* was introduced to the Lake Victoria basin in the 1950s and 1960s and eventually became one of the most valuable commercial species of East Africa's inland fisheries. Intense fishing-induced mortality may be contributing to dramatic ecological change in this species (reductions in body size and catch rate) and reinforcing patterns of ecological divergence in some lakes in the region. We used radio telemetry to characterize Nile perch movement and home range size in Lake Nabugabo, Uganda and quantified patterns of habitat selection by Nile perch in the heavily fished near-shore areas of this system. Nile perch exhibited high site tenacity with daily movement averaging ~400 m/day and home range size averaging 0.83 km^2. Body size and water temperature were both important predictors of Nile perch movement patterns. In the near-shore area of the lake, Nile perch selected regions characterized by low temperature and high oxygen conditions, and tended to prefer forest edge over wetland edge. The level of site tenacity exhibited by Nile perch suggests that ecological isolation between fish using forest and wetland ecotones may be higher than expected. These results also have important implications for development of territorial jurisdiction by Beach Management Units, the decentralized structure of fisheries management in the region.

INTRODUCTION

There is a growing body of evidence that size selective mortality, such as that produced by fishing, can lead to changes in life history traits of harvested species (Ricker 1981, Rijnsdorp 1993, Law 2000) and can bring about ecological change and divergence among populations (Grift et al. 2003, Conover et al. 2006, Reznick and Ghalambor 2005). Fisheries can lead to directional selection through a process known as 'fishing down' whereby large individuals in a population or community are lost in favor of smaller, shorter-lived fishes that are less fit and not as effective at maintaining stocks (Pauly et al. 1998, Conover and Munch 2002, Hsieh et al. 2010). For example, over-exploitation of North Atlantic cod stocks coincided with a 2-year decline in age at maturity between 1960 and 2000 (Hutchings 2005). Fishing-induced mortality can also have a number of indirect effects on ecological interactions between target species and their environment. Avoidance of fishing gears (Ona and Godø 1992, Handegaard and Tjøstheim 2005) and modifications in habitat use (Sundby and Godø 1994) have been documented in association with fishing pressure (reviewed in Heino and Godø 2002). Heterogeneous exploitation centered in optimal habitat zones of target species can fundamentally alter distribution and movement patterns of stocks leading fish to use sub-optimal habitats (Heino and Godø 2002). This has the potential of precipitating patchy intra-region divergence in ecological traits of harvested species. Depending on movement patterns, site tenacity, and home range sizes this ecological divergence could be transient, ontogenetic, or lead to distinct phenotypes within the population (Law 2000). Management of a sustainable fishery, therefore, partly depends on an understanding of movement patterns and habitat preferences of commercially harvested fish species, and how these patterns and preferences respond to fishing pressure (Mason and Lowe 2010, Gruss et al. 2011).

Relative to temperate marine systems, effects of exploitation on fishes in tropical inland waters have received little attention (Mkumbo et al*.* 2007, Welcomme et al. 2010, Cooke et al. 2011). Given the increasing population growth rates in many tropical nations, and accelerating pressure and reliance on inland fish resources, it is critical that we understand habitat requirements of major stock species, and both direct and indirect effects of fishing on habitat use and selection (Smith et al. 2005, Welcomme et al. 2010, Cooke et al. 2011). In this study we quantify home range sizes, movement patterns, and habitat selection of the intensively harvested Nile perch (*Lates niloticus* L.*),* an invasive, predatory fish that has fueled important freshwater fisheries in East Africa.

History of the Lake Victoria basin fishery

One of the world's most important inland fisheries is that of Lake Victoria in equatorial East Africa, the largest tropical lake in the world (Matsuishi et al. 2006, Balirwa 2007, Chapman et al. 2008). For many decades, Lake Victoria supported a productive multi-species fishery, but the 20th century brought massive ecological change to this region as human population density increased and demands on aquatic resources intensified (Ogutu-Ohwayo 2004). In the 1950's and 60's the large, piscivorous Nile perch (*Lates niloticus*) was released into Lake Victoria and other lakes in the region (e.g., Nabugabo, Kyoga) to boost overexploited native fisheries (Balirwa et al. 2003, Pringle 2005, Goudswaard et al. 2008). A dramatic increase in Nile perch in the 1980s and other perturbations to the lake system (e.g., eutrophication) led to the further decline of many native species and most notably, the disappearance of ~40% of the 500+ endemic haplochromine cichlid species (Witte et al. 1992, Seehausen et al. 1997). The upsurge of Nile perch fueled a rapid increase in fishing pressure, creating a productive fishery and an economically important export market for Uganda, Kenya, and Tanzania in the 1990s (Balirwa et al. 2003). However, intense fishing and other changes in the lake basin have led to a decline in catch rates per fisher, and an apparent reduction in Nile perch biomass in some regions of the lake (Balirwa et al. 2003, Matsuishi et al. 2006, Mkumbo et al. 2007, Hecky et al. 2010). There is mounting evidence that dynamics among fishers, Nile perch, and Nile perch prey have contributed to ecological and phenotypic change in the Nile perch including shifts in diet and habitat use, habitat-associated divergence in morphology and body size, and change in life history traits (Schofield and Chapman 1999, Paterson and Chapman 2009, Paterson et al. 2010, Nkalubo 2012). Documenting movement patterns and habitat use of Nile perch is critical to understanding habitat- and fishing-associated trait variation in Nile perch, and has implications for development of territorial jurisdictions by community-based Beach Managements Units, institutions created in the lake basin to shift fisheries management from central governments to individual fishing communities (Nunan 2006, vanderKnaap and Ligtvoet 2010).

Ecological change in Nile perch in Lake Nabugabo, Uganda.

We conducted our study in Lake Nabugabo, a satellite of Lake Victoria that also experienced Nile perch introduction, overfishing, and dramatic ecological change. Several studies in this lake have focused on the ecology of Nile perch in two major shoreline habitats: wetland edge (ecotones) and forest edge (exposed). Nile perch in exposed habitats have undergone a reduction in body size, decline in total catch, and reduced catch per unit effort (CPUE) (Balirwa et al. 2003, Chapman et al. 2003, Paterson and Chapman 2009). A larger percentage of Nile perch are now found near wetland ecotones (5 – 100 m offshore) than in the mid 1990s, Nile perch from near wetland ecotones are proportionately larger than fish captured in exposed waters, and diet of Nile perch differs dramatically between the two habitat types (Paterson and Chapman 2009). It is likely that the change in size and distribution of Nile perch reflect intense harvest in their preferred open water habitat (Schofield and Chapman 1999, Paterson and Chapman 2009). There is also evidence for habitat-associated morphological divergence in juvenile Nile perch with individuals from hypoxic wetlands having larger gills than those captured in well-oxygenated waters (Paterson et al. 2010). Taken together, these findings point towards the possibility that the cascading effects of heterogeneous fishing pressure may drive or reinforce divergence in Nile perch diet, morphology and other phenotypic traits between wetland edge and forest edge (exposed) habitats. This divergence may be transient if Nile perch move across habitats, ontogenetic if juveniles are more site tenacious than adults, or lead to distinct adult phenotypes if Nile perch movement is limited across all life-history stages. To maximize the effectiveness of management of this stock and to determine the likelihood of divergence in this population, a sound knowledge of movement behaviour, home range size, and habitat selection of Nile perch is required. In this study we used radio telemetry to track Nile perch movement patterns, characterize home range size, and quantify habitat selection of Nile perch in Lake Nabugabo to enhance our knowledge of the ecological interactions of Nile perch with its environment and to inform our understanding of habitat-associated trait divergence. We hope that this work will also lead to further development of Nabugabo’s Beach Management Unit by helping to define territoriality of the Nile perch and providing incentive to restrain members of the BMU overuse of fishery stocks.

MATERIALS AND METHODS

Study Site

Nile perch were tracked in Lake Nabugabo, Uganda, 4 km west of Lake Victoria between 0^{o}’20 and 0^{o}’24 S latitude and 31^{o} ‘51 and 31^{o} ’57 E longitude. Lake Nabugabo has a surface area of 33 km^2 (mean depth = 3.13 m) with an average surface temperature of 25.8 ^{0}C (±1.07, SD) and low water transparency (mean Secchi depth = 0.69 m, ±0.11, SD). High dissolved oxygen (DO) conditions prevail in the open waters with surface DO averaging 7.71 mg/L (±1.04, SD) but drop off near the bottom into a thick layer of sludgy anoxic water. This region experiences two rainy and two dry seasons with heavy rains extending from March to May and light rains from November to December; average rainfall in this region of Uganda ranges from 1500 - 2000 mm/year (Mwebaze 2006). Lake Nabugabo was formerly a bay of Lake Victoria, which became isolated from the main lake by an extensive swamp and sandbar approximately 5000 years ago (Stager et al. 2005). Now, much of the lake’s perimeter consists of a dense wetland (the Lwamunda Swamp) that is characterized by high structural complexity and low DO conditions (Schofield and Chapman 1999, Paterson and Chapman 2009). The Lwamunda Swamp is dominated by four types of emergent macrophyte: two grasses, *Miscanthidium violaceum* and *Vossia cuspidata* (hippo grass) and two floating emergents, the water lilies, *Nymphaea lotus* and *Nymphaea caerulea*.

The west side of the lake is edged by dense forest, fishing villages (three active fish landings) and small developments (three holiday centers and two churches) (Fig. 1). Mukene (*Rastrineobola argentea*), Nile perch, and Nile tilapia (*Oreochromis niloticus*) are currently the most important commercial and artisanal catches. Size selective gill netting (Nile perch and tilapia) and long lining (Nile perch) are the predominant methods of fishing on the lake for large-bodied fish. Mukene are fished with small hand-operated scoop seines at night. Fishing pressure on the lake has been intense, with both size and abundance of Nile perch in the catch declining (Paterson and Chapman 2009).

Nile perch can grow up to 200 kg and 2 m in length, although individuals are usually caught well before they reach this size. Nile perch feed on insects and crustaceans when young, but undergo an ontogenetic dietary shift to piscivory at a particular developmental stage (Ogutu-Ohwayo 1994). The timing of this dietary shift depends, in part, on food availability (Ogutu-Ohwayo 1993, Paterson and Chapman 2009). Nile perch is a free spawning species that breeds year round with a peak in the rainy seasons (Ogutu-Ohwayo 1994). Up to 16 million eggs can be produced by a large, fecund female over a breeding cycle (Ogutu-Ohwayo 1994). Recent estimates of L_{50} in Lake Victoria, are 45 – 49 cm TL for males and 50-54 cm TL for females (Nkalubo 2012).

Home range and movement patterns

Tag attachment

Live Nile perch were purchased from fishers immediately after capture and placed in a large basin of clean lake water. Nile perch condition was determined to be adequate for tagging if equilibrium and buoyancy were immediately established and maintained upon introduction to the basin. Fish were measured for total and standard length (cm), and weighed to the nearest 50 g. Radio transmitters were externally attached on the left hand side below the rear dorsal fin (see Fig. 2 inset) while the fish was held in clean lake water following methods described in Cooke (2003). Three sizes of radio transmitter were used: small (model BD-2, 1.2 g, 16 x 8 x 3.5 mm), medium (model PD-2, 2.5 g, 23 x 12 x 5 mm), and large (model RI-2C, = 6 g, 3 x 10 x 6 mm) (Holohil Systems Inc., Ontario, Canada). Fish over 34 cm (> 400 g) were given large tags and those under 27 cm (< 250 g) were given small tags. All other fish were given medium tags. This ensured that transmitters were always less than the recommended 2% of body mass (Brown et al. 1999). Fish were released approximately 200 m offshore of their capture location. The tagging process took less than two minutes, and total fish handling time from the moment of capture to return to the lake was under 5 minutes.

Tracking

We began tracking on 18 January, 2011 and located fish through 13 May, 2011. In January and February we relocated fish daily between 6:30 am and 7:00 pm, and in March, April and May fish were relocated daily during two weeks of each month. We recorded UTM (Universal Transverse Mercator) coordinates of each fish's location with a Garmin 72H™ (Garmin International, Inc., Olathe, KS, USA) global positioning satellite (GPS) unit. Average accuracy of locations (15.6 m ± 6.9, SD) was estimated by repeatedly (N = 9) locating a tag that was stationary on the lake bottom. This is similar to the average GPS error (12.9 m ± 6.7, SD) determined by marking locations (N = 9) at the same point on shore. Thus, location errors appeared to be attributable to GPS error, and we feel confident that fish were tracked within 7 m of their true location plus GPS error. Each day a novel tracking route was established to ensure fish were located at different times of day throughout the field season. Some days we tracked each fish twice, once in morning and once in afternoon. The minimum time between two consecutive relocations was 6.35 hours, and the average (not including 2-week gaps) was 25.1 hours. The longest time between two consecutive relocations including the approximate 2-week gaps was 458 hours (~19 days). At each Nile perch relocation point we recorded a number of environmental variables. Depth was measured with a weighted meter tape and water transparency with a Secchi disk. Temperature (°C) and dissolved oxygen (DO) concentration (mg/L) were measured at the surface and then every subsequent meter using a YSI Pro20 handheld probe. Distance offshore was measured in a *post hoc* analysis using ArcGIS 9.3 (described in detail below).

In numerous circumstances, radio tagged fish were captured by fishers after they had been returned to the lake and tracked, in part a reflection of the very intense fishing pressure in this system. In most cases we were able to retrieve the tag from the fish landing before it had been removed from the fish. This provided opportunity to visually assess the condition of the fish and damage to the scales and musculature. Similar to findings in Herke and Moring (1999) fish tag wounds appeared to be well healed after 4-5 days with only minor scale loss and dermal abrasion. In every case we asked the fisher where, when, and how each fish was caught. In only 3 cases out of 26, did the fisher find that the transmitter to be the likely cause of the fish's entrapment.

Home range and movement calculations

All fish locations from tracking data were plotted in a Geographic Information System (ArcGIS, v. 9.3) to quantify spatial distribution patterns of individual fish within the lake. Hourly movement was calculated for each Nile perch by dividing distance moved by number of hours between two subsequent relocations, and daily movement was defined as the distance (m) between fish positions within a 24 hour period.

Although we refer to observations between tracking times as distance moved per day or per hour, it is a conservative estimate as not all movements are expected to be uni-directional. To estimate mean distance from shore for each Nile perch, we averaged the distance of all relocation points in a home range to their nearest points on shore using ArcGIS v. 9.3.

Hawth's Analysis Tools v. 3.27 (Beyer, 2004) for ArcGIS was employed to determine home range area using two methods: minimum convex polygon (MCP), a polygon that connects the outermost relocation points for each individual (Vokoun 2003), and 50% and 95% fixed kernel utilization distribution (FKUD) that produces smoothed, concentric isopleths representing the area where an individual spends 50% and 95% of its time during tracking (Worton 1989, Lowe et al. 2003, Vokoun 2003, Topping et al. 2005)**.** The 95% isopleth estimates the greater region used by a fish over the study period, while the 50% isopleth identifies the core range of an individual (Worton 1989). Elapsed time between relocations (sampling interval) is an important consideration when performing home range analyses (Swihart and Slade 1985*a*, Vokoun 2003). The ideal sampling interval is unique for each species and avoids autocorrelation of data by ensuring statistical independence of successive relocation points (Vokoun 2003). We tested our data for autocorrelation using Schoener's ratio according to methods described in Swihart and Slade (1985*b*) and found that successive observations for all but two fish were independent at the $\alpha = 0.05$ level. Home range estimates from fixed kernel techniques are free from parametric assumptions, and are therefore not affected by auto-correlated data (important given that home range data for two Nile perch did not meet independence criteria), and provide an efficient method for smoothing locational data (Worton 1989). Fixed kernel density estimates require calculation of smoothing parameters (h) that control the amount of variation in each component of the estimate. We used Animal Space Use v. 1.3 (Horne and Garton 2009) to calculate an adjusted h (h_{ajd}) smoothing parameter as outlined by Wauters et al. (2007). h_{ajd} produces home ranges that are comparable to MCP and other FKUD estimators, but are less sensitive to small sample sizes and consistently produce biologically realistic core home ranges while minimizing over-smoothing of the 95% isopleth (Seaman and Powell 1996, Wauters et al. 2007).

Analyses

Linear regression was used to detect relationships between home range area and hourly movements (dependent variables), and fish characteristics (total length, standard length and weight) and environmental characteristics (temperature, DO, depth, Secchi depth, and distance from shore). All data were tested for normality with the Shapiro-Wilk goodness-of-fit test and adjusted using a log transformation if necessary. Differences in home range size and movement parameters between fish caught in distinct habitat types (wetland edge vs. forest edge) were assessed using an independent 2-tailed t-test to compare means of two groups. Equal variance between groups was tested using Levene's homogeneity of variance test. Due to the inherent nature of co-linearity among environmental parameters, a principal component analysis (PCA) was performed using SAS software (JMP 8) to condense the dataset into composite variables to assess the environmental variables important for home range size and movement patterns. We incorporated seven physico-chemical variables (surface water temperature, bottom water temperature, average water column temperature, surface DO, bottom DO, average water column DO, and turbidity) and two other environmental variables (depth, and average distance from shore). A Pearson's correlation matrix was used to detect relationships among PCA scores and environmental variables to detect variables that loaded most heavily onto PC axes.

Habitat selection in the near-shore environment

Habitat mapping

We generated a bathymetric map of Lake Nabugabo by integrating systematically collected depth sounding data with GPS positional data. To collect depth data we followed a pre-determined grid pattern heading N – S across the lake taking depth points at ~400 m intervals. We used ArcGIS 9.3 spatial analyst tools to rasterize the point data and create bathymetric contour lines (Fig. 1). We quantified shoreline vegetation by driving the boat around the lake's perimeter 10 m off shore and recording presence of major vegetation types (*Miscanthidium violaceum*, *Vossia cuspidata* (hippo grass), *Nymphaea lotus/Nymphaea caerulea* (water lily) and forest edge) every ~50 meters (548 vegetation data points total). We estimated the distance that water lily and hippo grass patches extend into the lake from the edge of the *Miscanthidium*, grassland, or forest edge. These data were used to create an ecological map in ArcGIS outlining exact locations of the different vegetation types around the lake (Fig. 1). Every 100 m along the 10 m shoreline perimeter we recorded abiotic environmental conditions (T, DO, depth, Secchi depth) using the same methods as described above. A second sampling perimeter 250 m offshore provided an indication of environmental conditions more likely to be used by Nile perch as they were rarely found within 10 m of shore. These sampling methods provided detailed information about both shoreline vegetation (extending approximately 100 m into the lake) and abiotic environmental conditions (extending approximately 250 m into the lake) in the near-shore zone of Lake Nabugabo.

Near-shore Habitat selection

We concentrated our analysis of the habitat selection behaviour of Nile perch to locations sampled in near-shore regions of the lake as these areas are currently the most intensively fished in Lake Nabugabo and are characterized by a higher level of habitat heterogeneity than open waters. Near-shore habitat selected by Nile perch was identified by comparing proportions of habitat available in the near-shore zone of Lake Nabugabo to proportions of habitat used by Nile perch when they were in near-shore regions. To evaluate *habitat availability*, abiotic variables (depth, Secchi depth, average water column DO, average water column temperature) were split into five categories (Appendix A), and perimeter data points falling into each category were tallied. Similarly, shoreline vegetation was split into forest edge (category 1) and wetland edge comprised of water lilies (2), *Miscanthidium violaceum* (3), and hippo grass (4). Every perimeter vegetation point was assigned a category based on the dominant vegetation type in that location. Proportions of shoreline vegetation category availability are presented in Appendix A. To evaluate *habitat used* by Nile perch we calculated proportion of time spent in the categories outlined above. To estimate use of abiotic environmental conditions, we used the temperature, DO, Depth and Secchi depth data associated with each Nile perch relocation point. Because our perimeter survey for abiotic environmental variables represented 250 m of the near-shore zone of the lake we only evaluated data associated with Nile perch relocation points that were within 250 m of shore (32% of all relocation points). To evaluate shoreline vegetation use we only used relocation points that are within 100 meters of shore (19% of all relocation points). ArcGIS 9.3 was used to generate near-tables linking each relocation point within 100 m of shore to the nearest vegetation point in the perimeter survey. We justify this 100 meter cut-off point in two ways: 1) The shoreline vegetation survey revealed that, in some areas, hippo grass and water lily beds extended 100 meters into the lake and 2) an analysis of long term sampling data (L. Chapman, unpublished data) indicates that faunal assemblages associated with shoreline vegetation drop off 100 meters offshore. We therefore suggest that up to 100 m from shore fishes can still be said to be 'using' shoreline vegetation, or benefitting from its proximity. Pearson's chi-squared tests were used to detect differences between proportional habitat use and availability. We conducted this analysis twice, once using all inshore fish relocation points and once with each fish equally represented in the data set (8 points/fish) to avoid overrepresentation of individuals who spent more time inshore. Although the direction and significance of the results were the same for both analyses, there were a number of minor differences between them, so both are presented in the results.

RESULTS

Movement and Home Range

We tagged a total of 38 Nile perch over 5 months in Lake Nabugabo, Uganda. Radio-tagged Nile perch ranged from 24.5 to 57.2 cm total length (TL) (mean = 37.8 ± 9.56 cm, SD) and weighed between 160 and 2100 g (mean = 742.0 ± 595.4 g, SD). Of 38 individuals, six were lost due to tag failure, and one died of natural causes (no evidence of having been netted or hooked). Twenty-six individuals were re-captured by fishers (15 before sufficient data could be attained for home range analysis), and five fish remained in the lake until the end of the study period (two without sufficient data). All individuals with too few relocation points (<11) were removed from the data set leaving a total of 14 Nile perch for home range analysis. Nile perch used in the analysis ranged in body size from 25 to 57 cm TL (mean = 39.9 ± 9.29 cm, SD) and weighed between 170 and 2100 g (831.8 ± 588.7g, SD) encompassing as much variation in body size as was represented by all 38 fish.

Tracking of radio-tagged Nile perch revealed that the average linear distance traveled in the first 4 days after tagging ranged from 85.5 m/hr on day 1 to 38.5 m/hr on day 4 (overall mean = 53.5 ± 21.6, SD) but then decreased and levelled off. After 4 days, hourly distances moved in any one day ranged from 1.55 m/hr to 28 m/hr (mean = 12.6 ± 6.6, SD). To avoid introducing a bias as a result of the tagging procedure, the first 4 days of tracking for each individual were excluded from the analysis so as not to overestimate movement patterns. A minimum of 11 and a maximum of 43 (mean 25) relocation points were used to estimate home range. This threshold of 11 relocations is less than the minimum of 30 suggested by Vokoun (2003). However, in this case, using a minimum of 30 relocations would have reduced the number of tagged Nile perch whose movements we could characterize (Gilroy et al., 2010). We instead used multiple home range estimation techniques that are well suited to small sample sizes (Wauters et al. 2007) to ensure consistency among different home range calculators. We further investigated this potential source of error by randomly selecting 11 data points from individuals with >20 relocations and calculating new home range estimates. These estimates were then compared to the originals to determine whether important differences could be detected. Although home range estimates tended to be smaller when only 11 points were used, there was no significant difference in mean home range area ($t_{(df)} = 1.84_{(13)}$, $p = 0.11$). Finally, linear regression showed no relationship between number of relocation points and home range size (MCP: $r^2 = 0.04$, $p = 0.51$, FKUD 50%: $r^2 = 0.009$, $p = 0.74$, FKUD 95%: $r^2 = 0.0004$, $p = 0.944$) or any other environmental variable or fish characteristic (data not presented, r^2: range = 0.001 to 0.22, p: range = 0.09 to 0.91).

Home ranges for Nile Perch in Lake Nabugabo ranged from 0.11 to 2.28 km^2 (mean = 0.80, ± 0.71, SD) when estimated with MCP, and 0.11 to 2.42 km^2 (mean 0.83, ± 0.72, SD) when measured with FKUD (Fig. 2), and MCP and FKUD home range estimates were strongly correlated ($r = 0.95$, $p < 0.0001$). Details on movement patterns, home range areas, and fish characteristics are presented in Table 1 and Fig. 2. Average distance moved per hour for individual fish over the entire tracking period ranged from 4.9 to 38.1 m/hr (overall mean = 18.9 ± 10.6, SD), and average distance moved per day ranged from 118.0 to 594.7 m/day (overall mean = 454.4 ± 256.6, SD). Average time between relocations was 25.1 hours, not including the 2 week intervals in March, April, and May when no tracking occurred. Site tenacity was evident for all 14 Nile perch with their movements staying within approximately 400 m of the center of their home range (mean = 416.6 ± 220.8, SD) and the 50:95 isopleth area ratio equalling 20%. Seventy-nine percent of Nile perch established home ranges within either forest edge (8 Nile perch) or wetland (3 Nile perch) ecotones, while only 3 individuals (21%) established home ranges that crossed the two habitat types.

Home range vs. fish and habitat characteristics

Linear regressions indicate that Nile perch with home ranges further offshore were characterized by greater movement distances ($r^2 = 0.40$, $p = 0.015$) and larger home ranges (MCP: $r^2 = 0.53$, $p = 0.003$**,** FKUD 50%: $r^2 = 0.58$, $F = 16.39$, $p = 0.002$, FKUD 95%: $r^2 = 0.52$, $F = 12.92$, $p = 0.004$) than those closer to shore (Fig. 3 a, b). Home ranges established by perch near wetland ecotones were larger (mean = 1.21 km^2 ± 0.73, SD) than those from the forest edge (mean = 0.32 km^2 ± 0.24, SD) ($t_{(df)} = 2.94_{(12)}$, $p = 0.0125$). Home ranges established by fish that were caught near wetland ecotones ranged from 0.152 km^2 to 2.42 km^2, and home ranges of fish from the forest edge ranged from 0.11 km^2 to 0.74 km^2.

Fish total length was positively related to individual home range area (MCP: r^2= 0.34, $F = 6.27$, $p = 0.0277$**,** FKUD 50%: $r^2 = 0.24$ $F = 3.81$, $p = 0.074$**,** KFUD 95%: $r^2 = 0.30$, $F = 5.26$, $p = 0.041$), average distance moved per hour ($r^2 = 0.33$, $F = 5.89$, $p = 0.032$) (Fig. 3 c, d), and average distance from shore (r^2=0.36, F =6.21, p=0.023) (not shown in the figure)**.** These relationships were similar when fish size was expressed as standard length or body mass confirming that larger fish have home ranges that are both larger and further from shore than smaller fish. Water temperature was related to Nile perch home range and movement patterns (Fig. 3 e, f). Average Nile perch home range area **(**MCP: $r^2 = 0.30$, $F = 5.17$, $p = 0.04$, FKUD 50%: $r^2 = 0.47$, $F = 10.64$, $p = 0.007$, FKUD 95%: $r^2 = 0.46$, F =10.25, $p = 0.008$) and average distance moved/hr ($r^2 = 0.35$, $F = 6.35$, $p = 0.027$) decreased with increasing water temperature (Fig. 3 e, f). We also found a negative relationship between fish TL and water temperature (r^2= 0.47, $F = 10.8$, $p = 0.007$) (Fig. 3 g) and a positive relationship between fish TL and the concentration of surface DO ($r^2 = 0.33$, F 5.93, $p = 0.031$) (Fig. 3 h). These relationships were similar when fish total length was replaced with either standard length or body mass indicating that larger fish are generally found in cooler waters characterized by high DO, while smaller individuals use warmer waters and lower DO conditions. Pearson's correlation showed that dissolved oxygen increased ($r = 0.18$ $p=0.0013$) and water temperature decreased ($r=0.16$ $p=0.005$) with distance from shore. Neither depth, Secchi depth, bottom DO, nor water column DO were significantly related to fish size or any home range estimate.

The principal component analysis on environmental and habitat variables generated two functions with eigenvalues >1.0, which cumulatively explained 77.4% of the variance (Table 2). Variable loadings for the first two PC axes are given in Table 3. Environmental factors that loaded most heavily on PC1 were temperature (surface, bottom and average) followed by shore distance (Table 3). Bottom DO concentration was the only factor that loaded heavily onto PC2 (Table 2). There was a negative correlation between PC1 and distance moved/hr ($r = 0.53$, $P = 0.0498$, $n=14$) and total length ($r = 0.69$, $P=0.0068$, $n=14$). There were no significant relationships between any fish characteristics and PC2.

Habitat Selection

Percent availability of each type of habitat category in the near-shore environment is presented in Appendix A. The habitat selection analyses for abiotic environmental variables and shoreline vegetation indicated significant preferences of Nile perch for some habitat types over others. For environmental variables, Nile perch in near-shore zones selected intermediate to low water temperatures ($\chi^2_{(df)} = 11.07_{(4)}$, $p= 0.03$) (Fig. 4a) and intermediate to high levels of dissolved oxygen ($\chi^2_{(df)} = 113.0_{(4)}$, $p <.0.0001$) (Fig. 4b). There was also significant selection for deeper waters ($\chi^2_{(df)} = 705.6_{(4)}$, $P < 0.0001$) (Fig. 4c). Here we report Chi-squared values for T and DO water column average values, but these relationships held for surface and bottom DO and T values as well. In terms of shoreline vegetation selection, results from the Chi-squared analysis reveal that Nile perch selected for forest edge habitat ($\chi^2_{(df)} = 15.17_{(3)}$, $p < 0.0017$) and against *Miscanthidium* and water lily habitats (Fig. 4d). We decided to exclude Secchi depth from this analysis due to minimal variation in Secchi transparency.

DISCUSSION

Radio telemetry of Nile perch in Lake Nabugabo provides evidence for high site tenacity, low daily movement, and small home range sizes. Although many aspects Nile perch ecology have been studied in detail (Ogutu-Ohwayo 1994, Schofield and Chapman 1999, Paterson and Chapman 2009, Nkalubo 2012), very little was known of their spatial dynamics prior to this study. This is the first telemetry study of Nile perch, and one of the only telemetry studies of a commercially important tropical freshwater species (but see Koehn et al. 2009, Heupel et al. 2011). Our results support many established aspects of Nile perch ecology and habitat use (preference for high-oxygen/low temperature conditions) but contradict some assumptions previously held about their spatial requirements and movement distances, which may be very important for informing operational fishing management areas. High levels of site tenacity may help to explain habitat-associated trait divergence in the Nile perch of Lake Nabugabo (See Chapter 2).

Home range and movement parameters

We found a high level of variability in home range sizes and movement distances among our tagged Nile perch (HR = 0.1 – > 2.0 km^2, distance = 0.06 to 141 m/hr). Variability in home range size has been documented in several other tropical fish species from both marine (Lowe et al. 2003, Topping et al. 2005, Bellquist et al. 2008) and freshwater environments (Koehn et al. 2009, Heupel et al. 2011). For example, Heupel et al. (2011) found home ranges from ~0 km^2 to 2.5 km^2 in Barramundi (*Lates calcarifer)*, a tropical species in the same genus and of comparable size to Nile perch. Commonly cited sources of variation in movement parameters are body size (Kramer and Chapman 1999), sex (Shpigel and Fischelson 1989, Koehn et al. 2009), and habitat structure (Ahrenstorff et al. 2009, Koehn et al. 2009). We tested how home range size varied with body size and different aspects of habitat variability. Lack of sexual dimorphism in Nile perch prevented analysis of sex as a factor affecting home range size.

In this study, Nile perch ranged in size from 25 to 57 cm TL, and body length explained 30% of the variation in home range size. Many other fish movement studies have found links between home range area and fish size both inter- and intra-specifically (Minns 1995, Kramer and Chapman 1999, Jones 2004). For example, Jones (2004) found positive associations between body size and home range size in five Caribbean wrasse species tracked in Tague Bay, St Croix (U.S. Virgin Islands). Koehn et al. (2009) also cited body size as being a key determinant of home range area in Murray cod in the Murray River drainage in Australia. Although mechanistic links between body size and home range have rarely been thoroughly investigated, it is commonly proposed that larger individuals establish greater home ranges to meet their increased need for resources (food, mating opportunities) (Jones 2004, McGrath and Austin 2012), or to accommodate their need to seek out high quality spawning grounds as they reach sexual maturity (Koehn et al. 2009). Whatever the case, the strong and common relationship between the spatial requirements of fish species and their body size emphasizes the role that life history plays in the ecology of fish and interactions with their environment. This may be especially important in species that go thorough ontogenetic changes in diet or habitat use. Nile perch are known to undergo ontogenetic dietary shifts from insect feeding to piscivory (Ogutu-Ohwayo 1993, 1994). Although the timing of this dietary shift depends on habitat type and prey availability (Chapman et al. 2003, Paterson and Chapman 2009), the increase in home range size and movement pattern with body size could be due, in part, to the higher mobility and larger spatial requirements of preferred prey species (haplochromine cichlids) of larger Nile perch. Increases in Nile perch home range size with body size could also be due to the tendency of larger Nile perch to establish home ranges further offshore (possibly in search of deeper, cooler waters) where high quality prey resources are less abundant (Chapman et al. 1996), and greater search effort is required.

Variation in Nile perch spatial requirements was also related to several environmental and habitat characteristics. Temperature accounted for 46% of the variation in Nile perch movement patterns with higher activity levels and larger home range sizes in cooler waters. These patterns are corroborated by habitat selection results for near-shore areas and may relate to the negative effect of increasing water temperature on aerobic performance that has been documented in many fish species (discussed further below) (Farrell 1997, Pörtner and Knust 2007). There was also a positive relationship between home range size and distance from shore. Differences in home range size between near-shore and offshore environments could reflect a larger search radius required to seek out pelagic prey species and/or be a by-product of larger fish inhabiting offshore zones where low temperature and high oxygen conditions can be found. Given the strong correlations between Nile perch body size, water temperature, and distance offshore it seems likely that these factors combine to effect larger home ranges in these areas.

We also found that Nile perch near wetland ecotones tended to have larger home ranges than those from forest edge environments. This relationship was unexpected for two reasons: 1) wetlands in Lake Nabugabo are thought to have a richer prey base and greater structural complexity than open water or forest edge zones (Chapman et al. 1996, Schofield and Chapman 1999) and 2) many studies provide evidence that predatory fishes occupying areas of high structural complexity (littoral refuge habitats) show restricted movement while those in less complex regions display higher movement rates (Savino and Stein 1982, Ahrenstorff et al. 2009). We suggest that Nile perch prey may be *more abundant* in highly structured habitats, but *less available* if dense vegetation provides physical and visual obstruction to predators and enhances escape probabilities of prey (Ryer 1988, Sass et al. 2006). Indeed, many studies have shown that foraging efficiency is inversely related to structural complexity in many species (Ryer 1988, Eklöv 1997). Although decreased foraging efficiency may translate into fish adopting a sit-and-wait strategy, it may be equally likely to prompt predators to increase search effort. For example, Flynn and Ritz (1999) showed that *Hippocamous abdominalus* (sea horse) adults in exposed regions only target prey items that come within reach but search actively in areas of high structural complexity. Nile perch near wetland ecotones may similarly use a more active foraging strategy while searching the ecotone for prey species emerging from the near-shore vegetation.

Implications for ecological divergence

Given its streamlined body morphology and hunting lifestyle, Nile perch has generally been assumed to be a relatively active species (Ligtvoet and Mkumbo 1990) with low chance of sub-group isolation within a lake or region. Results of this study, however, reveal that movement distances and home range sizes are restricted relative to some other freshwater fish species of comparable body size in both tropical and temperate systems (Gilroy et al. 2010, Heupel et al. 2011, Smith et al. 2011, Trested et al. 2011). For example, Australian bass (*Macquaria novemculata,* Perciformes) a closely related but smaller species was found to move an average of 35 m/hour (Smith et al. 2011); much greater than the 18.9 m/hr observed in Nile perch. The restricted movement of Nile perch is especially important when considered in the context of ecological change and possible sub-stock variation in this species. Only 21% of Nile perch in this study moved across wetland/forest edge habitat boundaries, and individual perch tended to remain within 400 m of the center of their home range with half of their relocation points falling within an area approximately 20% of their entire spatial distribution. This limited movement may mean that the intense selection imposed by fishing in Lake Nabugabo may be promoting ecological divergence in Nile perch between the two habitat types. It has been shown that phenotypic change in natural populations can be accelerated in situations where human actions create a greater degree of selection than is encountered in natural environments (Hendry et al. 2008) and that these rapid changes are often seen in heavily fished stocks (Stokes and Law 2000). In Lake Nabugabo, there is evidence that intense fishing of Nile perch is selecting against larger individuals and fish from more open habitat, thus shifting the population distribution towards wetland ecotones (Paterson and Chapman 2009). It has also been shown that wetland Nile perch exhibit unique phenotypic responses to their low-oxygen habitat (Paterson et al. 2010). Since smaller fish generally have smaller home range sizes, this trajectory may lead to an even lower chance of overlap between forest edge and wetland components of the population resulting in further habitat-specific phenotypic differentiation. This may increase the possibility for the development of a sub-stock of Nile perch that are smaller and better adapted to wetland ecotones. Some genetic variation exists between geographically separate populations in Lake Victoria (Mwanja and Mwanja 2008), but there is also evidence for an extensive amount of gene flow between different regions of the lake that may relate to the open water spawning style and/or lack of parental care of Nile perch (Mwanja and Mwanja 2008). In Lake Nabugabo, a system much smaller than Lake Victoria, it is unlikely that the observed habitat-associated divergence in Nile perch has a genetic basis; however, limited movement may facilitate the maintenance of habitat-associated phenotypic divergence.

Habitat selection in the near-shore zone

In the near-shore areas of Nile perch home ranges, we found evidence for selection of specific habitat types and environmental conditions. Our movement study shows that Nile perch in Lake Nabugabo prefer forest edge over wetland ecotones when occupying near-shore regions of their home range. In their study of Nile perch (5-35 cm TL) Paterson and Chapman (2009) found that the proportion of Nile perch near wetland ecotones relative to forest edge had increased over a 12-year period; however, there was no evidence for an increase in their abundance near the wetlands. They speculated the proportional shift in distribution reflected intensive fishing for Nile perch more open waters near the forest edge where Nile perch abundance declined over the same period, although quantitative evidence for historical heterogeneous harvest patterns is lacking. It is interesting that our radio-tagged Nile perch showed a preference for forest edge habitat given apparent declines in their abundance in this habitat since 1995. The difference between studies may relate to the size of Nile perch used and/or differences in defining habitat use and selection, and clearly highlights the importance of integrating methods. Our radio tracking study provides detailed information on individual habitat selection and intra-specific variation in behaviour that whole-population studies overlook. When these fine-scale movement data are combined with population-level abundance and density data a clearer and more well-rounded picture of Nile perch movement, habitat use and habitat selection may emerge (Mason and Lowe 2010). Paterson and Chapman (2009) focused their study on Nile perch of a smaller average and maximum size than in our telemetry study, which may point to the possibility of size-related shifts in habitat use.

Nile perch in this study also exhibited strong selection for waters with mid to high dissolved oxygen and mid to low temperatures when using near-shore areas of the lake. These results corroborate previous findings that temperature and oxygen are important in determining Nile perch distribution (Ogutu-Ohwayo 1994, Schofield and Chapman 1999). Many movement studies have documented evidence that environmental temperature is a key determinant of fish distribution (Perry et al. 2005, Farrell et al. 2008). Physiological processes operate optimally within a range of body temperatures specific to every organism (Pörtner and Farrell 2008). For fishes, this temperature range is limited by basal metabolic rate and oxygen availability, which is directly related to water temperature (Pörtner 2010). Temperatures below a species’ optimum cause a kinetic reduction in the functional capacity of its internal processes, while high temperature waters simultaneously increase basal oxygen demand and hold less dissolved oxygen than cooler waters (Farrell 1997, Pörtner and Knust 2007). Both scenarios lead to anaerobic respiration and temperature-induced hypoxemia in fishes (Pörtner and Knust 2007, Pörtner and Farrell 2008), which can reduce activity levels.

This may partly explain results from this study that show high water temperatures correlate with low rates of movement and small home ranges, as discussed above. In more extreme cases temperature-induced hypoxaemia can cause fish to seek out more favourable environmental conditions leading to serious shifts in habitat use. For example, Farrell et al. (2008) found that pacific salmon in the Fraser River system of British Columbia are restricted from accessing upstream reaches of their spawning grounds due to thermal stress limiting their aerobic swimming capacity. This thermal limitation could be part of the reason why Nile perch select specific temperature and oxygen regimes. Interestingly, oxygen- and capacity-limitation of thermal tolerance predicts an earlier loss of aerobic scope in larger fish (Pörtner and Farrell 2008, Pörtner 2010), which may explain, at least in part, why larger Nile perch are generally found in cooler, high DO waters.

Nile perch fishery management

Home range and movement parameters have long been of interest to fisheries managers and conservationists since distribution of stocks has direct application to species management. Studies of how movement affects fisheries management often examine the adequacy of marine protected areas (MPAs) or no-take reserves in protecting stocks and/or boosting yields of important marine fisheries (Roberts and Polunin 1991, Allison et al. 1998). Results from these studies have provided overwhelming evidence that MPA efficacy depends largely on features of life history, home range size, and movement parameters of the managed species (Kramer and Chapman 1999, Pastor et al. 2009, Gruss et al. 2011). For example, Pastor et al. (2009) demonstrated that high site tenacity and specialized habitat use of dusky groupers in the Natural Marine Reserve (Cerbère-Banyuls, France) heightens the reserve ability to shelter this species and provides valuable information for placement of future reserves.

Because Nile perch in East African lakes are intensively targeted by fishers, knowledge of the spatial dynamics of this species is needed to improve our ability to predict changes in stocks and to initiate effective management strategies (Mason and Lowe 2010). Although issues surrounding management of Nile perch are much different than those encountered in marine fisheries, there is still an inherently spatial quality to the management schemes currently in place. In recent years, efforts have been made to improve fisheries management in the Lake Victoria basin by shifting responsibilities away from a central governing body to individual fishing communities through the creation of locally regulated beach management units (BMUs) where fishers and other stakeholder groups are responsible for management decisions and enforcement (Nunan 2006, vanderKnaap and Ligtvoet 2010). A major challenge to the success of this co-management scheme is in defining BMU boundaries that are both socially and biologically meaningful (Allison and Ellis 2001). Research on the functioning of BMUs therefore requires an interdisciplinary approach to assess both the social range of the fishers and also the distribution and mobility of key fished species in the lake. Knowing that Nile perch, one of the most important commercial catches in the Lake Victoria basin, have definable home ranges provides a biologically relevant rationale for the insertion of territorial boundaries for BMUs. Clearly defined resource-use boundaries may provide additional incentives for members to follow fishery rules and may prove to be instrumental in improving BMU efficacy. More research is required both spatially and temporally to evaluate the consistency of Nile perch movement behaviours between lakes and over longer time scales, and to determine how movement patterns compare to Lake Victoria’s much larger and more socially and environmentally complex fishery.

Conclusions and Caveats

Measuring habitat selection and generating information on effects of environmental variables on movement and home range size of Nile perch provide details that have direct management implications (Kramer and Chapman 1999, Gilroy et al. 2010) and also provide insight into our understanding ecological divergence in this population. Nevertheless, it is important to note that these data are not completely comprehensive. Although we accounted for low sample sizes of individual Nile perch and of relocation points as much as possible in our analyses, the rate at which Nile perch were removed from the system by fishers made it very difficult to track fish for longer than a few months. These low sample sizes combined with the limited temporal scale over which data were collected restrict our ability to extrapolate to other lake systems (Gu and Swihart 2004). This study, however, still provides important and novel ecological information on a commercially fished and economically important species in a large tropical fresh water fishery.

One further caveat is that the largest fish tracked in this study (57 cm) was much smaller than a full-grown Nile perch. Very large individuals (> 1 m) will likely have more extensive home ranges and movement distances than those reported here if the positive relationship between size and home range does not plateau. This could mean greater regions of overlap between the largest and most fecund individuals in Lake Nabugabo, an important consideration for future management decisions. Furthermore, movement patterns of Nile perch in larger lakes with different environmental conditions and habitat variability could be very different than those found in Nabugabo. Future studies should focus on home ranges on the extremes of the size continuum, and on expansion of movement studies to nearby lakes to determine if movement patterns are equally restricted in larger lakes (Lake Victoria) and if the same habitat preferences and environmental limitations apply.

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FIGURE CAPTIONS

Figure 1 – Bathymetric map of Lake Nabugabo showing the distribution of shoreline vegetation and the positions of three fish landings, and a map showing the location of Lake Nabugabo relative to Lake Victoria and other major lakes in Uganda (inset).

Figure 2 – 50% and 95% fixed kernel utilization distribution (FKUD) home range estimates for 14 Nile perch in Lake Nabugabo, and a schematic diagram indicating the location of externally attached radio transmitters on Nile perch (inset).

Figure 3 – Simple linear regressions of a) average distance from shore with 95% fixed kernel utilization distribution (FKUD) home range (HR) area; b) average distance from shore with movement distance/hour; c) Nile perch Total length (TL) with 95% FKUD HR area; d) TL with movement distance/hour; e) 95% FKUD HR area with average water column temperature; f) distance moved/hour with average water column temperature; g) TL with average water column temperature, and h) TL with average water column dissolved oxygen (DO). Grey lines represent the least squares regression line. All relationships are significant at $p < 0.05$.

Figure 4 – Differences in observed (used habitat in near-shore zones) and expected (available habitat in near-shore zones) values based on four environmental variables: a) water column average temperature, b) water column average dissolved oxygen (DO) and c) depth and d) shoreline vegetation. Positive values indicate selection for a category, and negative values indicate selection against a category

Table 1 – Summary of fish characteristics, home range areas (minimum convex polygon; 50% and 95% fixed kernel utilization distribution), and movement parameters for 14 Nile perch tracked in Lake Nabugabo. All movement distances are in m and all home range area estimates in km^2.

Date of tracking start	Fish ID#	TL (cm)	SL (cm)	WT (g)	points	MCP	FKUD 95%	FKUD 50%	mean dist. from shore	mean dist. moved per hr
25-Jan-11	1	25.0	22.0	170	42	0.118	0.108	0.022	121.58	4.92
09-Feb-11	2	26.0	22.5	230	20	0.187	0.152	0.034	269.77	9.95
31-Jan-11	3	28.0	24.0	260	34	0.264	0.193	0.042	365.03	8.85
24-Jan-11	4	28.0	24.0	250	18	1.253	1.392	0.336	583.41	30.04
24-Jan-11	5	29.0	25.0	250	11	0.530	0.792	0.202	510.65	38.18
28-Jan-11	6	30.0	25.0	250	16	0.147	0.152	0.041	308.63	6.20
22-Jan-11	7	33.5	27.0	430	43	2.281	1.886	0.287	563.07	14.95
01-Feb-11	8	34.0	28.4	480	11	0.395	0.459	0.126	444.14	24.78
27-Jan-11	9	34.4	29.1	400	43	0.708	0.311	0.045	359.19	13.82
20-Jan-11	10	36.0	30.0	500	35	2.275	2.429	0.770	760.22	37.54
22-Feb-11	11	38.0	32.0	700	30	0.915	1.006	0.162	701.48	14.65
10-Feb-11	12	42.0	35.0	750	24	0.930	1.440	0.213	193.32	19.66
22-Feb-11	13	49.0	42.0	1700	16	0.780	0.744	0.119	475.64	19.45
11-Apr-11	14	57.2	48.0	2100	12	0.479	0.607	0.091	516.35	22.09

Table 2 – Principal component analysis scores for environmental measurements. Nine variables were condensed into two PCs with eigenvalues greater than 1.0. Numbers in bold represent variables loading heavily on each component (>0.60).

Axes	**% variance explained**	**test statistics**	**surf. DO**	**bot. DO**	**avg. DO**	**surf. T**	**bot. T**	**avg. T**	**depth**	**Secchi**	**shore dist.**
PC 1	51.57	Pearson's	**-0.652**	0	-0.549	**0.928**	**0.908**	**0.939**	-0.435	0.418	**-0.85**
		sig (2-tailed)	0.012	0.999	0.042	<.0001	<.0001	<.0001	0.12	0.137	<.0001
		N	14	14	14	14	14	14	14	14	14
PC 2	25.81	Pearson's	0.585	**0.954**	-0.593	0.246	0.288	0.275	-0.49	-0.451	-0.179
		sig (2-tailed)	0.028	<.0001	0.025	0.396	0.317	0.342	0.075	0.106	0.541
		N	14	14	14	14	14	14	14	14	14

FIGURES

Figure 1

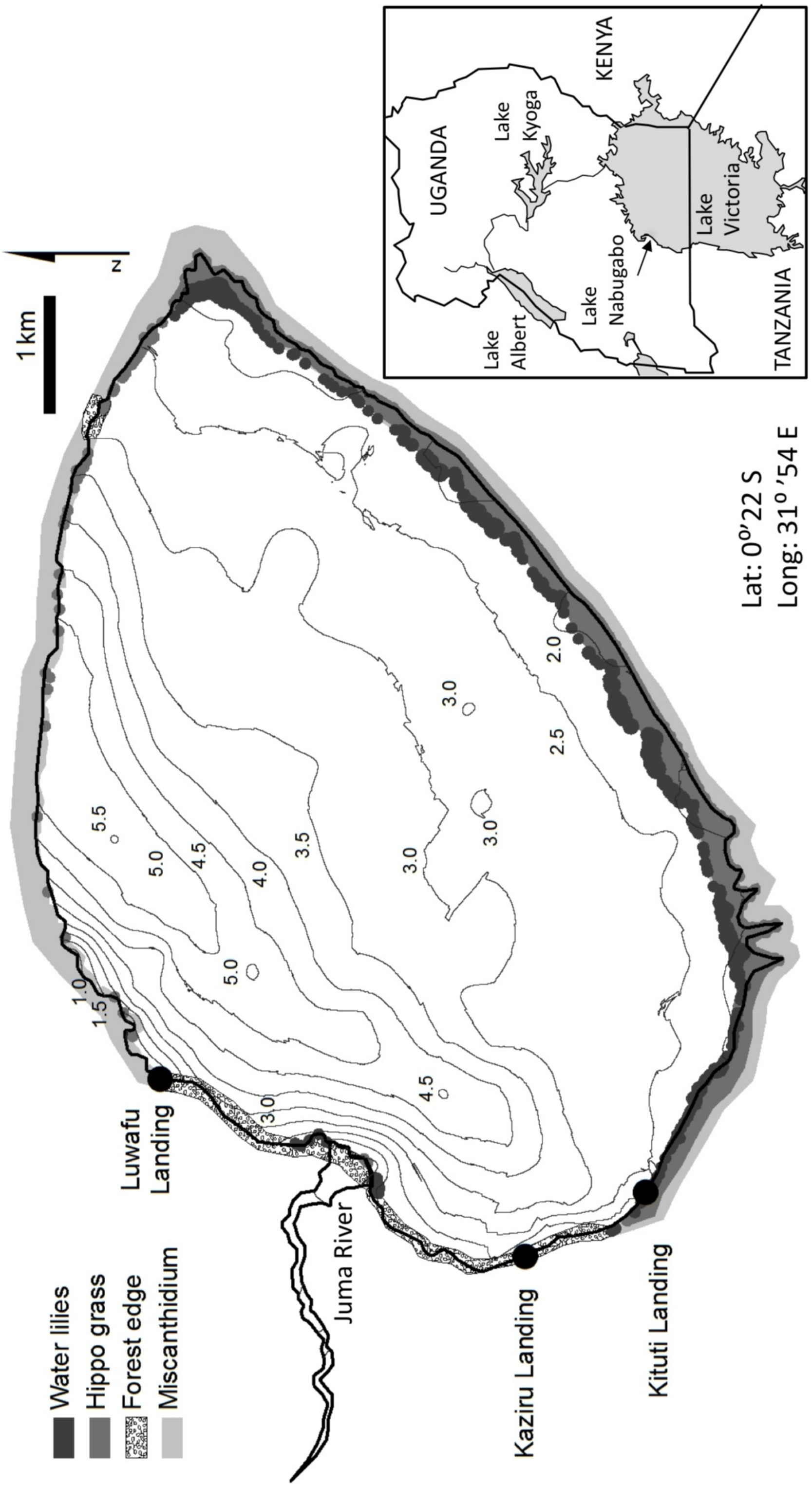


Figure 2

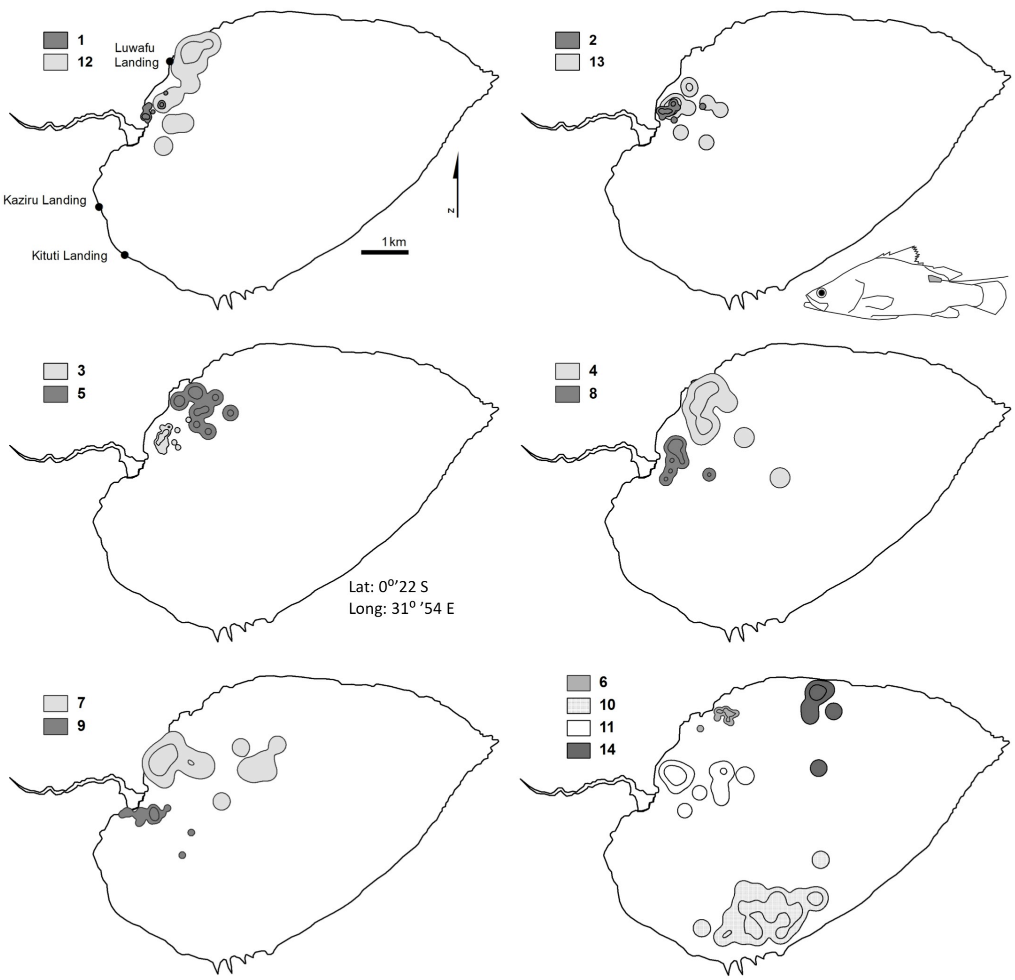
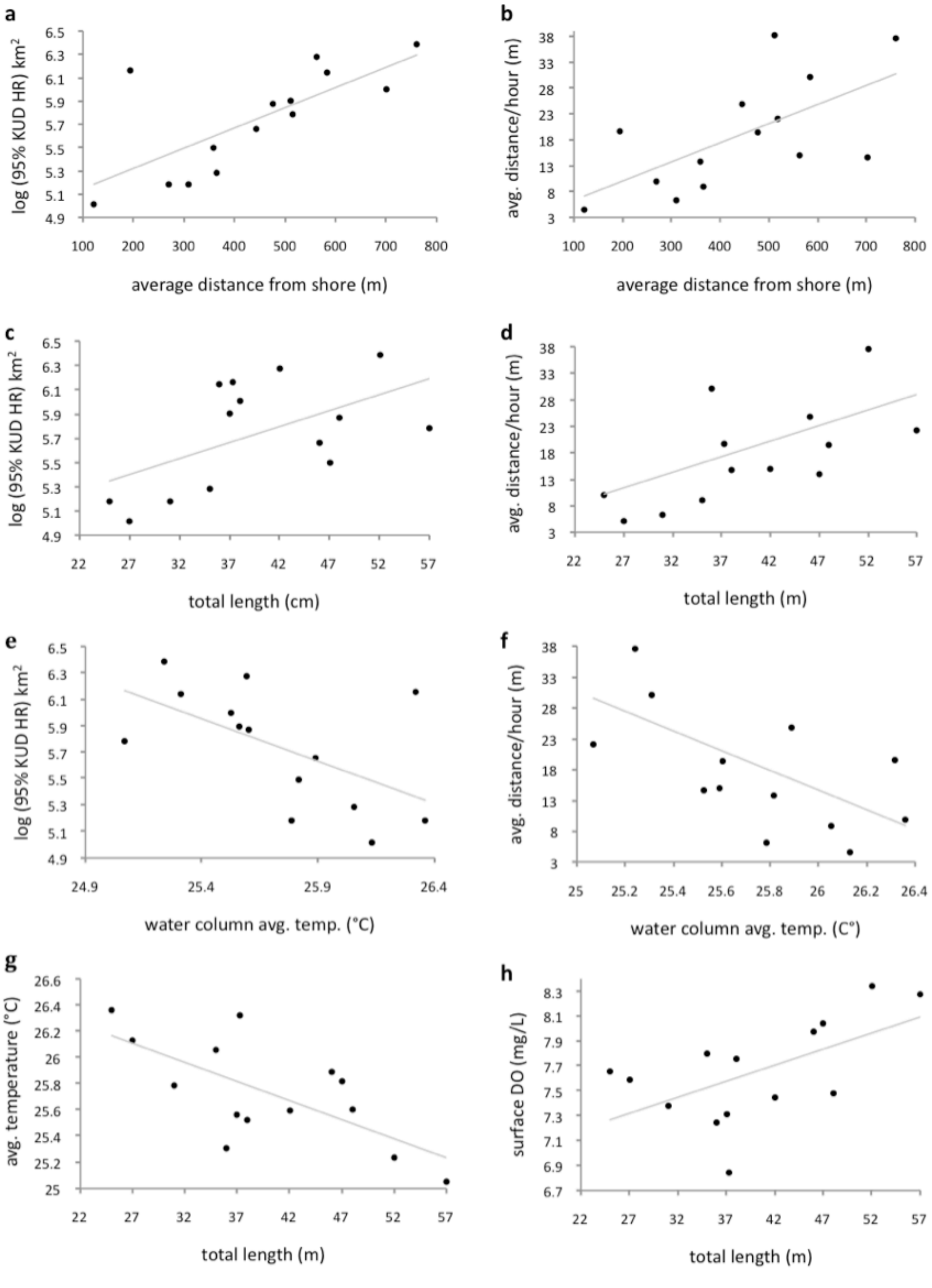
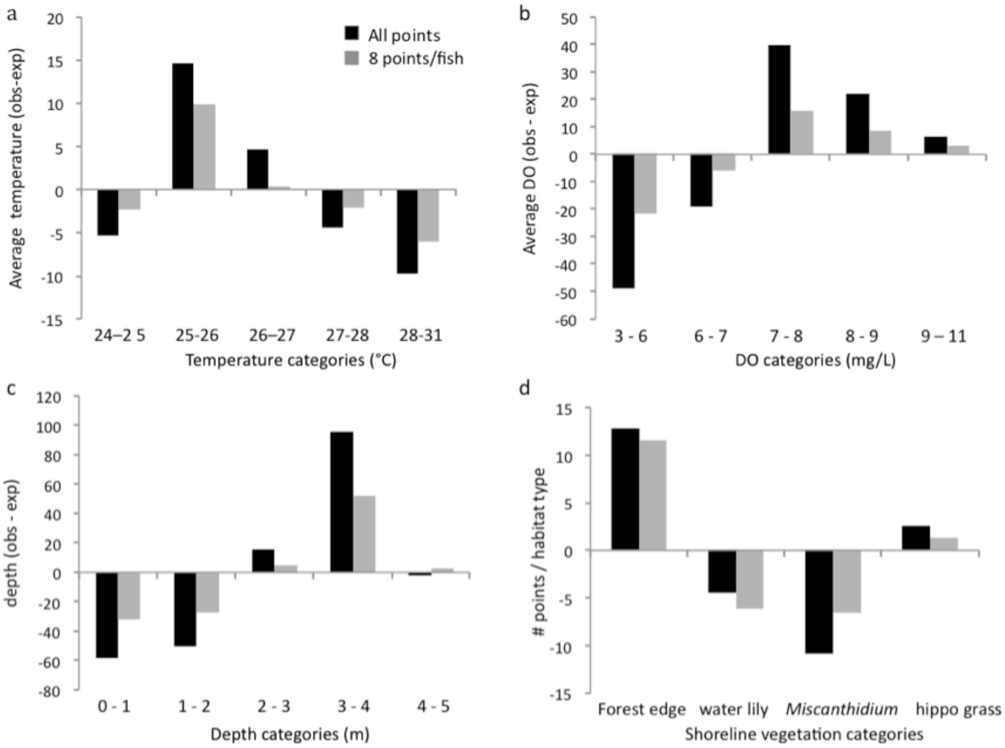

1
12
Luwafu Landing
Kaziru Landing
Kituti Landing
N
1km
2
13
3
5
4
8
Lat: 0°'22 S
Long: 31° '54 E
7
9
6
10
11
14

Figure 3



a
log (95% KUD HR) km²
6.5
6.3
6.1
5.9
5.7
5.5
5.3
5.1
4.9
100
200
300
400
500
600
700
800
average distance from shore (m)
b
avg. distance/hour (m)
38
33
28
23
18
13
8
3
100
200
300
400
500
600
700
800
average distance from shore (m)
c
log (95% KUD HR) km²
22
27
32
37
42
47
52
57
total length (cm)
d
avg. distance/hour (m)
22
27
32
37
42
47
52
57
total length (m)
e
log (95% KUD HR) km²
24.9
25.4
25.9
26.4
water column avg. temp. (°C)
f
avg. distance/hour (m)
25
25.2
25.4
25.6
25.8
26
26.2
26.4
water column avg. temp. (C°)
g
avg. temperature (°C)
26.6
26.4
26.2
26
25.8
25.6
25.4
25.2
25
22
27
32
37
42
47
52
57
total length (m)
h
surface DO (mg/L)
8.3
8.1
7.9
7.7
7.5
7.3
7.1
6.9
6.7
22
27
32
37
42
47
52
57
total length (m)

Figure 4


a
20
15
10
5
0
-5
-10
-15
Average temperature (obs-exp)
All points
8 points/fish
24–2 5
25-26
26–27
27-28
28-31
Temperature categories (°C)
b
50
40
30
20
10
0
-10
-20
-30
-40
-50
-60
Average DO (obs - exp)
3 - 6
6 - 7
7 - 8
8 - 9
9 – 11
DO categories (mg/L)
c
120
100
80
60
40
20
0
-20
-40
-60
-80
depth (obs - exp)
0 - 1
1 - 2
2 - 3
3 - 4
4 - 5
Depth categories (m)
d
15
10
5
0
-5
-10
-15
points / habitat type
Forest edge
water lily
Miscanthidium
hippo grass
Shoreline vegetation categories

APPENDIX A

Table A.1 – Definitions and proportions of available habitat in each habitat selection category (1 – 5; wetland (W) or forest edge (FE)) of environmental variables (temp, DO, depth, Secchi depth) and shoreline vegetation.

Environmental variables	**Cat,**	**Definition**	**% avail**
water column temp °C	1	24 - 25	19.3
	2	25 - 26	35.1
	3	26 - 27	24.6
	4	27 - 28	14.0
	5	28 - 31	7.0
water column DO ($^{\text{mg L}^{-1}}$)	1	3 - 6	31.6
	2	6 - 7	36.8
	3	7 - 8	19.3
	4	8 - 9	10.5
	5	9 - 11	1.8
depth (m)	1	0 - 1	35.1
	2	1 - 2	40.4
	3	2 - 3	12.3
	4	3 - 4	7.0
	5	4 - 5	5.3
Secchi depth (M)	1	0 - 0.55	21.1
	2	0.55 - 0.65	24.6
	3	0.65 - 0.75	24.6
	4	0.75 - 0.85	28.1
	5	0.85 - 1.0	1.8
Shoreline vegetation	FE	forest edge	27.1
	W	water lily	34.8
	W	*Miscanth.*	21.7
	W	hippo grass	16.4

Connecting Statement

The first chapter of this thesis demonstrated that Nile perch are site tenacious with small home ranges and relatively restricted movement patterns. These findings have important implications for fisheries management and the potential for habitat-associated ecological divergence in this species. The introduction of the Nile perch to the inland waters of the Lake Victoria basin was partly responsible for massive ecological change in this region, coinciding notably with dramatic loss of endemic fish species. Although a subset of native species escaped predation by using wetlands as ecological refugia, relationships between Nile perch and their prey species continue to be dynamic. Recent studies have provided evidence for fishing induced ecological change in Nile perch and habitat-associated divergence in gill size, pointing towards the possibility that directional selection by fishers may select for smaller and more wetland resistant Nile perch. In the second chapter of this thesis, I take a second approach to explore habitat-associated divergence in Nile perch by quantifying phenotypic traits that might be expected to differ between wetland edge and more open habitats based on literature review and qualitative observations. I used geometric morphometrics and colour analyses to detect differences in body shape and skin colour between wetland and forest edge individuals, and examined patterns across size class to detect whether trait divergence persists through ontogeny. The findings, presented in Ch. 2, shed light on the nature and extent of phenotypic divergence, and permit inference on potential environmental drivers of divergence. Interestingly, the high site tenacity of Nile perch (Ch. 1) suggests that individuals do occupy spatially and ecologically distinct habitat types that may contribute to the maintenance of habitat-associated phenotypes that are explored in the Chapter 2.

Habitat-associated divergence in morphology and colour of Nile perch (*Lates niloticus*) in Lake Nabugabo, Uganda

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Key words: Introduced predator; East Africa; Lake Victoria basin; ecological divergence; geometric morphometrics; body shape; skin colour

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Note: in preparation for *Evolutionary Ecology*

ABSTRACT

Divergent natural selection is a potent evolutionary force that can generate and maintain ecologically significant trait variation in natural populations. Habitat-associated trait divergence can have a genetic and/or plastic basis and may vary across ontogeny if there are strong size-related shifts in selection pressures. In this study we used geometric morphometric and colour analyses to quantify patterns of phenotypic divergence in Nile perch from ecologically distinct wetland edge and forest edge habitats in Lake Nabugabo, Uganda, and compared patterns across size class to determine if trends are consistent through Nile perch ontogeny. We found substantial morphological and colour differences in Nile perch between habitats, but not all trends were consistent across size classes. Small Nile perch (8-30 cm SL) from wetland edge habitats had much darker skin pigmentation than those from forest edge, however no significant colour differences existed between large Nile perch (>30 cm SL). Differences observed in juvenile skin colour may reflect camouflage strategies between habitats with divergent background coloration. Divergence in body shape was consistent between small and large Nile perch and fits with eco-morphological patterns for fish inhabiting complex vs. simple habitats. Nile perch from forest edge ecotones displayed a more streamlined body shape that may facilitate sustained swimming in open waters, while those from wetlands had a more developed caudal region for high maneuverability and fast burst swimming. The source of the observed phenotypic variation is unknown at present but may reflect genetic differences and/or phenotypic plasticity. The latter is more likely, particularly for colour patterns that converge in Nile perch of larger sizes.

INTRODUCTION

Divergent natural selection is a potent evolutionary force that can generate and maintain ecologically significant trait variation in natural populations (Endler 1986, Schluter 2000, Bolnick et al. 2009). This variation can be due to genetic and/or plastic responses to different selective pressures encountered across heterogeneous environments (Schluter 2000, Rundle and Nosil 2005). Divergent selection can lead to reproductive isolation or ecological speciation between components of a population (Schluter 1996, Hendry 2001); however, gene flow through migration and population mixing may constrain genetic diversification (Hendry et al. 2002, Lenormand 2002, Moore et al. 2007, Crispo 2008). Thus, there can be tight linkages between movement within and across life stages and the potential for habitat-associated trait divergence.

There is a rich body of literature on intraspecific variation in freshwater fishes; and body shape and colour are well-studied examples of phenotypic traits that vary widely within taxa. These traits are under strong evolutionary pressure as they are often heritable and regulate growth, survival, and propagation of species (Kingsolver et al 2001; Leclercq et al 2010). In freshwater fishes, common examples of studies exploring divergent selection on traits related to body shape include comparisons of benthic, limnetic, and littoral forms (e.g. Schluter 1993; Svanbäck and Eklöv 2002; Ruzzante et al 1998), lotic and lentic systems (e.g., Hendry et al 2000; Langerhans et al 2003), and the presence or absence of predators (e.g. Johnson and Belk 2001; Langerhans and DeWitt 2004). A number of conserved patterns of habitat-associated divergence have been noted both within and across fish taxa (Robinson and Wilson 1994). For example, it is commonly observed that individuals inhabiting regions with low habitat complexity (i.e. limnetic zones, simple littoral zones) tend to exhibit a fusiform body shape, long fins and streamlined caudal peduncle, which are adaptations for sustained swimming through open waters (Langerhans and Reznick 2010). Conversely, those in structurally complex regions (benthic or littoral zones with high rugosity and dense vegetation) tend to have deeper bodies and well developed caudal regions that assist in maneuverability (Webb 1982, 1984, Robinson and Wilson 1994, Walker 1997, Langerhans and Reznick 2010, Ruehl et al. 2011). Habitat-associated variation in colour patterns of fishes has also received much attention. Many studies have investigated how environmental variation and social interactions can affect skin colour and ultimately bring about species divergence (Gray and McKinnon 2007, Seehausen et al. 2008). Skin colour in fishes can be affected by diet, intra- and interspecific interactions, and abiotic environmental conditions. Colour patterns act as signals for mating and agonistic interactions (Höglund et al. 2000, Mann et al. 2004) or reflect adaptations for camouflage or mimicry in prey capture and predator avoidance (Cott 1957, Donnelly and Whoriskey 1991, Khoda and Hori 1993). Skin colour of fishes also shows repeated trends across distinct habitat types (Leclercq et al. 2010). Fish in high predation conditions will often recruit melanin (black/brown) pigments for camouflage and crypticity in areas of darker background colour (Donnelly and Whoriskey 1991), and those in habitats with a prey base rich in carotenoids exhibit higher degrees of skin redness (Ibrahim et al. 1984, Gosse and Wroblewski 2004).

These repeated phenotype-environment associations suggest that patterns of morphological and colour variation are adaptive (Schluter 2000, Leclercq et al. 2010) and allow predictions to be made about phenotypic traits in fishes between discrete environmental conditions. Establishing the genetic vs. plastic basis for phenotypic trends is difficult, however, and ecological processes such as migration and gene flow can constrain or limit local adaptation (Hendry et al. 2002, Svanbäck and Eklöv 2002, Crispo 2008, Ruehl et al. 2011). In addition, many freshwater fishes, particularly piscivores, exhibit strong ontogenetic shifts in diet and habitat use (Winemiller 1989, Montiero et al. 2005, Nunn et al. 2007) that can cloud the role of divergent selection in driving phenotypic divergence. Therefore, an important consideration in mapping patterns of intraspecific variation is exploring the relationship between ontogenetic shifts in ecological traits with habitat-associated trait divergence. The invasive, predatory Nile perch (*Lates niloticus* L.) in the Lake Victoria basin of East Africa provides an excellent system in which to explore habitat-associated phenotypic divergence, because of the broad range of habitat types occupied by the predator, dramatic ontogenetic dietary shifts, and strong divergence in diet and body size across ecologically distinct habitats (Paterson and Chapman 2009). We use this system to investigate the interaction between size and habitat in explaining patterns of habitat-associated phenotypic divergence. Understanding trends of habitat-associated phenotypic divergence in this species is critical for understanding and predicting its ability to establish and flourish in many lakes where it has been introduced.

Nile perch history and ecological interactions in its introduced range

The Nile perch was released into Lake Victoria and other lakes in the region such as Nabugabo and Kyoga in the 1950s and 1960s to compensate for depleting commercial fisheries and to develop a sport fishing industry (Balirwa et al. 2003, Pringle 2005, Goudswaard et al. 2008). In Lake Victoria, the Nile perch population increased dramatically in the 1980s and became an important part of the fishery yield (Ogutu-Ohwayo 1994, Goudswaard et al. 2008, Paterson and Chapman 2009). The upsurge in

Nile perch in Lake Victoria coincided with a further decline of native species and the disappearance of an estimated 40% of the unique flock of endemic haplochromine cichlids (Witte et al. 1992, Seehausen et al. 1997, Balirwa 2007); similar faunal collapse was observed in lakes Kyoga and Nabugabo. A subset of the native species persisted in the face of Nile perch predation through use of ecological refugia that act as barriers to Nile perch dispersal and/or behavioural shifts (Chapman et al. 1996a, Chapman et al. 2002, Balirwa et al. 2003, Olowo et al. 2004). For example, in Lake Nabugabo, a satellite of Lake Victoria, the abundant wetland habitat functions as structural and low-oxygen refugia for fishes that are smaller and more tolerant to hypoxia than the Nile perch (Chapman et al. 1996 b, Schofield and Chapman 1999).

As a valuable economic species, Nile perch are subject to heavy fishing pressure that appears to be reducing Nile perch biomass and catch per unit effort (Balirwa et al. 2003, Matsuishi et al. 2006) and contributing to shifts in its distribution and diet (Paterson and Chapman 2009). Studies conducted in the 1990s in Lake Nabugabo showed Nile perch to be rare in wetland ecotones (Chapman et al. 1996ab, Schofield and Chapman 1999) and more prevalent in forest edge or exposed habitats. In a more recent study in Lake Nabugabo Paterson and Chapman (2009) found that the proportion of Nile perch near wetland ecotones relative to forest edge had increased over a 12-year period, although there was no evidence for an increase in their abundance near the wetlands. They speculated the proportional shift in distribution reflected intensive fishing for Nile perch more open waters near the forest edge where Nile perch abundance declined over the same period. A number of behavioural and morphological differences have been observed between Nile perch near wetland edge and forest edge that may be reinforced by heterogeneous fishing pressure. In waters near wetland ecotones, the size at which Nile perch undergo ontogenetic shifts from insectivory to piscivory is smaller, the mean size of Nile perch is larger, and the gill size of juvenile Nile perch is larger, associated with more hypoxic conditions (Paterson and Chapman, 2009, Paterson and Chapman 2010). Colour polymorphism has also been observed in Nile perch with skin colour ranging from completely silver to completely brown.

The question of whether Nile perch exhibit habitat-associated phenotypic divergence, and the persistence of this divergence through Nile perch life stages, is of ecological importance to this system. The decline in Nile perch biomass has coincided with a modest resurgence of some haplochromine cichlids (Witte et al. 2000, Balirwa et al. 2003). Evidence that Nile perch are capable of top down control of native fauna in the Lake Victoria basin is controversial (Kolding et al. 2008), but raises concerns that distribution shifts and possible adaptation to wetland ecotones in Nile perch could threaten the ecological refugia responsible for the preservation of some native fauna (Paterson et al. 2010).

In this study we use geometric morphometrics and colour analyses to determine whether variation exists in the morphology and skin pigmentation of Nile perch between inshore forest edge and wetland habitats in Lake Nabugabo, Uganda. We compared divergent trends across size classes to determine whether habitat-associated differences are transient, ontogenetic, or represent distinct phenotypes within the population. Based on established eco-morphological and colour patterns relating to diet, predator-prey relationships, locomotion and oxygen availability, we made specific predictions about patterns of morphology and colour of individuals collected from structurally complex, low-oxygen (wetland ecotone) habitats versus high oxygen (forest edge/exposed) habitats with limited inshore structure (Keast and Webb 1966, Webb

1984, Winemiller 1991, Domenici 2003, Langerhans and Reznick 2010). We predicted that Nile perch collected from near wetland ecotones would have deeper bodies and well-developed caudal regions to improve maneuverability, have deeper and longer heads to accommodate larger gills, and have a dark brown body colouration to improve crypsis. In forest edge or open water habitats we predicted fusiform body shapes with narrow caudal peduncles for streamlining, and a lighter skin colour to blend with brighter more exposed conditions.

MATERIALS AND METHODS

Study location

Nile perch were sampled from Lake Nabugabo, Uganda, 4 km west of Lake Victoria just south of the equator. Lake Nabugabo is a relatively small and shallow lake (surface area = 33 km^2; mean depth = 3.13 m) (Nyboer and Chapman, this thesis). The lake is characterized by a high surface temperature (25.8 ^{o}C; ±1.07, SD) and low water transparency (mean Secchi depth = 0.69 m; ±0.11, SD) (Nyboer and Chapman, this thesis). Lake Nabugabo was once a bay of Lake Victoria but has been isolated from the main lake by an extensive swamp and sand bar for approximately 5000 years (Stager et al. 2005). Approximately ¾ of the lake's perimeter consists of dense wetland characterized by high structural complexity and low oxygen conditions; and Nile perch diet reflects a fish-rich prey base near wetland ecotones (Schofield and Chapman 1999, Paterson and Chapman 2009). The west side of the lake is edged by dense forest and fishing villages (three active fish landing sites) and is characterized by low structural complexity and high oxygen conditions; Nile perch diet shows a greater proportion of insect prey near the forest edge.

Specimen collection and photography

Nile perch between 7.8 to 84.5 cm standard length (SL) were sampled from both wetland edge (n = 135) and forest edge (n = 75) habitats in Lake Nabugabo. Nile perch < 30 cm were collected between June 2011 to November 2011 with beach seines and experimental gill nets. Since our experimental gears did not catch larger fish, some Nile perch >30 cm were sampled from Lake Nabugabo from January – November 2011 at fish landing sites. Fishers identified where each fish was caught, so that we could determine whether they were captured near wetland ecotones or forest edge. Each fish was measured for total length (TL) and standard length (SL) to the nearest 0.1 cm, weighed to the nearest 0.1 g, and labeled with location and ID number. Fish were separated into either large (fish > 30 cm SL) or small (fish < 30 cm SL) size classes. The size at which Nile perch in Lake Nabugabo shifts to piscivory from a primarily insectivorous diet differs between habitats, but is less than 30 cm across all habitats (Schofield and Chapman 1999, Chapman et al. 2003, Paterson and Chapman 2009). These two size-class categories also differed in body shape allometry (see results). Final counts for fish were: small, wetland: 56; small, forest edge: 54; large, wetland: 81; large, forest edge: 28. Nile perch were placed on a standard grid-ruled background (small fish: 1.8 x 1.8 cm; large fish: 4 x 4 cm) and photographed on the left side of the body with a Canon Powershot® G10 camera. The camera was pointed straight down approximately 2 m above the fish to minimize fisheye effect. Fish were photographed in full shade between 9:00 am and 11:00 am to ensure consistent lighting.

Measuring colour

Sixty wetland edge (30 large, 30 small) and 58 forest edge (28 large, 30 small) images were randomly selected from the photo bank for colour analysis (except in the case of large forest edge perch for which all available photos were used to create a near-even sample size). Nile perch images were opened in Adobe Photoshop CS5® in random order and processed by one individual who was unaware of the capture locations of the fish. Images were corrected for minor differences in ambient light quality by using the white balance tool to standardize photograph hue (Mann et al. 2004). The fish was then clipped from the background, which was deleted. To ensure that only pigments present in the scales were included in the analysis, fins and eyeballs were clipped from the image as well as any flecks of dirt or leaves that were on the body of the Nile perch when it was photographed. If the mouth and gills were distended, as was often the case for large Nile perch caught on long lines by fishers, these were excluded as well (See Appendix A, Fig. A.1 for an example).

To calculate colour scores, we used methods similar to those outlined in Mann et al. (2004) whereby we defined a range of colours that encompassed pigments of interest observed in Nile perch scales. This colour range was then used to determine the proportion of skin surface area containing these pigments. We created the colour range using Adobe Photoshop CS5® swatch tools by selecting 13 swatches representing the range of black - brown pigments present in Nile perch scales. Using the eyedropper tool we selected all pixels in the Nile perch image that fell within this colour range. The number of coloured pixels was then divided by total pixels in the Nile perch body yielding a percentage of body colouration falling within this pre-determined range. We developed this Photoshop technique as an alternative to the usual Sigma Scan Pro®

method because the colour range required for this analysis was not available in the Sigma Scan Pro® software.

Geometric morphometrics and linear measurements

To prepare photographs for geometric morphometrics and analyses of linear metrics related to body shape, all images were opened with Adobe Photoshop CS5®, straightened, and corrected for remnant fisheye effects with a lens correction filter specific to the Canon Powershot G10. Nine of the 28 large, forest edge Nile perch that were sampled from fish landing sites could not be used for body shape analyses because of large distended gills that made it impossible to accurately place landmarks. This reduced the sample size of large, forest edge Nile perch to 19.

Measuring body shape

Geometric morphometric techniques were used to analyze body shape variation among fish from different habitats. All photographs were processed with TPSDig software (v.2.16 © Rohlf 2010), which was used to digitize 18 discrete homologous landmarks on each specimen (Fig. 1a) based on recommendations from Zelditch et al. (2004) and B. Langerhans (pers comm). We tested repeatability by randomly re-digitizing landmarks on a subset ($n=30$) of photographs of both large and small specimens. Measurement error was universally low with correlations between repeated estimates of landmark XY coordinates falling between $r = 0.97 – 1.0$, $p < 0.0001$. We used TPSRelw (v. 1.49 © Rohlf 2010) to calculate centroid size (the square root of the sum of the squared distances of all landmarks to the center point), which we used as an estimate overall body size (Bookstein 1991). A consensus configuration was then established using generalized least squares Procrustes superimposition, which scales and rotates each configuration of landmarks such that the sum of the squared distances between homologous landmarks is minimized (Zelditch et al. 2004). TPSRelw was then used to compare each individual configuration of landmarks to the consensus, and deviations from the consensus were calculated as partial warps (PWs) (non-uniform) and uniform components (UCs). The direction and orientation of warps were then specified by two-dimensional vectors (warp scores) that represent localized variation on individual landmark positions. Finally, TPSRelw was used to calculate relative warps (RWs), which are principal components of body shape that include all PWs and UCs, to explore overall shape variation on a reduced set of axes.

Following methods of Ruehl and DeWitt (2007), we digitized an additional landmark on the distal tip lower jaw (L J – see Fig. 1a) and used TPSdig to calculate the distance between 'L J' and '1' to estimate gape width for each individual. We divided gape width by centroid size, and used this value as a covariate in our analyses to statistically account for changes in head shape that are artifacts of having been photographed with an open mouth.

Linear measurements

TPSDig was used to perform linear measurements (LMs) on specific body shape traits known to be related to swim performance (body depth, caudal depth and length, fin lengths) as well as traits related to variation in gill size in other fish species (2 measures of head depth, head length), and foraging (jaw length, eye width) (Fig. 1b). The standard length (SL) line was drawn first extending from the tip of the upper jaw to the point on the caudal peduncle at which the lateral line meets the caudal fin. Head depth and body depth measures were then carried out perpendicular to the SL line. Most linear measures used points previously defined by landmarks for the origin or end point of the lines. Exceptions were: 1) posterior head depth (PHD), which is placed exactly half way between the lines for anterior head depth (AHD) and anterior body depth (ABD), 2) caudal length (CL), which ends at the posterior body depth (PBD) line and 3) caudal width (CW), which passes perpendicularly through the standard length (SL) line at the narrowest point in the caudal peduncle (Fig. 1b). These sliding landmarks were only used in the linear trait analyses, and not in the formal geometric morphometric analysis.

Statistical analyses

Colour

Spearman rank correlation was used to detect relationships between body size (total length (TL), standard length (SL) and weight, (W)) and body colour (percent brown). Analyses were done separately for Nile perch from the two major habitat types (wetland edge and forest edge). We used a non-parametric analysis, as our data did not meet assumptions of normality and linearity. Data from each habitat were then split into large (>30 cm) and small (<30 cm) size classes. To determine whether within-size-class means in percent brown differed across habitats we used independent t-tests with habitat as the predictor variable and percent brown as the variable of interest. We also used t-tests to ensure that mean TL, SL, and W of fish in the two size classes did not differ across habitats to ensure that ‘small’ fish from wetland ecotones are not larger than ‘small’ fish from the forest edge. After log transformation, all variables except for percent brown in the ‘small’ category fit the normal distribution. We therefore used the non-parametric Wilcoxon rank sum test to determine whether percent brown differed across habitats for small perch. Finally, Nile perch from each habitat were split into 10 cm size classes, and average percent brown was compared across habitats for each size category.

Geometric morphometrics

Data were split into large (>30 cm) and small (<30 cm) fish for all geometric morphometric analyses. Our initial analysis indicated slope heterogeneity across habitats when all size classes of fish were considered as one group. When size classes were treated separately, slopes were homogeneous. To identify the effect of habitat on body shape independent of allometry and gape size, we conducted a MANCOVA with body shape variables (30 PWs and 2 UCs) as independent variables, centroid size and gape width/centroid size as covariates, and habitat as a fixed factor. We initially ran the MANCOVA with all possible interaction terms (tests for slope heterogeneity) but removed them from the model, as they were not significant for either size class. We could therefore conclude that the relationship between body shape and centroid size, and body shape and gape width did not differ between habitat types within the two size classes. We used Wilks partial η^2 to calculate the relative importance of the remaining factors (centroid size, gape width/centroid size, and habitat) (Langerhans & DeWitt, 2004). We then used MANCOVA to generate a canonical variate (CV) for habitat to describe the relative positions of wetland and forest edge groups along the axis. Using this canonical axis, thin plate spline grid transformations were generated using TPSRegr (v. 1.37 © Rohlf 2009) and used to visualize this variation in shape for small and large size classes separately. The thin plate spline method allows for complete interpretation of partial warps by combining all uniform and non-uniform components over the entire form. To test for habitat effects on relative warps (RWs) we conducted analyses of covariance (ANCOVAs) on the first 6 RWs with centroid size and gape as covariates. As with the PWs, none of the interactions terms were significant and were therefore removed from the final analysis. Univariate analyses were used in this instance, as relative warps are independent of one another.

Linear measurements

MANCOVA was used to identify the effect of habitat on body shape with the 15 linear measurements as independent variables, standard length as a covariate, and habitat as a fixed factor. Data were split into large (>30 cm) and small (<30 cm) fish for analyses of linear traits. The habitat x SL interaction term was removed from the model as it was not significant for either size class. Univariate ANCOVAs were used to explore the effect of individual traits. We tested all interaction terms between the main effect and the covariate, and none of them were significant for any of the traits and were therefore removed from the model. For all MANCOVAs and ANCOVAs, we performed Levene's test for equality of error variances, and in no case was the error variance assumption violated. We also used Box's test to compare variance-covariance matrices between groups and found a significant result for small Nile perch (p = 0.046) only, but because sample sizes are equal we assume that the multivariate tests used are robust to violations of this assumption.

RESULTS

Colour analysis

Small fish from the wetland edge were characterized by a higher proportion of black-brown (melanophore) colouration in their scales (mean 46.3%, ± 22.4%, SD) than small fish from forest edge environments (mean = 24.2% ± 19.9%, SD) (Table 1), however, this pattern disappeared in large fish with no significant difference in the proportion of black-brown pigment between wetland ecotone (mean = 29.1% ± 12.7%, SD) and forest edge (mean = 34.5% ± 17.7%, SD) fish (Table 1). No other characteristics (total length, standard length, or body mass) differed between habitats for large or small size classes; and therefore it is unlikely that differences detected between habitats were due to the size structure of the samples (Table 1). Plots of average percent brown of 10 cm size categories compared across habitats show that the proportion of brown pigment in scales converges as perch grow larger. This convergence appears to occur at the 20-30 cm SL range (Fig. 2). Spearman's rank correlations of the relationship between percent brown and fish size showed a weak negative relationship for wetland edge fish with proportion of brown declining with standard length (SL: $r = -0.233$, $p = 0.07$). For fish from the forest edge, the relationship was positive with proportion brown increasing with standard length (SL: $r = 0.471$, $p = 0.0003$).

Geometric morphometrics

MANCOVA revealed significant morphological divergence in Nile perch body shape between habitats in both large and small size categories, independent of body size and gape width (Table 2). The habitat canonical axis explained 67% of the variation for small and 79.7% for large Nile perch. The covariates in our model (centroid size and gape width) were significant for both size classes of Nile perch (Table 2). For small fish, inspection of the visualizations along the habitat canonical axis revealed that individuals with increasingly positive scores (forest edge fish) showed a fusiform body shape with a shortened and deepened head, an anterior deepening of the body, and a streamlined caudal region (Fig. 3). Individuals with negative scores (wetland edge fish) show a narrower, longer head and deepening of posterior body depth in the caudal region (Fig. 3). For large fish, individuals with increasingly negative scores (forest edge fish) again showed a deepening of the anterior body relative to wetland fish, however the difference between habitats was not as extreme as in the smaller fish (Fig. 4). Differences in the streamlining of the caudal region were also much less obvious in larger fish. The most important differences between habitats in larger fish appear to be in head shape. Fish with increasingly positive scores (wetland edge fish) possessed longer heads and snouts and a more ventrally placed eye (Fig. 4), while those from forest edge habitats were characterized by a compressed head morphology with the eye placed nearer to the dorsal midline (Fig. 4).

For Nile perch < 30 cm, the first 6 RWs accounted for 70% of the variation in body shape, however variation in RWs 1 and 2 (26.8% and 11.74 %, respectively) were primarily driven by centroid size (Table 3), and RWs 3 and 4 (9.9 % and 8.7 %, respectively) were related to gape size (Table 3) and are therefore not considered further. The habitat effect was significant for RW 5 and 6 explaining 7.1 and 5.8 % of the variation, respectively (Table 3). Although the combined percentage of these two RWs (12.9%) is small, visualizations support results of the partial warp analyses (Fig. 5). Visual inspection of body shape extremes along the RW5 axis reveals that Nile perch with increasingly positive scores (wetland edge fish) show a greater posterior body depth in the caudal region (Fig. 5), whereas those with negative scores (forest edge fish) show a greater overall body depth and streamlining of the caudal region (Fig. 5). Apart from further corroborating previously described body depth differences, variation in RW 6 was difficult to detect even when visualizations were exaggerated (Fig. 5).

For Nile perch >30 cm, the first 6 RWs accounted for 73.8 % of the variation in body shape. RW 1 and 4 (34.7% and 7.3%, respectively) were primarily related to gape size (Table 3), and RWs 3 and 6 (9.0% and 5.1%, respectively) were related to centroid size (Table 3) and are therefore not considered further. RWs 2 and 5 accounted for 11.1% and 6.54% of the variation, respectively, and were related to habitat (Table 3, Fig. 6). RW 2 was related primarily to head shape and placement of body depth. Individuals with increasingly positive scores (forest edge) showed a constriction of the anterior portion of the head, an anterior and dorsal displacement of the eye, and an anterior displacement of body depth (Fig. 6). Negative scores (wetland) indicated an increase in head length and a lengthening of the caudal peduncle (Fig. 6). Variation in RW 5 was less pronounced, however it showed a constriction of the caudal peduncle and an increase in anterior body depth in fish with increasingly positive scores (forest edge fish) (Fig. 6).

Linear measurements

MANCOVA indicated significant differences between forest edge and wetland edge fish in linear measures (Table 4). Results of univariate analyses on linear traits revealed patterns of divergence between habitat types that support trends derived from the geometric morphometric analyses. Because the multivariate test established significance for the group of traits, we did not correct for multiple comparisons. In the smaller size class, Nile perch from forest edge showed a marginally deeper anterior body depth (p = 0.1), longer anal and posterior dorsal fins, and deeper heads than Nile perch from wetland ecotones (Table 5). In the large size class, Nile perch from wetland habitats were characterized by longer caudal fins, wider eyes, and smaller jaw length than Nile perch from forest edge environment (Table 5).

DISCUSSION

This study revealed clear phenotypic differences in morphology and colour between Nile perch captured near wetland and forest edge ecotones. Although some trends changed through ontogeny, several patterns of habitat-associated morphological divergence were consistent across size classes. Wetland edge and forest edge habitats differ in structural complexity, prey base, and dissolved oxygen concentration (Chapman et al. 1996ab, Schofield and Chapman 1999), but may have a number of other differences common to complex vs. simple habitats such as divergence in light regime and background hue (Kirk 2011). In general, inter-habitat variation in Nile perch body shape and colour met *a priori* predictions, suggesting that the patterns observed in Nile perch are a response to divergent selection pressures encountered across a heterogeneous landscape.

Divergence in colour patterns

Results from this study showed a strong pattern of colour divergence in small (<30 cm) Nile perch between wetland edge and forest edge habitats. Wetland edge fish had higher proportions of black/brown pigmentation in their skin, and those from forest edge or exposed habitats displayed a higher proportion of silver/iridescent pigmentation. This pattern of divergence was not maintained in the large (>30 cm) Nile perch size class. Colour patterns become more uniform across habitats and appeared to converge when fish grew to approximately 20-30 cm in length.

Intraspecific diversity in fish colour is common, and pigmentation is often under strong selection (Endler 1983, Gray and McKinnon 2007, Seehausen et al. 2008, Leclercq et al. 2010). Skin colour functions in mimicry, camouflage, and mate attraction; and variation in pigmentation is often correlated with environmental conditions such as background colour, water transparency, and predator-prey interactions (Endler 1978, 1983, Donnelly and Whoriskey 1991, Kekäläinen et al. 2010). Skin colour in fishes is mediated by a number of different types of chromatophores, cells containing pigments that absorb or reflect a range of light wavelengths, and translate to colour patterns detectable by other fishes (Sugimoto 2002, Leclercq et al. 2010). The main chromatophores present in Nile perch skin are likely to be melanophores, cells that contain light-absorbing pigments (melanins) that produce dark black/brown colours, and iridophores, cells that contain light-reflecting platelets that produce metallic/iridescent tones. Melanin is one of the most important pigments for freshwater fish and is commonly used for camouflage, photo-protection, and visual communication (reviewed in Sugimoto 2002, Leclercq et al. 2010).

Small Nile perch associated with wetland ecotones may recruit more melanin pigments than those from forest edge or exposed habitats to enhance crypticity in complex environments. Although we know little about the variation in light regimes between wetland edge and forest edge habitats in Lake Nabugabo, dense macrophyte structures in wetlands can alter the spectral quality of light in water and can cause darker background hues than would be found in exposed conditions (Loiselle et al. 2008, Kirk 2011). Many fish species have been shown to increase melanophore concentrations in their skin when set against darker backgrounds to enhance camouflage (Donnelly and Whoriskey 1991, Sugimoto 2002). Increased camouflage in wetland ecotones may be of advantage to small Nile perch both to improve their efficiency as piscivores, but also to avoid predation by larger Nile perch. In wetland edge habitats where fish prey are abundant, juvenile Nile perch undergo an ontogenetic dietary shift from insectivory to piscivory at ~10-15 cm, sooner than the average 30 cm documented for Nile perch in open waters where haplochromines are rare (Schofield and Chapman 1999, Paterson and Chapman 2009). This early switch to piscivory may be one advantage of cryptic colouration for small Nile perch in wetland habitats as it may enhance their ability to avoid detection by prey. Camouflage has been shown to improve foraging efficiency in a number of fish species. For example, Khoda and Hori (1993) found that pale-dark dichromatism in predatory cichlid fishes in Lake Tanganyika optimizes prey capture across habitats that vary in light condition and complexity; dark morph predatory cichlids targeted prey from rocky habitats, while pale morphs searched for prey in open water.

Another potential advantage of cryptic colouration for Nile perch is predator avoidance, since small Nile perch are subject to cannibalism. It has long been known that cryptic coloration is highly adaptive as a means to avoid predation in aquatic systems (Sumner 1935ab). For example, Donnelly and Whoriskey (1991) found that brook trout (*Salvelinus fontinalis*) acclimated to a brown background experienced higher mortality due to predation when against a tan-background than tan-acclimated trout. Interestingly, diet studies in Lake Nabugabo show a higher frequency of cannibalism in forest edge habitats indicating that juvenile Nile perch may successfully evade predation in wetland habitats through camouflage with their surroundings; although this may also reflect density of juvenile perch across habitats.

In contrast to smaller Nile perch, larger conspecifics from wetland ecotones did not exhibit colour patterns divergent from forest edge-dwelling conspecifics. Larger wetland Nile perch do not penetrate as far into near-shore vegetation as their smaller counterparts (Paterson and Chapman 2009). The benefits to recruiting melanin pigments may be more limited for Nile perch not using wetland ecotonal structure, as strategies for crypticity change in pelagic waters where background colour is likely brighter. Pelagic fishes often exhibit camouflage strategies such as pale or counter-shaded skin with darker pigments either absent or concentrated in the dorsal surface, a strategy that may reduce conspicuousness by concealment of shadows cast on the body (Thayer 1896, Cott 1957). Counter-shading is commonly observed in large Nile perch from both habitat types, and may reduce detection by their prey.

Divergence in morphological traits

We found evidence for habitat-associated divergence of morphological traits for both small and large Nile perch, although not all trends were consistent across size classes. The morphological variation observed across wetland edge and forest edge habitats is consistent with well-documented and highly conserved eco-morphological patterns that are thought to reflect habitat complexity, although some trait variation in Nile perch is also consistent with body shape variation indirectly induced by divergent aquatic oxygen regimes.

Morphological divergence: Small size class

The most striking pattern consistent across size class was an anterior displacement of maximum body depth in forest edge Nile perch relative to wetland individuals. This pattern is commonly observed in fishes occupying simple vs. complex habitat types as development of the anterior portion of the body maximizes hydrodynamic efficiency and reduces energetic costs of sustained swimming through open waters (Keast and Webb 1966, Webb 1984, Langerhans and Reznick 2010). In addition, we found variation in the shape of the caudal region, especially pronounced small Nile perch. Wetland edge individuals were characterized by a highly developed posterior region, resulting in a steeply angled transition to the caudal peduncle. In contrast, individuals from forest edge or exposed environments have a streamlined caudal region. The caudal region of fishes is used to generate rapid forward thrust (c-starts) (Webb 1984, Langerhans et al. 2004, Langerhans and Reznick 2010) and to increase control over fine movement in structurally complex habitats (Keast and Webb 1966, Webb 1982, 1984, Winemiller 1991, Domenici 2003, Langerhans and Reznick 2010, Ruehl et al. 2011). A strong caudal region combined with a shallower anterior body depth has been shown to contribute to better survival of fishes in complex habitats (Langerhans et al. 2004). Increased c-start speed improves escape from predators (Webb 1982, Walker 1997), and is likely to enhance foraging ability or hunting efficiency in such habitats (Walker 1997). These findings suggest that some of the variation in body shape in small Nile perch may be an adaptive response to differences in habitat complexity between wetland edge and forest edge habitats.

Wetland edge fish were also characterized by a longer head than forest edge fish, a pattern that was more pronounced in small Nile perch, but also evident in the larger size class. Recent studies have shown that juvenile Nile perch in hypoxic wetlands have larger gills than those in well-oxygenated forest edge habitats (Paterson et al. 2010). A number of studies have reported proliferation of gill size in hypoxic habitats to be associated with larger head size, most like to accommodate the larger branchial basket (Langerhans et al. 2007, Crispo and Chapman 2011). For example, Crispo and Chapman (2011) found that larger heads in cichlid species raised under low-oxygen conditions were due, in large part, to an increase in gill size. The elongated heads of Nile perch in wetland edge habitats may, therefore, constitute morphological change due to indirect effects of low dissolved oxygen, which has been linked to diversification in Nile perch gill size across forest edge and wetland habitats (Paterson et al. 2010).

Results from analysis of linear measures captured a number of patterns not readily apparent in the geometric morphometric analyses. Small Nile perch from forest edge conditions had longer anal and posterior (soft) dorsal fins than those from wetlands. Median fins (dorsal, anal and caudal) have an important function in acceleration and maintenance of steady swimming (Lauder and Drucker 2004). The soft dorsal fin, in particular, has been shown to maintain body stability during propulsion, and can improve flow regimes over the caudal peduncle (Lauder and Drucker 2004). The longer dorsal and anal fins in forest edge Nile perch may be beneficial in improving stability and reducing drag during sustained swimming in open waters (Arbour et al. 2011). These results are consistent with diversification in body shape that may facilitate differences in swimming style (sustained swimming vs. high maneuverability) across habitats that vary in structural complexity.

Morphological divergence: Large size class

Results from geometric morphometric analyses on Nile perch in the larger size class revealed some similar trends as seen in small individuals: anterior displacement of body depth (RW 2 & 5, PW), a narrower caudal peduncle (RW 5, LM,) and shortening of the head (RW2) in forest edge fish relative to wetland conspecifics. However, inter-habitat variation in these traits was not as extreme as in the smaller size class. Although large Nile perch are less likely to penetrate as far into near-shore vegetation as juveniles, the divergence across habitats in the larger perch may still relate to differences in swimming strategy between simple and complex habitats. Larger wetland Nile perch are thought to spend the majority of their time off the wetland ecotone, but approach the macrophyte structure to seek high quality prey items (Schofield and Chapman 1999, Paterson and Chapman 2009). Furthermore, Nile perch > 24 cm TL were observed inside water lily and hippo grass stands during telemetry tracking, providing evidence that Nile perch do, at times, enter wetland edge vegetation. This may partly explain the retention of a high-maneuverability body shape in wetland adults, while forest edge individuals continue to show a pelagic fusiform morphology to maximize prolonged swimming ability (Domenici 2003).

The most striking patterns of trait variation in large Nile perch were related to both the placement and size of the eye. Eyes of forest edge fish were situated closer to the dorsal midline and smaller in width. A growing number of studies have documented habitat-associated intraspecific variation in eye placement in fishes (Langerhans et al. 2004), that has been linked to divergent light conditions, the fish's position in the water column (Helland et al. 2007, Herler 2007), and differences in predator regime (Langerhans et al. 2004, Langerhans and DeWitt 2004). For example, fish from high predation habitats commonly display a relatively posterior, ventral position of the eye in comparison to predator-free populations (Langerhans et al. 2004), which may facilitate a wider range of vision and influence predator detection. Since it is unlikely that large Nile perch need be concerned with non-human predation, divergence in eye position may instead reflect divergent selection associated with differences in prey detection between the two environments (Langerhans et al. 2004). Divergence in eye size is also common within fish species. Large eyes may be adaptations to low light conditions by improving prey capture abilities in deeper or shadier regions of the lake (Helland et al. 2007). The larger eyes of Nile perch in wetland ecotones may increase hunting efficiency when searching for prey against a darker background that may characterize this habitat.

Implications of divergent trends

Habitat-associated divergence in morphology and colour in Nile perch across forest edge and wetland habitats fits well with established eco-morphological trends repeated across numerous fish species inhabiting regions of lakes that differ in structural complexity, dissolved oxygen concentration, and (possibly) light regime. The source of the observed phenotypic variation is unknown at present but may reflect genetic differences and/or phenotypic plasticity. The latter is more likely, particularly for colour patterns that converge in Nile perch of larger sizes. One might expect high rates of population mixing in this small lake that could buffer local adaptation and select for high levels of phenotypic plasticity; future common garden studies will be informative in addressing mechanisms contributing to trait variation in this population. Although we cannot be certain about the plastic or genetic basis of the divergence, documenting habitat-associated differences in Nile perch is an important step in understanding patterns of diversification that may be occurring, and how these differences might affect the ecosystem.

Nile perch plays an important ecological role in both their native and introduced range. In lakes of the Victoria basin where they have been introduced, they appear to exert considerable top-down control over some (but not all) other fish species that serve as their prey (Kaufman 1992, Witte et al. 1992, Kitchell et al. 1997, Schindler et al. 1998, Balirwa 2007). Divergence in foraging preferences of predators can have dramatic consequences on the dynamics of ecological communities (Schmitz and Suttle 2001). For example, Palkovaks and Post (2009) found that even in early stages of divergence phenotypic differentiation between anadromous and landlocked alewives led to divergence in zooplankton prey communities in experimental ponds. Ecological divergence of Nile perch is of concern from a biodiversity conservation perspective, as divergent selection may lead to Nile perch that are increasingly well adapted to wetland ecotones, which may compromise the effectiveness of these areas as refugia for native species in the region.

Conclusion

Results from this study provide evidence to suggest that divergent habitats in Lake Nabugabo may promote phenotypic divergence in Nile perch. Although the functional morphology of fish swimming, feeding, foraging, oxygen intake and camouflage suggests adaptive roles for morphological and colour differences in Nile perch, selection in nature is highly complex, and both body shape and colour are likely to be under the control of a number of competing factors. This is, however, the first study to empirically examine habitat-associated divergence of external morphology and colour patterns in Nile perch, and therefore a critical step towards outlining patterns of diversification in this species. To better evaluate the importance of divergent habitats in shaping the morphology and colour patterns of Nile perch I suggest 3 areas for future research. Future studies should 1. experimentally test links between morphology/colour, performance and fitness across alternative environments, 2. investigate whether similar patterns of divergence are found in other Nile perch populations where similar ecological gradients are encountered, and 3. conduct common garden rearing experiments to tease apart the plastic or genetic basis of these changes. Studies such as this can help to determine the nature of the phenotypic divergence, the degree to which shifts in distribution are encouraging this divergence, and whether the divergence is adaptive and likely to result in ecologically distinct components of the population.

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FIGURE CAPTIONS

Figure 1 – Diagram depicting a) landmark positions and b) linear measurements on Nile perch for morphological analysis. Panel A depicts positions used for geometric morphometric analyses. The 18 landmarks are: anterior tip of upper jaw (1), anterior edge of bony eye orbit where it meets the dorsal midline (2), posterior edge of bony eye orbit (3), indentation on dorsal profile of the anterior opercle flap (4), indentation at the posterodorsal end of head (5) origin of 1st ray of spiny dorsal fin (6) origin of 1st ray of soft dorsal fin (7), insertion of soft dorsal fin (8), origin of caudal fin membrane at dorsal midline (9), origin of caudal fin membrane at lateral line (10), origin of caudal fin membrane at ventral midline (11), insertion of anal fin (12), origin of anal fin (13), origin of pelvic fin (14), intersection of operculum edge with ventral midline (15), end of upper jaw (16), upper anterior insertion of pectoral fin (17), posterior margin of operculum (18). Panel B depicts linear measurements: jaw length (JL), eye width (EW), head length (HL) standard length (SL), anterior (a.) head depth (AHD), posterior (p.) head depth (PHD), anterior (a.) body depth (ABD), posterior (p.) body depth 2 (PBD), caudal length (CL), caudal width (CW), caudal fin length (CFL), posterior dorsal fin length (PDFL) and anal fin length (AFL). Total length (TL) is the sum of SL and CFL.

Figure 2 – Mean % brown pigment for size classes of Nile perch in two habitat types (forest edge and wetland ecotone) in Lake Nabugabo. Error bars represent standard errors.

Figure 3 – Morphological divergence in body shape for small Nile perch between wetland and forest edge habitat types. Symbols represent mean scores (with standard error). Thin plate spline transformations depict landmark configurations that correspond to the maximum and minimum scores for the habitat CV, with visualizations magnified 3x for ease of interpretation.

Figure 4 – Morphological divergence in body shape for large Nile perch between wetland and forest edge habitat types. Symbols represent mean scores (with standard error). Thin plate spline transformations depict landmark configurations that correspond to the maximum and minimum scores for the habitat CV, with visualizations magnified 3x for ease of interpretation.

Figure 5 – Morphological divergence in body shape for small Nile perch between wetland and forest edge habitat types along RW5 and RW6. Symbols represent least-squares means (with standard error). Thin plate spline transformations depict landmark configurations that correspond to the maximum and minimum scores for each RW.

Figure 6 – Morphological divergence in body shape for large Nile perch between wetland and forest edge habitat types along RW2 and RW5. Symbols represent least-squares means (with standard error). Thin plate spline transformations depict landmark configurations that correspond to the maximum and minimum scores for each RW.

TABLES

Table 1 – Analysis of differences between Nile perch in body size (TL, SL and W) and body colour (% brown) between two habitats (forest edge and wetland ecotones in Lake Nabugabo). *significance at the 0.05 level.

Grouping	Test	Variable	Z / t	P	df
All	Wilcoxon rank sum	TL	0.085	0.932	1, 111
	Wilcoxon rank sum	SL	-0.429	0.668	1, 111
	Wilcoxon rank sum	W	-0.363	0.716	1, 107
	Wilcoxon rank sum	% brown	-2.48	0.013	1, 111
Small	independent t-test	TL	-1.065	0.292	47
	independent t-test	SL	-0.426	0.672	49
	independent t-test	W	-0.353	0.725	44
	Wilcoxon rank sum	% brown	-3.677	<0.001*	1, 57
Large	independent t-test	TL	-0.221	0.825	53
	independent t-test	SL	0.581	0.563	53
	independent t-test	W	0.977	0.333	53
	independent t-test	% brown	-0.971	0.336	53

Table 2 – Results of MANCOVAs to detect differences in body shape for small and large size classes of Nile Perch between forest edge and wetland ecotone habitats in Lake Nabugabo. Dependent variables were partial warps (PWs) derived from geometric morphometric analyses of 18 landmarks.

Size class	Source of variation	F	d.f.	P	Partial Eta squared
Small	Habitat	1.912	32,75	0.011	0.449
	Centroid size	13.735	32,75	<0.0001	0.814
	Gape	10.236	32,75	<0.0001	0.854
Large	Habitat	3.536	32, 65	<0.0001	0.635
	Centroid size	8.173	32, 65	<0.0001	0.873
	Gape	13.964	32, 65	<0.0001	0.801

Table 3 – Results of ANCOVAs to detect differences in body shape of small (left) and large (right) size classes of Nile perch between forest edge and wetland ecotone habitats in Lake Nabugabo as represented by the first six relative warps (RWs). Relative warps were derived from geometric morphometric analyses of 18 landmarks.

	SMALL				**LARGE**			
Source of variation	**d.f.**	**F**	**P**	**partial Eta squared**	**d.f.**	**F**	**P**	**partial Eta squared**
RW1								
Habitat	1	0.643	0.425	0.006	1	0.296	0.588	0.003
Centroid size	1	**63.55**	**<0.0001**	**0.375**	1	17.515	<0.0001	0.154
Gape	1	34.131	<0.0001	0.244	1	**40.517**	**<0.0001**	**0.297**
RW2								
Habitat	1	0.146	0.703	0.001	1	**8.667**	**0.004**	**0.083**
Centroid size	1	**18.539**	**<0.0001**	**0.149**	1	33.311	<0.0001	0.258
Gape	1	3.829	0.053	0.035	1	19.936	<0.0001	0.172
RW3								
Habitat	1	0.01	0.921	<0.0001	1	0.071	0.79	0.001
Centroid size	1	1.283	0.26	0.012	1	**17.559**	**<0.0001**	**0.155**
Gape	1	**6.816**	**0.01**	**0.06**	1	3.261	0.074	0.033
RW4								
Habitat	1	1.393	0.241	0.013	1	0.112	0.738	0.001
Centroid size	1	0.038	0.846	<0.0001	1	5.069	0.027	0.05
Gape	1	**5.258**	**0.024**	**0.047**	1	**7.684**	**0.007**	**0.074**
RW5								
Habitat	1	**7.467**	**0.007**	**0.128**	1	**3.799**	**0.05**	**0.038**
Centroid size	1	0.136	0.713	0.001	1	0.832	0.364	0.009
Gape	1	7.542	0.007	0.066	1	5.466	0.021	0.054
RW6								
Habitat	1	**15.608**	**<0.0001**	**0.066**	1	0.36	0.55	0.004
Centroid size	1	3.406	0.068	0.031	1	**13.252**	**<0.0001**	**0.121**
Gape	1	8.538	0.004	0.075	1	0.129	0.72	0.001

Table 4 – Results of MANCOVAs to detect differences in body shape of small and large size classes of Nile perch between forest edge and wetland ecotone habitats of Lake Nabugabo. Dependent variables included 13 linear measurements (see Fig. 1 for details of linear metrics).

Size class	Source of variation	F	d.f.	P	Partial Eta squared
Small	habitat	3.06	12, 95	0.001	0.279
	standard length	573.85	12, 95	<0.0001	0.986
Large	habitat	2.27	12, 86	0.018	0.235
	standard length	1059.09	12, 86	<0.0001	0.997

Table 5 – Results of ANCOVAs to detect differences in linear measurements related to body shape of large and small Nile perch between forest edge and wetland ecotones habitats of Lake Nabugabo. *significant at the 0.05 level.

Size	Traits	F (sd)	W (sd)	p
Small	anal fin length (AFL)	0.208 (0.075)	0.142 (0.102)	0.017*
	a. body depth (ABD)	0.608 (0.071)	0.561 (0.079)	0.100
	p. body depth (PBD)	0.532 (0.068)	0.489 (0.080)	0.579
	caudal depth (CD)	0.153 (0.068)	0.115 (0.082)	0.607
	caudal fin length (CFL)	0.328 (0.069)	0.285 (0.087)	0.620
	caudal length (CL)	0.649 (0.066)	0.610 (0.080)	0.812
	p. dorsal Fin length (PDFL)	0.337 (0.074)	0.267 (0.093)	0.001*
	eye width (EW)	0.046 (0.047)	0.032 (0.056)	0.721
	a. head depth (AHD)	0.371 (0.046)	0.338 (0.057)	0.083
	p. head depth (PHD)	0.542 (0.065)	0.495 (0.072)	0.003*
	head length (HL)	0.666 (0.055)	0.636 (0.072)	0.394
	jaw length (JL)	0.271 (0.058)	0.230 (0.066)	0.064
Large	anal fin length (AFL)	0.681 (0.084)	0.702 (0.132)	0.584
	a. body depth (ABD)	1.060 (0.094)	1.079 (0.127)	0.288
	p. body depth (PBD)	1.010 (0.091)	1.028 (0.129)	0.570
	caudal depth (CD)	0.640 (0.084)	0.652 (0.126)	0.100
	caudal fin length (CFL)	0.797 (0.075)	0.824 (0.110)	0.055
	caudal length (CL)	1.125 (0.085)	1.143 (0.119)	0.265
	p. dorsal Fin length (PDFL)	0.818 (0.093)	0.845 (0.132)	0.171
	eye width (EW)	0.171 (0.058)	0.220 (0.063)	0.001*
	a. head depth (AHD)	0.716 (0.090)	0.729 (0.093)	0.813
	p. head depth (PHD)	0.959 (0.088)	0.978 (0.120)	0.281
	head length (HL)	1.073 (0.094)	1.091 (0.114)	0.140
	jaw length (JL)	0.643 (0.092)	0.675 (0.111)	0.037*

FIGURES

Figure 1

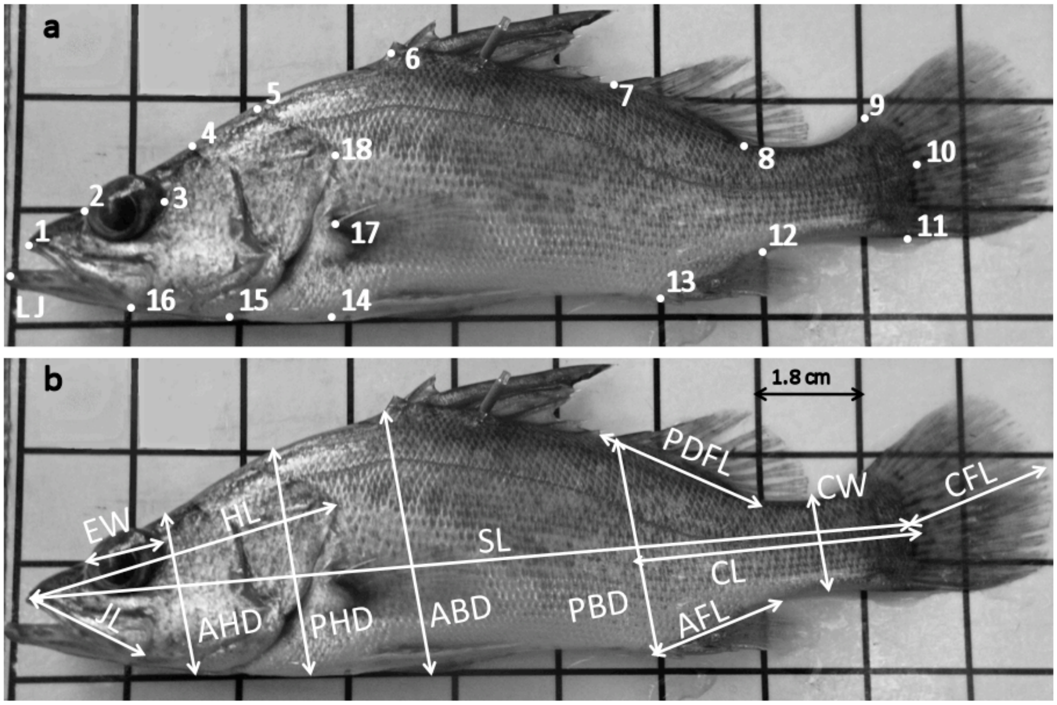


Figure 2

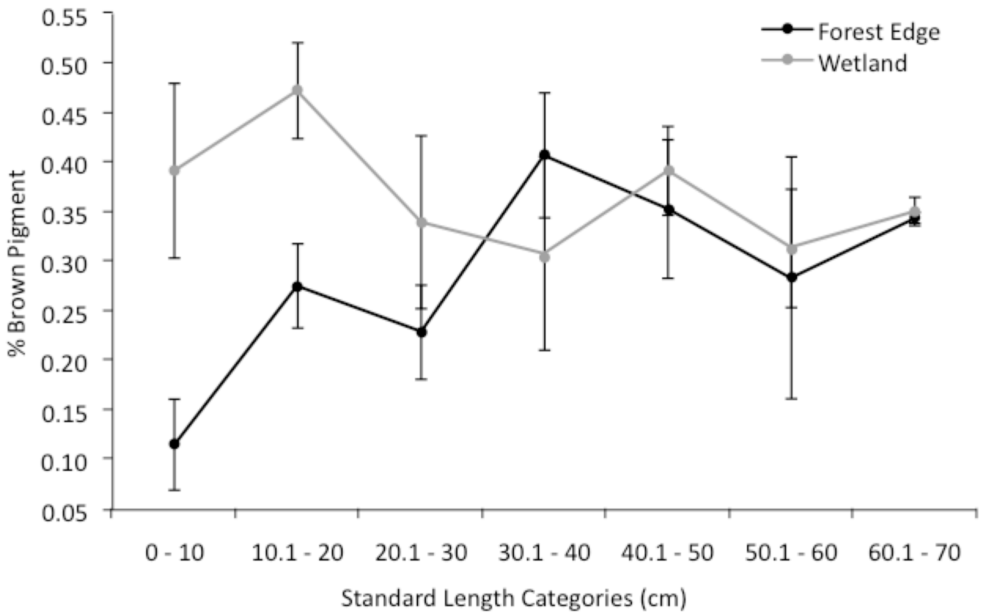

Forest Edge
Wetland
% Brown Pigment
0.55
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0 - 10
10.1 - 20
20.1 - 30
30.1 - 40
40.1 - 50
50.1 - 60
60.1 - 70
Standard Length Categories (cm)

Figure 3

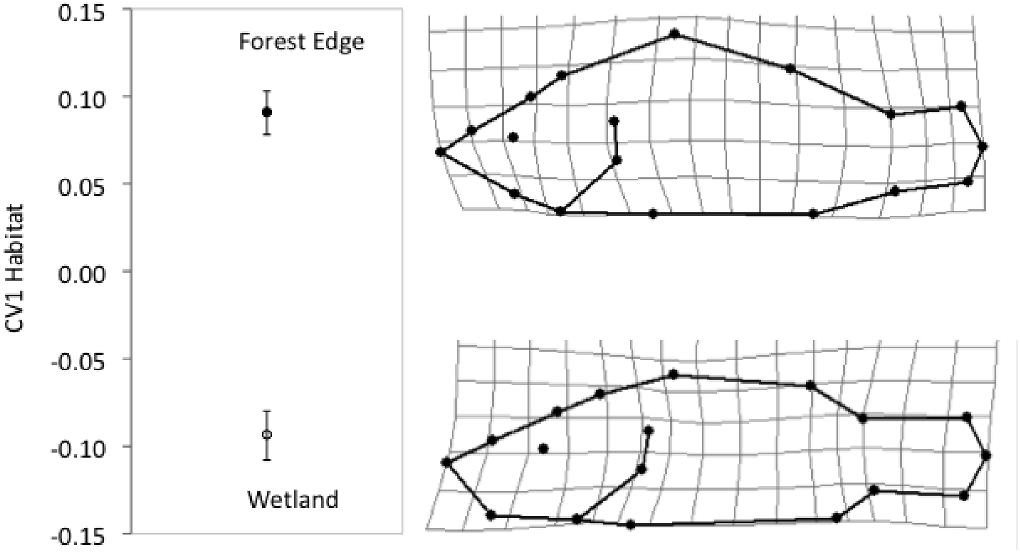


Figure 4

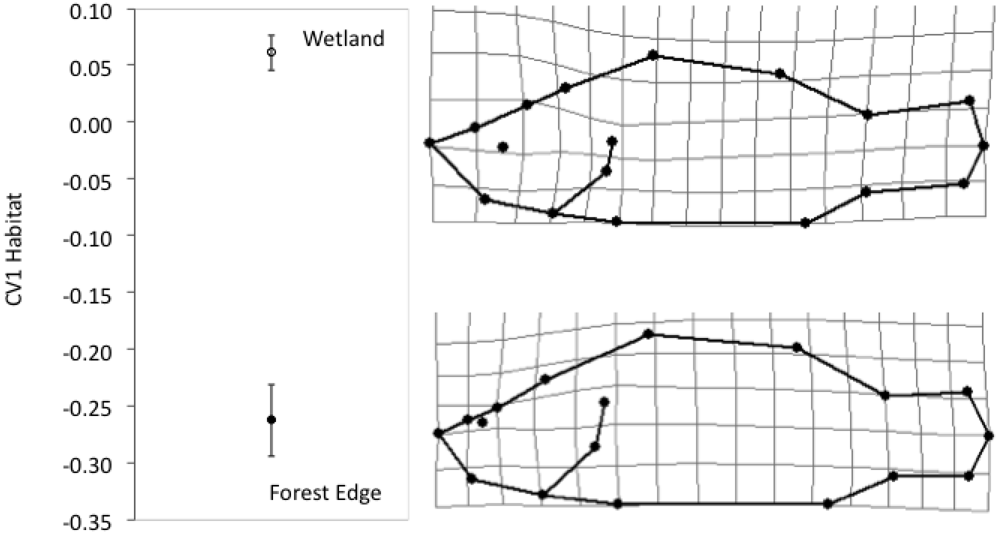

0.10
0.05
0.00
-0.05
-0.10
-0.15
-0.20
-0.25
-0.30
-0.35
CV1 Habitat
Wetland
Forest Edge

Figure 5

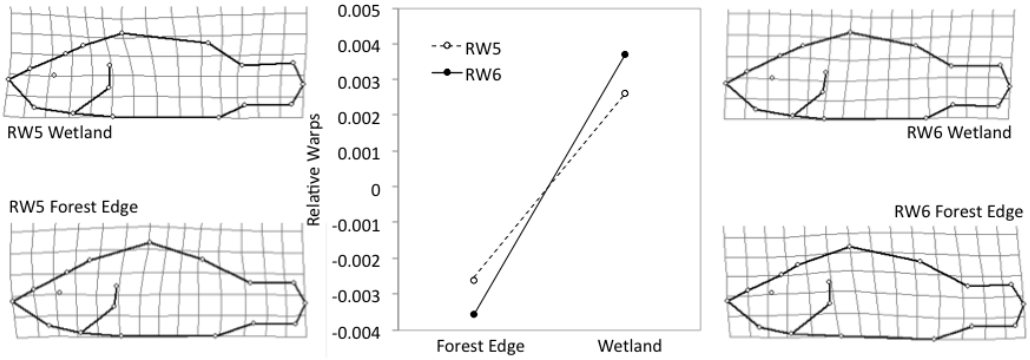
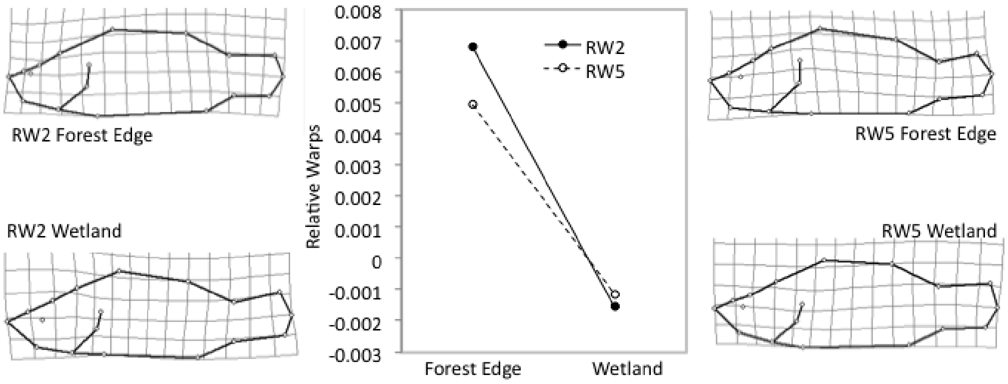

RW5 Wetland
RW5 Forest Edge
0.005
0.004
0.003
0.002
0.001
0
-0.001
-0.002
-0.003
-0.004
Relative Warps
RW5
RW6
Forest Edge
Wetland
RW6 Wetland
RW6 Forest Edge

Figure 6


RW2 Forest Edge
RW2 Wetland
RW5 Forest Edge
RW5 Wetland
Relative Warps
0.008
0.007
0.006
0.005
0.004
0.003
0.002
0.001
0
-0.001
-0.002
-0.003
Forest Edge
Wetland
RW2
RW5

APPENDIX A

Figure A.1 – A representative image of a large Nile perch specimen cut out in preparation for colour analysis.

Figure A.2— Representative examples of small dark (a) and light (b) Nile perch morphs from wetland and forest edge habitats in Lake Nabugabo.

a

b

General Conclusion

Humans rely heavily on inland aquatic resources, and are responsible for major changes in these ecosystems through deterioration of water quality, introduction of invasive species, and overharvesting of fishes, all of which contribute to alteration of food web structure and loss of biodiversity (Welcomme et al. 2010, Cooke et al. 2011). Tropical inland fisheries are some of the most important and highly threatened resources in the world, yet they have received little attention relative to temperate marine systems, and many are still effectively managed as open access resources. This thesis provides important and novel ecological information on Nile perch (*Lates niloticus* L.), a commercially fished and economically important species in a large tropical freshwater fishery. Nile perch was introduced to the Lake Victoria basin in the 1950s and 1960s and eventually became one of the most valuable commercial species of East Africa's inland fisheries (Balirwa et al. 2003). Intense fishing-induced mortality may be contributing to dramatic ecological change in this species (reductions in body size and catch rate) and reinforcing patterns of ecological divergence in some lakes in the region (Balirwa et al. 2003, Matsuishi et al. 2006, Paterson and Chapman 2009, Paterson et al. 2010). In this thesis I quantified Nile perch movement patterns and habitat selection, and explored patterns of habitat-associated phenotypic divergence between wetland and forest edge habitats in Lake Nabugabo.

In the first chapter I used radio telemetry to characterize Nile perch movement and home range size in Lake Nabugabo, Uganda, and quantified patterns of habitat selection by Nile perch in the heavily fished inshore areas of this system. Nile perch exhibited high site tenacity with daily movement averaging ~400 m/day and home range size averaging 0.83 km^2. Body size and water temperature were both important predictors of Nile perch movement patterns. In the near-shore area of the lake, Nile perch selected regions characterized by low temperature and high oxygen conditions, and tended to prefer forest edge to wetland ecotones. The level of site tenacity exhibited by Nile perch suggests that ecological isolation between fish using forest and wetland ecotones may be higher than expected. These results also have important implications for development of territorial jurisdiction by Beach Management Units, the decentralized structure of fisheries management in the region. Knowledge of the spatial dynamics of this species is needed to improve our ability to predict changes in stocks and to initiate effective management strategies (Mason and Lowe 2010). In recent years, efforts have been made to improve fisheries management in the Lake Victoria basin by shifting responsibilities away from a central governing body to individual fishing communities through the creation of locally regulated beach management units (BMUs) (Nunan 2006, vanderKnaap and Ligtvoet 2010). One of the major challenges in implementing BMUs is in defining boundaries that are both socially and biologically meaningful (Allison and Ellis 2001). Understanding the distribution and mobility of key fished species in the lake is therefore of utmost importance to the development of territorial jurisdiction in the BMUs of the Lake Victoria basin.

In the second chapter I used geometric morphometric and colour analyses to quantify patterns of phenotypic divergence across size classes in Nile perch from ecologically distinct wetland and forest edge habitats in Lake Nabugabo. Nile perch exhibited significant morphological and colour differences between habitats, but not all trends were consistent across size classes. Whether or not the variation in body shape and colour is adaptive is unknown; however, observed patterns of trait divergence are consistent with hypotheses for adaptive variation. Small Nile perch captured near wetland ecotones had much darker skin pigmentation than those from forest edge that may reflect camouflage strategies associated with divergent light regimes and background coloration. Divergence in body shape was relatively similar between large and small Nile perch and consistent with eco-morphological patterns commonly observed to facilitate performance for fish inhabiting complex vs. simple habitat types. Nile perch from forest edge ecotones displayed fusiform streamlined body shape for sustained swimming in open waters while those from wetlands had more developed caudal region for high maneuverability and fast burst swimming. There was also evidence for enlarged heads for small fish in wetland ecotones, which could be due to indirect effects of low oxygen concentration as head shape often co-varies with gill size. Given that some aspects of trait divergence, particularly colour, did not persist across size classes, it is likely that observed diversification in these traits has a strong element of phenotypic plasticity. However, the fact that some patterns of trait divergence were consistent between small and large Nile perch, and the site-tenacious nature of Nile perch movement patterns suggest the possibility of genetic differentiation. There are numerous examples of natural populations of fish species undergoing sympatric ecological divergence (Endler 1986, Schluter 2000, Kawecki and Ebert 2004, Bolnick and Fitzpatrick 2007), and in some cases speciation (Schluter 2000, Rundle and Nosil 2005), in divergent environments. The demonstration of habitat-associated divergence in Nile perch has implications for biodiversity conservation in lakes with introduced Nile perch. If fishing pressure is selecting for an increasingly wetland adapted Nile perch, the ecotonal wetlands may become more limited in their role as effective habitat refugia for native prey from Nile perch predation. Furthermore, knowledge of adaptive responses of aquatic organisms to environmental change is important for stock management. Since anthropogenic stressors continue to disturb the inland waters of the Lake Victoria basin, management strategies should adjust to these changes (Kaufman and Schwartz 1992, Kaufman et al. 1997). It is therefore very important to continue monitoring the ecological and evolutionary responses of Nile perch to a continuously changing environment.

Future studies should explore Nile perch movement patterns in bays of Lake Victoria to determine whether individuals in a larger system with greater habitat heterogeneity have similarly restricted movement patterns. In terms of ecological divergence, future studies should experimentally test links between morphology/colour, performance and fitness across alternative environments, investigate whether similar patterns of divergence are found in other Nile perch populations, and conduct common garden rearing experiments to tease apart the plastic or genetic basis of these changes. Studies such as this can help to determine the consistency of these findings across greater spatial and temporal scales, and can provide insight into the nature of the phenotypic divergence, the degree to which shifts in distribution are encouraging this divergence, and whether the divergence is adaptive and likely to result in ecologically distinct components of the population.

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