Phenotypic response to anthropogenic stressors in the African cyprinid *Rastrineobola argentea*

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To my loving parents, and my “little ones,” Ian and Victoria

Abstract

Humans are now undoubtedly a potent evolutionary force, yet we still know relatively little about the extent and potential consequences of human-induced phenotype change in nature. My doctoral research explores phenotypic responses to two stressors that constitute major threats to freshwater communities worldwide: fishing and the introduction of non-native species. In a quantitative review, I find that fishing appears to be a ubiquitous driver of contemporary life history change in commercial fish stocks, and is significantly associated with declining size and age at maturity in the majority of global stocks for which long-term phenotypic data are available. For the remainder of the dissertation, I focus on *Rastrineobola argentea*, a commercially-important cyprinid fish endemic to the Lake Victoria basin (East Africa) that has been subject to multiple anthropogenic stressors over the past half century, yet still thrives in Lake Victoria. In each chapter, I exploit spatial and temporal variation in the presence of fishing and an introduced predator (the Nile perch, *Lates niloticus*) to test for phenotypic responses to these two stressors. My first major finding is that *R. argentea* populations that had been subjected to fishing and Nile perch predation generally show reductions in mean body size and length at maturity, and increases in size-specific reproductive investment, relative to unperturbed populations. These trends are consistent with global patterns of fisheries-induced change, and also with predictions from life history theory. Second, I find some evidence that the Nile perch may also have driven changes in overall body morphology, in a direction that would be expected to improve burst swimming ability, although these effects are subtle, and context-dependent. Third, I find some evidence for cascading effects of the Nile perch introduction on the diet and trophic morphology of *R. argentea* through time, but not across space. Taken together, my results suggest that contemporary phenotypic change has likely played an important role in *R. argentea's* persistence in the face of multiple stressors in Lake Victoria. The rate and direction of change in life history traits; however, raises concerns for the sustainability of the *R. argentea* fishery, now the most important (by mass) in Lake Victoria. This work provides critical insights for

management of the *R. argentea* stock in Lake Victoria, and also broadens our understanding of global patterns of human-induced phenotypic change.

Résumé

Alors qu'il est désormais clair que les activités humaines soient une force évolutive importante, on ne sait toujours que relativement peu de la généralité et des conséquences potentielles des changements phénotypiques de nature anthropogène. Ma recherche de doctorat explore les changements phénotypiques associés à deux perturbations anthropiques qui menacent fortement les communautés aquatiques dans le monde entier: la pêche et l'introduction d'espèces exotiques. Dans une revue de littérature quantitative, je montre d'abord que la pêche est une cause commune de changement contemporain dans les traits d'histoire de vie des populations de poissons exploitées commercialement: la pêche est significativement associée à une réduction de la taille et de l'âge à la maturité au sein des stocks globaux pour lesquels des données phénotypiques à long terme sont disponibles. Pour le reste de ma thèse, je me concentre sur *Rastrineobola argentea,* un poisson cyprinidé commercialement important et endémique au basin du lac Victoria, en Afrique de l'Est. *R. argentea,* bien que toujours abondant dans le Lac Victoria, a été soumis à de multiples perturbations anthropiques au cours du dernier demi-siècle. Dans chaque chapitre, j'utilise la variation spatiale et temporelle dans l'intensité de pêche et la présence d'un prédateur introduit (la perche du Nil, *Lates niloticus*) pour mettre en évidence des réponses phénotypiques à ces deux perturbations. Mon premier résultat principal est que les populations de *R. argentea* qui ont été soumises à la pêche et à la prédation par la perche du Nil montrent une réduction de la taille et de la taille à la maturité et une augmentation de l'effort reproducteur relatif. Ces résultats sont en accord autant avec les changements phénotypiques mondiaux associés à la pêche commerciale qu'avec les prédictions de la théorie des traits d'histoire de vie. Deuxièmement, je montre des résultats qui suggèrent que la perche du Nil ait aussi causé des changements dans la morphologie générale de *R. argentea*. Ces changements vont dans la direction prévue car ils pourraient améliorer l'habileté de *R. argentea* à nager rapidement; par contre, ces effets sont subtils et dépendent du contexte. Finalement, j'obtiens des résultats montrant un effet indirect de l'introduction de la perche du Nil sur le régime alimentaire et la morphologie

trophique de *R. argentea* à travers le temps (mais pas à travers l'espace). Ensemble, ces résultats suggèrent que les changements phénotypiques contemporains aient joué un rôle important pour la persistance de *R. argentea* dans le Lac Victoria en dépit de multiples perturbations anthropiques. Par contre, la magnitude et la direction des changements dans les traits d'histoire de vie sont inquiétantes pour la durabilité de la pêcherie de *R. argentea*, maintenant la plus considérable de la région. Cette thèse arrive à des conclusions importantes à la fois pour la gestion de la pêche de *R. argentea* dans le lac Victoria que pour notre compréhension des patrons mondiaux de changement phénotypique anthropogène.

Table of Contents

List of Tables

List of Figures

List of Appendices

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argentea in Tanzania in the 1980s was an important source of inspiration for this work.

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Contribution of authors

This dissertation consists of four manuscripts, which are either published (Chapters 1 and 2), or in preparation for submission (Chapters 3 and 4). As the primary author on all chapters, I developed the research questions, conceived and executed the experimental design, collected the majority of the data, carried out the statistical analyses, and wrote the main draft of each manuscript. My advisor, Dr. Lauren Chapman, has contributed greatly to the dissertation, by assisting with the development of research questions and experimental design, analysis of data, interpretation of results, and making improvements to the manuscripts. A number of other collaborators have made important contributions to particular chapters, and these are detailed below.

Chapter 1 developed out of a paper that I wrote for Andrew Hendry's graduate-level course, Advanced Evolutionary Ecology (BIOL 594) in the fall of 2007. Andrew guided me in the development of this paper, and encouraged me to pursue it beyond the course by participating in an invited symposium on fisheries-induced evolution at the American Fisheries Society Meeting in the summer 2008, which then led to an invitation to refine the work into an article to be included in a Special Issue of Evolutionary Applications on fisheries-induced evolution in 2009. This meta-analysis served as an important foundation for the other chapters of the dissertation.

Chapter 2 benefited greatly from the collaboration of Mr. S.B. Wandera, a senior scientist at the National Fisheries Resources Research Institute (NaFIRRI) in Uganda. Mr. Wandera contributed unpublished data on *R. argentea* from the early 1990s, which allowed us to make key historical comparisons. Mr. Wandera also shared a wealth of knowledge about the natural history and biology of *R. argentea* that helped guide us in the interpretations of our results.

Chapter 3 developed out of a pilot study conducted by Dr. Lauren Chapman, Dr. Brian Langerhans and Etienne Low-Décarie in 2007. At that time, Lauren and Brian analyzed some preliminary photographs from the museum collections in Uganda, while Etienne digitized these photographs and conducted a preliminary analysis. When I expanded on the pilot study in 2011 (by adding additional historical populations and a new spatial comparison), all three co-authors assisted with advice and feedback on the statistical analysis and manuscript.

Chapter 4 was done in collaboration with Dr. Lauren Chapman, who assisted with the sampling design, analysis and interpretation of the data, and writing.

Original contributions to knowledge

In Chapter 1, I reviewed published studies of life history changes in commercial fish stocks, and showed that, across a large number of stocks, rates of phenotypic change in two key life history traits were significantly correlated with the intensity of fishing. This study is the first to quantitatively relate rates of phenotypic change to rates of fishing mortality, and to test for statistical relationships between them. In doing so, I provide strong empirical support for the hypothesis that fishing is a major driver of contemporary life history change in commercial fish stocks.

In Chapter 2, I tested for the effects of fishing and the presence of an introduced predator (Nile perch) on life history traits in *R. argentea*. This study provides the first empirical evidence of fisheries-induced phenotypic change in *R. argentea*, and is (to my knowledge) the first published example of fisheries-induced change in a tropical, freshwater fish stock. This is also one of the first studies to detect life history changes in a fish stock that is harvested using relatively unselective gears. This provides empirical support for the view (Abrams and Rowe 1996) that high levels of mortality (regardless of selectively) can drive life history change.

In Chapter 3, I tested whether the introduction of the Nile perch was associated with changes in the overall body morphology of *R. argentea*. This study is the first to examine body shape variation in *R. argentea.* It also provides one of only a few known examples of contemporary morphological change in a native prey species in response to an introduced predator, as well as an important empirical test of existing eco-morphological predictions in a taxonomically and geographically distinct taxon.

In Chapter 4, I tested for cascading effects of the Nile perch introduction on the diet and trophic morphology of *R. argentea*. This is the first in-depth study of niche width and individual specialization in *R. argentea*, as well as the first study to quantitatively link variation in diet and trophic morphology in this species. More generally, this is one of the first studies to examine the *indirect* phenotypic consequences of an introduced predator on native prey, and to test predictions of the Niche Variation Hypothesis (Van Valen 1965) in the context of a biological invasion. This study clearly demonstrates how biological invasions can be used to empirically test long-standing theoretical questions in ecology in a novel way.

In summary, this thesis significantly advances our knowledge of the ecology, morphology, and reproductive biology of *R. argentea* in Lake Victoria, a species which has been relatively under-studied to-date despite its considerable socio-economic importance. My findings provide specific insights for the management of the *R. argentea* fishery, which we have shared with colleagues and managers in Uganda. More broadly, as detailed above, this work makes a number of novel contributions to our understanding of the phenotypic impacts of fishing and introduced species, and provides a framework for integrating ecological and evolutionary theory with fisheries management and conservation biology.

Animal ethics

Field collections of fish were carried out in compliance with McGill University’s animal care policies (Animal Use Protocol No. 5029). Permission to conduct research in Uganda was granted by the Uganda National Council for Science and Technology and the Office of the President, and permission to export samples from Uganda was granted by the Ugandan Commissioner for Fisheries.

0 General introduction

Human impacts on the Earth's ecosystems are pervasive and accelerating: from large-scale land use change and alterations to the major biogeochemical cycles that control the climate, to over-harvesting and homogenization of the planet's biota through species introductions (Vitousek et al. 1997). One of the most alarming consequences of these myriad anthropogenic stressors has been the loss of biodiversity on a global scale. Current extinction rates for various taxa are estimated to be 100-1000 times higher than background levels from the fossil record (Pimm et al. 1995), with the greatest losses occurring in tropical rainforests (Reid 1997) and in freshwater ecosystems (Ricciardi and Rasmussen 1999). A more subtle consequence of global anthropogenic change, and one which has only recently begun to be appreciated, is that human activities can also impose very strong selection on natural populations. This selection can in turn drive phenotypic and/or evolutionary changes, often on contemporary time-scales, i.e. in less than a few centuries (Reznick and Ghalambor 2001; Stockwell et al. 2003; Hendry et al. 2008). Palumbi (2001) has gone so far as to argue that humans may now be "the world's dominant evolutionary force." Indeed, the most rapid known rates of contemporary phenotypic change have been associated with anthropogenic perturbations (Hendry et al. 2008), and in harvested populations (Darimont et al. 2009). Studying phenotypic responses to anthropogenic stressors can provide important insights on several fronts. First, these contexts provide a rare opportunity to observe evolutionary processes on contemporary time scales in nature, and thereby test basic questions in evolutionary ecology in more direct and powerful ways. Second, from a conservation and natural resource management perspective, understanding the rate, limits, and ubiquity of adaptive phenotypic responses is essential for predicting species' persistence in the face of continuing anthropogenic disturbance.

My doctoral research explores patterns of contemporary ecological and phenotypic change in *Rastrineobola argentea*, a commercially-important cyprinid fish endemic to the Lake Victoria basin, in East Africa. I focus on detecting responses to two stressors that constitute major threats to freshwater communities worldwide (fishing and the introduction of non-native species), and then test whether these stressors have driven changes in the life history (Chapter 2), body morphology (Chapter 3), and/or trophic ecology and morphology (Chatper 4) of *R. argentea*. Below, I briefly review our current state of knowledge on the phenotypic/evolutionary consequences of fishing and biological invasions, before outlining how the Lake Victoria ecosystem provides a fitting "natural laboratory" in which to explore these questions.

0.1 Fishing: a "massive uncontrolled experiment in evolutionary selection"

Fishing can drastically reduce the abundance of targeted species, and can also alter the structure and functioning of entire aquatic communities. This has been particularly well-documented in the marine realm, where approximately half of fish stocks are now fully exploited, and another 32% are over-exploited, depleted or recovering (FAO 2010). Population declines in marine fishes have been widespread (Hutchings and Baum 2005), sometimes leading to complete fisheries collapses, as in the case of Newfoundland's Atlantic cod (*Gadhus morhua)* stocks (Hutchings and Myers 1994). It is estimated that industrial fishing has reduced the biomass of large, predatory marine fishes to less than 10% of pre-exploitation levels (Myers and Worm 2003), resulting in the profound alteration of many coastal ecosystems over the past centuries (Jackson et al. 2001). Data from inland fisheries are much scarcer, but the available evidence indicates that, in general, freshwater fisheries in Asia and Africa are already fully exploited, with fishing driving significant population and community-level ecological changes (Welcomme et al. 2010).

As early as the 1950s, fisheries biologists began to speculate that fishing might also be selecting for phenotypic changes in exploited fish populations (Miller 1957; Borisov 1978; Ricker 1981; Law and Grey 1989; Stokes et al. 1993). In particular, it was thought that fishing could lead to changes in life history traits, such as age and size at maturation, because these traits are especially sensitive to altered mortality schedules (Stearns 1992). The study of *fisheries-induced evolution* has emerged as an important new research area over the past 10-15 years, with several goals, including: (i) documenting the prevalence, rates, and underlying mechanisms of contemporary phenotypic changes in commercial fish stocks; (ii) using fisheries as a model to test basic evolutionary questions about life history evolution, and (iii) understanding how contemporary trait changes will influence fisheries yield and the long-term sustainability of stocks.

With respect to the first goal, there has been growing interest in understanding whether life history changes in commercial fish stocks may be restricted to a few heavily-exploited populations, or are a more general phenomenon. Similarly, there is interest in determining which types of traits are most likely to evolve (Heino and Godo 2002), at what rate (Jørgensen et al. 2007; Darimont et al. 2009; Sharpe and Hendry 2009; Devine et al. 2012), and under what type of selective regime (Law and Grey 1989; Ernande et al. 2004). Finally, there is considerable debate over the extent to which observed phenotypic changes may reflect genetic change (evolution), phenotypic plasticity, or some combination of the two; and how to best to disentangle these sources of phenotypic variation (Heino and Dieckmann 2008).

With respect to the second goal, life history theory seeks to understand the fundamental trade-offs between survival and reproduction that determine the timing of, and allocation to, reproductive events in an organisms' life cycle (Stearns 1992). One question of particular theoretical interest within this field has been how alterations to the mortality regime affect reproductive timing and allocation (Gadgil and Bossert 1970; Law 1979; Michod 1979). This question has been successfully explored empirically both in laboratory experiments (e.g., in *Dapnia pulex*, Spitze 1991), and in natural populations experiencing different levels of predation (e.g., in Trinidadian guppies, *Poecilia reticulata,* Reznick and Endler 1982). Fisheries provide another promising avenue for empirical tests, because fishing mortality is intense (often 2 to 3 times greater than natural mortality), and usually highly selective (Stokes and Law 2000). Fishing has thus been aptly described as a "massive uncontrolled experiment in evolutionary selection" (Stokes and Law 2000), and a "world-wide experiment in life history evolution" (Law 2000)

With respect to the third goal, fisheries biologists have traditionally been concerned with managing fish stocks based on demographic indicators such as stock biomass, recruitment, and mortality. However, the awareness that life history traits can evolve rapidly in commercially-exploited fish stocks – sometimes in only a few decades – has prompted research into the extent to which fisheries-induced evolution may impact yields (Edley and Law 1988; Heino 1998), population fitness (Walsh et al. 2006), and the potential for recovery after over-fishing (Hutchings 2005; Conover et al. 2009; Enberg et al. 2009; Kuparinen and Hutchings 2012).

0.2 Biological invasions: replicated, unplanned natural experiments in adaptation

Human-mediated biological invasions have increased by several orders of magnitude over the past few centuries, to the extent that few places on Earth now remain free of introduced species (Mack et al. 2000). Freshwater ecosystems have been particularly heavily invaded (Hall and Mills 2000; Strayer 2010); for example, there are hundreds of non-native species in Laurentian Great Lakes alone (Ricciardi 2006). Although many non-native species fail to establish or have little or no impact on local communities, those that do become invasive often cause serious and irreversible ecological damage. Invasive species are widely believed to one of the major drivers of contemporary global biodiversity loss, second only to habitat destruction (Wilcove et al. 1998; Sala et al. 2000; Clavero and Garciá 2005; but see Gurevitch and Padilla 2004). Some of the greatest losses in native biodiversity have been due to predator introductions: for example, the introduction of mammalian predators has led to widespread extinctions of birds across hundreds of oceanic islands (Steadman 1995; Blackburn et al. 2004). However, invasive species may also affect natives in a variety of other ways, including via competitive exclusion (e.g., in whitefish, Bøhn et al., 2007), habitat modification (e.g., zebra mussels, MacIsaac, 1996), hybridization (e.g., rainbow trout, Vitule et al. 2009) or as vectors or disease (e.g., Dutch elm disease, Brasier 2001).

Like fishing, biological invasions can also be a potent form of novel selection. There is growing interest in understanding the extent to which selection pressures induced directly or indirectly by invasive species may be driving plastic and/or evolutionary changes in native species (Mooney and Cleland 2001; Strauss et al. 2006; Carroll 2007). For example, native prey may adapt to introduced predators via the adoption of novel predator-avoidance behaviours (e.g., Kiesecker and Blaustein 1997; Losos et al. 2004), the evolution of morphological defences (e.g., Vermeij 1982), and/or altered life history tactics (e.g., Fisk et al. 2007). Native consumers may adapt to novel resources provided by invasive species: for example, Australian soapberry bugs have evolved longer mouthparts that allow them to consume the fruits of exotic balloon vines (Carroll et al. 2005).

Understanding the extent to which native species may be able to rapidly adapt to novel threats from invasive species (e.g., predation) is of clear conservation importance. This is especially true in closed ecosystems like lakes, where native species can rarely migrate away from a novel threat, and instead must adapt *in-situ*, or go extinct. Biological invasions also provide rich ground for testing new and existing theory in ecology and evolution. In many instances, introductions provide replicated natural experiments on large spatial scales, allowing for more direct deduction of causal relationships, and for the observation of processes, such as adaptation, that might naturally occur over much longer time scales (Sax et al. 2007).

0.3 Rastrineobola argentea in Lake Victoria: a case study for understanding phenotypic responses to anthropogenic stressors

My dissertation explores both direct and indirect phenotypic responses to fishing and introduced species, using *Rastrineobola argentea*, a resilient fish native to the Lake Victoria basin of East Africa, as a case study. Lake Victoria is the largest tropical lake in the world, and Africa’s most important source of inland fisheries production, supporting an estimated 22 million people in the three riparian states that share its waters: Kenya, Uganda, and Tanzania (LVFO 2011). Lake Victoria provides an excellent opportunity to explore the effects of anthropogenic stressors, as it has undergone dramatic ecological changes over the past century associated with overfishing of commercially important indigenous species, habitat degradation, eutrophication, and species introductions (reviewd in Kaufman 1992; Balirwa et al. 2003; Chapman et al. 2008). During the first half of the 20th century, the development of railways and urban centres, the introduction of synthetic gill nets, and the progressive use of increasingly smaller mesh sizes led to the rapid depletion of Lake Victoria's most important native fisheries, including those of the tilapiines *Oreochromis esculentus* and *O. variabilis*, the African lungfish *Protopterus aethiopicus*, and the migratory cyprinid *Labeo victorianus* (Ogutu-Ohwayo 1990; Balirwa et al. 2003). To supplement these declining catches, a series of non-native fishes were introduced in the 1950s and 60s, including four species of tilapias, and the large, predatory Nile perch, *Lates niloticus* (Pringle 2005). Concurrently, rapid increases in the human population in the catchment led to eutrophication, algal blooms, and increasing frequency of hypolimnetic hypoxia and anoxia (Ochumba and Kibaara 1989; Verschuren et al. 2002; Hecky et al. 1994; 2010). This combination of stressors resulted in the extinction or extirpation of hundreds of indigenous fish species in the mid to late 1980s, including approximately 40% of the 500+ haplochromine cichlids endemic to Lake Victoria (Witte et al. 1992; Kaufman and Ochumba 1993; Seehausen et al. 1997). Many other native species also suffered further declines during this period, including the African lungfish, *P. aethiopicus* (Goudswaard et al. 2002), the native tilapiines *O. variabilis* and *O. esculentus* (Goudswaard et al. 2002), and several native catfishes, including *Bagrus docmak, Clarias gariepinus, Synodontis afrofischeri,* and *Synodontis victoriae* (Goudswaard and Witte 1997). As a result, a once diverse and complex community of over 500 species was replaced by a much simpler community dominated by only three species: the native cyprinid *Rastrineobola argentea,* and the introduced Nile perch and Nile tilapia, *Oreochromis niloticus*. Similar patterns of biodiversity loss following overfishing and species introductions have been documented in other lakes in the region, including lakes Kyoga (Mbabazi et al. 2004; Schwartz et al. 2006), and Nabugabo (Ogutu-Ohwayo 1993; Chapman et al. 2003).

0.4 Rastrineobola argentea

*Rastrineobola argentea (*known as *mukene* in Uganda; *dagaa* in Tanzania, and *omena* in Kenya) is one of the few native species that has managed to thrive through this period of ecological upheaval (Fig. 0.1). *R. argentea* is a small (5-7 cm) pelagic zooplanktivore, originally thought to be endemic to lakes Victoria, Kyoga, Nabugabo, and the Nile River (Greenwood 1966). However, we discovered six new populations in small satellite lakes of the Kyoga basin during the course of my Ph.D. research, and it is possible that they are even more widespread than this, as few systemic surveys have been carried out. Although *R. argentea* is briefly mentioned in early accounts from Lake Victoria (Graham 1929; Corbet 1961); it was not until the 1980s and 1990s, when it began to increase almost exponentially in abundance in Lake Victoria (Wanink 1999), that it became the subject of more detailed scientific study (Wanink 1998; Wandera 1992). *R. argentea* is now the dominant fish species in Lake Victoria, accounting for approximately 57% of the fish biomass of the lake (NaFIRRI 2008). Although *R. argentea* managed to persist through this period of massive ecological change, it seems likely that it experienced considerable selection both from fishing, and from the introduced Nile perch. Contemporary phenotypic change in response to these stressors is a realistic possibility for *R. argentea*, because it has a short generation time (0.3-0.9 yr, Wanink 1998), and rapid phenotypic changes have been previously documented in this species in one region of Lake Victoria (Wanink 1998).

R. argentea was undoubtedly affected by the introduced Nile perch both directly (as an important prey of the perch), and indirectly (as the mass extinction of the haplochromines cichlids may have released it from competition). In terms of direct effects, predation pressure from the Nile perch likely peaked in the mid 1980s when, after depleting its preferred prey, the haplochromine cichlids, the Nile perch began to prey on *R. argentea* throughout its invaded range (Hughes

1986; Ogutu-Ohwayo 1990b; Ogutu-Ohwayo 1993; Mbabazi 2004). In terms of indirect effects, several authors have speculated that *R. argentea* may have undergone competitive release following the decline of the haplochromine cichlids, which declined from approximately 80% of the biomass of experimental trawls in the 1970s (Kudhongania and Cordone 1974) to less than 1% in the late-1980s (Witte et al. 2000). This group included more than 20 species of zooplanktivorous cichlids, which *R. argentea* has arguably now “replaced” in Lake Victoria (Goldschmidt et al. 1993; Ojwang et al. 2010; Wanink 1998; Wanink and Witte 2000).

Fishing pressure on *R. argentea* also has increased steadily over the past few decades, and the commercial fishery for *R. argentea* has now grown to be the largest in the region, with *R. argentea* accounting for over half of the total lake-wide catches (by weight) in 2006 (NaFIRRI 2008; LVFO 2011). *R. argentea* is harvested at night, using light attraction from floating kerosene lanterns to concentrate schools of fish at the surface, which are then surrounded with fine-meshed (3-10mm) surface seines, locally known as *lampara nets* (Fig. 0.1). Most of the fishery is operated from paddled dug-out canoes, and thus the is generally restricted to sheltered inshore areas (Taabu 2004). In Uganda, *R. argentea* is the least expensive fish available and, in contrast to the Nile perch, is not exported outside of East/Central Africa (Odongkara et al. 2006). Fishing employs roughly 300,000 Ugandans, and fish is the most important and affordable source of animal protein in the country (Kirema-Mukasa and Reynolds 1991). Ensuring the sustainability of the *R. argentea* fishery is therefore critical for food security, poverty alleviation, and socio-economic development both in Uganda, and more broadly in the Lake Victoria basin.

0.5 Structure of the dissertation

In Chapter 1, I review the evidence that fishing is driving rapid life history changes in commercially-exploited fish stocks globally. Using a meta-analytic approach, I summarize the rate and direction of observed trends in age and size at maturity in global commercial fish stocks, and test whether variation in rates of phenotypic change across these stocks can be explained by fishing mortality. For the remainder of the dissertation, I focus on *R. argentea* in Lake Victoria, which I use as a case study to understand the ways in which fishing and introduced species can drive contemporary phenotypic change in a natural population. In each chapter, I exploit spatial and temporal variation in both the presence of the invasive Nile perch and the fishery for *R. argentea* in this system to test for phenotypic responses to these two stressors. Specifically, I examine patterns of phenotypic variation spatially - across 10 Ugandan lakes that differ in Nile perch invasion history and the presence of *R. argentea* fisheries; and temporally - before versus after the introduction of the Nile perch and onset of commercial *R. argentea* fishing in Lake Victoria. In Chapter 2, I use this design to test whether increased predation and fishing-induced mortality are associated with changes in maturation and reproductive investment in *R. argentea*. I also use empirical data on life history change in *R. argentea* to make specific recommendations for the management of the *R. argentea* fishery in Uganda. In Chapter 3, I test whether predation from the introduced Nile perch is correlated with shifts in overall body morphology with increased predation. In Chapter 4, I consider the indirect effects of the Nile perch introduction on *R. argentea*, and test whether the simplification of the fish community by this novel predator has selected for niche expansion and associated morphological change in *R. argentea*.

Fig. 0.1 *Rastrineobola argentea* is a small (5-7cm) pelagic cyprinid (left). The *R. argentea* fishery uses light attraction to attract and capture schools of *R. argentea* at the surface at night (right).

0.6 References

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CHAPTER 1

1 Life history change in commercially exploited fish stocks: an analysis of trends across studies

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1.4 Abstract

Age and size at maturation have declined dramatically in many commercial fish stocks over the past few decades - changes that have been widely attributed to fishing pressure. We performed an analysis of such trends across multiple studies, to test for the consistency of life history changes under fishing, and for their association with the intensity of exploitation (fishing mortality rate). We analyzed 143 time series from 37 commercial fish stocks, the majority of which originated from the North Atlantic. Rates of phenotypic change were calculated for two traditional maturation indices (length and age at 50% maturity), as well as for probabilistic maturation reaction norms (PMRNs). We found that all three indices declined in heavily exploited populations, and at a rate that was strongly correlated with the intensity of fishing (for length at 50% maturity and PMRNs). These results support previous assertions that fishing pressure is playing a major role in the life history changes observed in commercial fish stocks. Rates of change were as strong for PMRNs as for age and size at 50% maturity, which is consistent with the hypothesis that fishing-induced phenotypic changes can sometimes have a genetic basis.

1.5 Introduction

It has long been hypothesized that fishing can cause phenotypic changes in exploited fish populations (Miller 1957; Borisov 1978; Ricker 1981; Law and Grey 1989; Stokes 1993). In particular, fishing may lead to changes in life history traits, such as age and size at maturation, because these traits are especially sensitive to altered mortality schedules (Stearns 1992). Matching this expectation, substantial changes in age and size at maturation have been observed in many commercial fish stocks over the past few decades (see reviews by Miller 1957; Policansky 1993; Trippel 1995; Rochet 1998; Law 2000; Stokes and Law 2000; Heino and Godo 2002; Hutchings and Baum 2005; Jorgensen et al. 2007; Fenberg and Roy 2008; Heino and Dieckmann 2008). Despite the apparent ubiquity of these trends, it has proven difficult to confirm that fishing per se is actually the cause - because competing explanatory factors are hard to rule out in observational studies. In particular, long-term environmental trends (e.g., increasing sea surface temperatures) have coincided with increasing exploitation in many fish stocks, and these environmental factors can influence maturation in fishes (e.g., Cox and Hinch 1997). Although a few studies have formally considered some environmental factors, and ruled them out statistically (Ricker 1981; Rijnsdorp 1993; Barot et al. 2004), many other studies have not rigorously accounted for them. Moreover, some studies have concluded that the principal drivers of life history changes in particular fish stocks are environmental variables other than fishing pressure (e.g., Cox and Hinch 1997; Cardinale and Modin 1999). We suggest that one way to inform the importance of fishing per se is to test, across multiple fish stocks, whether the rate of phenotypic change in life history traits is correlated with the intensity of exploitation. If fishing truly is a powerful and common driver of phenotypic change in nature, then lightly-fished stocks should exhibit little or no change in life history traits, whereas heavily-fished stocks should show rapid and dramatic changes.

We surveyed the literature on commercial fish stocks to calculate rates of life history change. We then used this data set to ask (1) whether rates of phenotypic change in life history traits are correlated with the intensity of exploitation, and (2) whether any such correlations are in the *direction* expected from theory. We therefore now briefly review theory concerning life history change in response to fishing.

1.5.1 Mechanisms and responses:

Fishing may drive life history changes via at least two different mechanisms – in addition to the immediate numerical effects of mortality (Nelson and Soulé 1987; Stokes 1993; Smith 1994; Trippel 1995; Law 2000; Heino and Godo 2002). First, fishing may induce plastic changes in life history traits. For example, heavy fishing pressure often leads to drastic declines in population size (Hutchings and Baum 2005), which in turn can lead to the relaxation of intraspecific competition, and thus increase individual growth rates of the survivors (Policansky 1993). As a result of these accelerated growth rates, fish in heavily exploited stocks can mature at younger ages, and can show associated changes in size at maturation (Heino and Godo 2002; Kuparinen and Merila 2007). Second, fishing may induce evolutionary (genetic) changes in fish stocks by selecting against particular life histories. The potential for fisheries-induced evolution seems strong given that (1) almost all modern commercial fisheries are highly selective, especially with respect to age and size (Heino and Godo 2002); (2) fisheries sometimes remove as much as 50% of the individuals in populations annually (Stokes and Law 2000); and (3) life history traits in fish are at least moderately heritable (h^2 for age at maturation = 0.31±0.19, mean from 8 studies; h^2 for length at maturation = 0.30±0.21, mean from 17 studies (reviewed by Law 2000)). Furthermore, laboratory selection experiments using salmonids (e.g., Gjedrem 1983) and Atlantic silversides (*Menida menida*) (Conover and Munch 2002; Conover et al. 2005; Walsh et al. 2006) have demonstrated that life history traits can evolve in response to selection. Finally, rapid genetic divergence in life history traits driven by altered mortality schedules has also been documented in the wild for introduced populations of guppies (*Poecilia reticulata*) (Reznick et al. 1990; Reznick and Ghalambor 2005) and mosquito fish (*Gambusia affinis*)

(Stearns 1983). All of these results support the possibility of life history evolution on contemporary time scales in nature.

The effects of these two mechanisms (plasticity or genetic change) can be jointly visualized using *probabilistic maturation reaction norms* (PMRNs). PMRNS are functions that describe the probability that an immature individual of a given age and size will mature during a specified time interval (Heino et al. 2002; Dieckmann and Heino 2007). Under this conceptual framework, plastic responses are visualized as shifts along the reaction norm mediated by changes in growth rate, whereas genetic changes are visualized as a shift in the position or shape of the maturation reaction norm itself. Empirical studies are therefore increasingly examining changes in PMRNs, instead of just size or age at 50% maturity, although the inferential strength of this method depends on accurately removing all of the important plastic effects (if any).

Plastic and genetic changes can both occur in harvested populations, although they may operate on different time scales, at different rates, and even in different directions. In terms of genetic responses, life history theory generally predicts that fishing should select for earlier maturation at smaller sizes (Jorgensen et al. 2007). This expectation arises because most commercial fisheries are highly size-selective; typically targeting individuals above a certain size threshold (Kuparinen and Merila 2007). This selectivity can result from the use of particular types of fishing gear, such as trawls, or specific regulations, such as minimum slot sizes (Jorgensen et al. this issue). As a result, individuals that manage to reproduce at a small size/young age will often have higher fitness (e.g., Ratner and Lande 2001; Ernande et al. 2004; de Roos et al. 2006; Andersen et al. 2007). Moreover, even fisheries that impose non-selective mortality can select for reduced age and size at maturation (e.g., Law and Grey 1989; de Roos et al. 2006), although not under all conditions (Abrams and Rowe 1996). One exception to the above prediction can occur when only sexually mature individuals are targeted, such as on spawning grounds. Under this type of harvest regime, selection favours increased age at maturation, because fish that remain longer on the feeding grounds will grow larger, and thus have greater reproductive potential when they do mature and enter the spawning grounds where mortality is high (Law and Grey 1989; Heino 1998; Ernande et al. 2004). However, this latter exploitation pattern is unusual (Andersen et al. 2007), and the majority of fisheries likely select for reduced age and size at maturation.

As introduced above, genetic responses to fisheries-induced selection can be accompanied by plastic shifts in life history traits, which can either reinforce, or mask, evolutionary trends. For age at maturation, plastic increases in growth rate in heavily-fished stocks should lead to earlier maturation (Policansky 1993; Trippel 1995; Law 2000; Heino and Godo 2002), thus reinforcing the pattern expected from genetic change alone. For length at maturation, increased growth rates typically result in greater size at maturation (Abrams and Rowe 1996), thus potentially masking any evolutionary trends towards smaller size at maturation. However, models that incorporate both plastic and genetic effects still generally predict small increases in length at maturation when fishing mortality is low, but rapid selection for decreased length at maturation when fishing mortality is high (de Roos et al. 2006).

Overall, we predict that the dominant trend across commercial fish stocks should be a shift towards earlier maturation at smaller sizes. This pattern should manifest itself via negative rates of phenotypic change for length at 50% maturity, age at 50% maturity, and PMRNs. Furthermore, we predict that the rates of change in each of these life history traits across different fish stocks will be positively correlated with fishing mortality.

1.6 Methods

1.6.1 Data collection

We searched the peer-reviewed literature (Web of Science) for time series data on life history traits in commercial fish stocks. We did not place any restrictions on the date of publication or the source journal, and we used various permutations of the following search terms: change, trends, ‘age at maturity’, ‘length at maturity’, fish, maturation, ‘life history’, and fishing. We also included data from any relevant technical fisheries reports that were brought to our attention, particularly those published by the Canadian Department of Fisheries and Oceans (DFO) and the North Atlantic Fisheries Organization (NAFO). For simplicity, we focused on commercial finfish species (marine or freshwater). Although we did not impose any *a priori* geographical restrictions, the majority of studies we found in the peer-reviewed literature focused on temperate, marine systems from the North Atlantic. Because of the nature of our statistical analyses, we only included stocks for which both phenotypic time series and reliable fishing mortality statistics were available (see below). This requirement greatly reduced the number of time series that we were ultimately able to analyze to 143 time series from 16 different studies. Although this data set was certainly not exhaustive, inclusion or exclusion of studies was independent of the observed phenotypic changes, fishing intensities, and combinations thereof.

Phenotypic data were gathered for three different response variables: length at 50% maturity (L_{50}), age at 50% maturity (A_{50}), and midpoints of PMRNs. L_{50} and A_{50} are derived from *maturity ogives* – demographic functions that describe the probability of being mature at a given age or size, and which depend not only on maturation, but also on mortality and growth rates. In contrast, PMRNs describe the maturation process after removing effects due to variation in growth rates and mortality, and thus disentangle some, but not all, of the environmental effects on maturation (Dieckmann and Heino 2007). PMRN mid-points represent the lengths at which the individuals of a given age have a 50% probability of maturing. Studies reporting trends in length-at-age, weight-at-age, or mean age or size in commercial catches were not included (with one exception; see Appendix A), because they do not directly describe maturation, and they may vary with the selectivity of fishing gear. We chose not to collect data on growth rates, as they were less widely reported and potential changes in growth in response to fishing are more difficult to predict and interpret. However, there is evidence that growth rates have declined in a few commercial fish stocks (Jorgensen et al. 2007).

For each time series, we estimated the phenotypic value at the beginning (Z_0) and end (Z_1) of the study period, as well as the duration of the study ($t_1 - t_0$ =

Δt). To account for year-to-year fluctuations in time series, we estimated ($t_{0,}$ Z_0) and ($t_{1,}$ Z_1) as the mean of the first and last three data points in each time series, respectively. Alternatively, if the authors had fit linear regressions to their time series, we used the (x,y) co-ordinates at the start and end of these regressions to estimate t_0 and t_1 and Z_0 and Z_1 respectively. In some cases, the time series spanned a significant change in fishing intensity such as the imposition of a complete fishing moratorium. In these cases, we considered the pre- and post-moratorium periods separately, as in Olsen *et al.* (2004). We did not include data in cases where Δt was less than the generation length of the species. The rate of phenotypic change for each trait was calculated in *darwins*, a common index for measuring rates of phenotypic change (Haldane 1948; Gingerich 1993; Hendry and Kinnison 1999). This index represents the proportional change per million years and is calculated as:

$$d = \frac{\ln(Z_1/Z_0)}{(\Delta t \times 10^{-6})}$$

An alternative phenotypic rate metric, the haldane, was not used because it required data (i.e., standard deviations in each time step) that were not available for many time series. We did, however, consider one important element of haldanes by also considering elapsed time as the number of generations (years divided by generation lengths). Generation lengths were estimated from stock status reports, published data, and from consultation with fisheries scientists (see Appendices A-C for details). These estimates generally reflect *pre*-exploitation conditions, and would likely change as age at maturation changes during exploitation.

Fishing intensity was estimated as the instantaneous rate of fishing mortality (F, year^{-1}). While data on fishing mortality are often scarce, F is a good proxy for the strength of selection imposed by a fishery, because it measures the proportion of a population that is removed by the fishery at a given time. Unlike other more widely-reported metrics of fishing intensity (e.g., total landings, catch per unit effort), F is a per capita rate with no other dimensions than time, and therefore has the advantage of being readily comparable across studies. F values were rarely reported in the studies we examined, and so they were obtained from other sources, including stock status reports, online databases, and consultation with fisheries scientists (see Appendices A-C for details). Overall fishing mortality (year^{-1}) for each stock was calculated as the average of yearly estimates of F over the time series (or fraction thereof if some years were missing). In cases where age-specific F estimates were available, we used those for the age classes most heavily targeted by the fishery (i.e., the highest F values). Given potential uncertainty in these estimates of F, we also assigned categorical levels of fishing intensity for each stock: LOW for $F < 0.3$, MED for $0.3 \leq F < 0.6$, and HIGH for $F \geq 0.6$.

1.6.2 Analyses

Not all of the rate estimates in our initial data set were strictly independent: for example, some came from males and females in the same stock, from different age cohorts in the same stock, or from different studies of the same stock. We reduced this non-independence by retaining only a single rate estimate for each life history trait for each stock, based on the criteria outlined below. Although stocks are often arbitrary management units and may not always represent genetically distinct populations their use here is justified on several grounds: a) life history traits often vary substantially among stocks (e.g., COSEWIC 2003; Busby et al. 2007), b) fishing intensity often varies among stocks (Appendices A-C, this paper), c) data are typically reported on a stock by stock basis (see for example Department of Fisheries and Oceans Canada stock status reports), and d) management decisions are usually made at the stock level (e.g., imposition of moratoria, see Appendices A-C, this paper). We experimented with reducing our data set in various ways (e.g., selecting the maximum or mean rate per stock, selecting one random entry per stock), but it made no important difference to our results (not shown), so we settled on the following protocol for eliminating pseudoreplicated entries. If time series were available for both sexes from a given stock, we included rate estimates for females only. If PMRN midpoints were reported for multiple ages from the same stock, we selected the time-series with the best resolution and smallest confidence intervals (generally the middle of the range of ages reported). If two separate studies reported time series for the same stock, we included whichever series was the longest. If multiple rate estimates were calculated from the same time series (e.g., pre and post-moratorium for the same stock), we excluded one at random. Finally, even within these reduced stock-level data sets, one might argue for non-independence of different stocks within a species. We therefore generated a further reduced data set that included only one rate estimate per species, selected at random from the stock-level data set.

To test for the effects of fishing on the rate of phenotypic change in each trait (L_{50}, A_{50}, PMRN) we fit four separate general linear models in R (v. 2.6.1., R 2007). The explanatory variables were fishing mortality (continuous or categorical) and time interval (log10 years or number of elapsed generations), and the response variable was the magnitude of phenotypic change (darwin numerator). We first fit a full model, but the interaction between fishing mortality and time was almost always not significant. These models were fit separately for each trait and for the stock-level and species-level data sets. Sample sizes were: 18 (stocks) and 8 (species) for length at 50% maturity, 25 (stocks) and 7 (species) for age at 50% maturity, and 11 (stocks) and 4 (species) for PMRNs.

1.7 Results

Rates of phenotypic change for length at 50% maturity retained for our stock-level analysis (i.e., after elimination of pseudoreplicated entries) ranged from -24.8 x 10^3 to + 5.7 x 10^3 darwins (mean ± sd = -10.6 ± 9.6). The vast majority (17 out of 18) of these rates were negative (Appendix A), significantly more so than expected from chance (Fisher's exact test, p = 0.007). Increasing fishing mortality (F) had a strong negative effect on length at 50% maturity, with the most heavily exploited stocks shifting most rapidly towards smaller sizes at 50% maturity (Fig. 1.1A and 1.2A). This relationship was significant for the stock-level data sets, regardless of the fishing mortality metric (continuous or categorical F), and the time metric (years or generations) (Table 1.1). The direction of the trend remained the same for the species-level dataset (Fig. 1.1B), but statistical significance was lost. Given comparable variances explained between the stock-level and species-level analyses, the reduced significance in the latter was probably the result of the smaller sample size and narrow range of F values (Table 1.1).

Rates of phenotypic change for age at 50% maturity retained for our stock-level analysis ranged from -41.2 x 10^3 to + 12.6 x 10^3 darwins (mean ± sd = -12.6 ± 12.3). The majority (23 out of 25) of these rates were negative (Appendix B), significantly more so than expected from chance (Fisher's exact test, p = 0.001). In contrast to the pattern observed for length at 50% maturity, fishing mortality had no substantial effect on the rate of change in age at maturity among stocks (Fig. 1.1C and 1.2B). Fishing mortality explained almost none of the variation among rates when considered as a continuous variable (Table 1.2) and although it was statistically significant when treated categorically (Table 1.2), there was substantial overlap among categories (Fig. 1.2B). Similar patterns were observed at the species-level (Fig. 1.1D), with no significant effect of fishing mortality regardless of the time metric used (Table 1.2).

Rates of phenotypic change for PMRNs retained for our stock-level analysis ranged from -27.5 x 10^3 to + 7.3 x 10^3 darwins (mean ± sd = -9.2 ± 10.6). The majority (8 out of 11) of these rates were negative (Appendix C), although this was not significantly more than expected from chance (Fisher's exact test, p = 0.387). Increasing fishing mortality had a very strong negative effect on PMRNs, with the most heavily exploited stocks showing the most rapid declines in PRMN midpoints (i.e. shifts towards maturation at smaller size for a given age) (Fig. 1.1E and 1.2C). This relationship was significant for the stock-specific analyses, regardless of the fishing mortality metric (continuous or categorical F), and the time metric (years or generations) (Table 1.3). The direction of the trend remained the same for the species-level dataset (Fig. 1.1F), but there were insufficient data (n=4) to conduct any statistical tests. In contrast to the other traits, the interaction between fishing mortality and time was significant in some models (Table 1.3).

1.8 Discussion

The rates of phenotypic change that we estimated for life history traits in commercial fish stocks are generally consistent with previous estimates (Jorgensen et al. 2007), but are higher than many evolutionary rates previously reported in the literature for other traits, taxa, and contexts (Hendry and Kinnison 1999; Kinnison and Hendry 2001; Hendry et al. 2008). This result supports the intuition that exploitation is a very strong selective force, probably outside the normal intensities of selection in most natural populations (Darimont et al. 2009). It is also true, however, that the particularly rapid rates of change observed here may be partly due to the relatively short duration of time series for harvested species (1-16 generations), given that rates of phenotypic change scale negatively with time interval (Gingerich 1993; Gingerich 2001; Kinnison and Hendry 2001). One potential reason is that short studies may coincide with periods of intense selection that, in longer studies, would be averaged with periods of stasis and reversals (Grant and Grant 2002).

It is important to acknowledge that the rapid rates of phenotypic change reported here could reflect plasticity – rather than genetic change. This might be particularly likely for age and size at 50% maturity, both of which are known to show substantial plasticity (Stearns 1992). PMRNs, however, are meant to remove at least some of these plastic effects by accounting for variation due to changes in growth and mortality (Dieckmann and Heino 2007). Thus, shifts in age-size PMRNs have been frequently interpreted as representing genetic, rather than plastic, changes in maturation schedules (e.g., Olsen et al. 2004), although such an inference must be made with caution (Dieckmann and Heino 2007; Kraak 2007). In our study, PMRNs often changed as rapidly as age and size at 50% maturity, suggesting that plastic effects of growth are not the sole driver of changes in life history traits.

How well do the observed trends fit theoretical predictions for fisheries-induced life history change? For length at 50% maturity, we observed downward trends in the vast majority of stocks. This pattern is consistent with either genetic responses to fishing-induced selection (Ratner and Lande 2001; Ernande et al.

2004; Andersen et al. 2007), or a combination of genetic and plastic effects (de Roos et al. 2006). However, this pattern is the opposite of what we would generally expect from plastic effects alone - in which case *increases* in size at maturation would have been most likely (Abrams and Rowe 1996). Plastic decreases in size at maturation might be theoretically observed in species with positively-sloped PMRNs; however, almost all PMRNs calculated to-date exhibit negative slopes (Heino and Dieckmann 2008). We also found that the intensity of fishing-induced mortality had a significant positive effect on the rate of change in length at 50% maturity, with the most heavily exploited populations experiencing the most precipitous declines in length. This correlation supports the hypothesis that fishing morality is a major driver of observed changes in size at 50% maturity across a diversity of commercial fish stocks.

For age at 50% maturity, we also observed declining trends in the majority of stocks, which is consistent with either genetic or plastic responses to fishing (Heino and Godo 2002; Ernande et al. 2004). However, variation in the rate of decline among stocks was not significantly correlated with fishing mortality, suggesting that trends in age at 50% maturity may be influenced by variables not considered in the present study. For example, strong temporal trends in temperature, large changes in growth rate, or high levels of natural mortality may be the primary drivers of changes of age at 50% maturity in certain stocks. Additionally, significant shifts in age at 50% maturity may have occurred earlier in the exploitation history of some stocks (i.e., before life history data were collected systematically), and further decreases may not be physiologically possible, despite continued high levels of mortality (Trippel 1995).

For PMRNs, we observed declines through time for most stocks, in agreement with predicted genetic responses to size-selective harvesting (Ernande et al. 2004). *Increases* in PMRN midpoints were typically observed only in post-moratorium situations (e.g., Olsen et al. 2005), or when fishing mortality was low (e.g., Norwegian spring-spawning herring prior to 1955). The rate of decline in PMRNs was positively correlated with fishing mortality, and this relationship was stronger than for age and size at 50% maturity. Overall, our results point to commercial fishing as a major driver of life history change (at least for length at 50% maturity and PMRNs), even across diverse fish stocks and species.

The above interpretations are subject to a number of caveats, stemming from the biases and uncertainties inherent in the data compiled for this review. First, our data set suffers from a strong geographical bias, with the majority of data coming from temperate, marine stocks from the Northwest Atlantic. As a result, we should be wary of generalizing our results beyond this region. It would be valuable to collect more data from other fish stocks, particularly from tropical and freshwater populations, which have been severely under- represented in this, and many earlier, reviews. Second, the literature is dominated by work on only a few major commercial species, most notably Atlantic cod, that have captured the public and scientific imagination because of the dramatic declines they suffered as a result of over-fishing. Such stocks might exhibit anomalous or extreme trends, and thereby have an inordinate effect in combined analyses. On a related note, only a few families are represented in our data set, most notably the Pleuronectidae, Gadidae, and Salmonidae. Given that life history characteristics are often conserved within families, and that different life history characteristics influence vulnerability to fishing (Jennings et al. 1999), the set of families that we considered are probably not representative of all possible responses to fishing. Third, we used stocks defined for fisheries management as our units of replication – and these stocks may not be demographically or evolutionarily independent. We attempted to address these last two issues by conducting analyses with reduced data sets that included only one rate estimate per species. Statistical power was lacking in these analyses, but qualitative trends did not change, suggesting that any biases may not be too severe.

Another set of caveats relate to our estimates of fishing mortality (F). These estimates came from a variety of different sources, showed considerable temporal variation, and were often available for only part of a given time series. Another limitation was that some data sources reported F estimates averaged across the entire stock, whereas others reported it only for the most heavily exploited age classes. Finally, the majority of F estimates do not include mortality due to by-catch from other fisheries, or discards at sea, which can be substantial (Jennings and Kaiser 1998). We attempted to minimize these uncertainties by also assigning categorical levels of fishing mortality to each stock. In all cases, results were similar between the continuous and categorical analyses, suggesting that uncertainties about the magnitude of F may not be an overwhelming problem.

Finally, we recognize that such a broad-brush analysis of trends necessarily ignores a great deal of biological complexity. We here wish to highlight two major complexities that might be particularly important. First, many stocks were exploited for centuries before any data on life history traits were collected. This past selection, which cannot be assessed, has presumably shaped the starting point for evolution in response to recent fishing. This consideration also implies that post-moratorium rates must be interpreted with caution, as any phenotypic change during these periods may be influenced by the prior periods of intense exploitation. Most notably, many stocks were at very low population densities at the time moratoria were imposed, and this could certainly have plastic effects on life history traits. However, we think that the inclusion of post-moratorium data is justifiable on several grounds. As mentioned above, even pre-moratorium estimates (usually 1960s-early 1990s) come after long periods of fishing pressure (hundreds of years in the case of some cod stocks), for which we have little or no quantitative data. Relying on these estimates exclusively would likely still introduce biases. In addition, excluding all post-moratorium estimates would dramatically reduce the range of F values for our analyses, because almost of all our “low” fishing mortality estimates come from post-moratorium contexts. Of course it would be preferable to have long-term maturity data from unexploited or lightly exploited fish populations, but to the best of our knowledge, such data are scarce. Thus, estimates from post-moratorium stocks provide virtually the only data on life history change in populations experiencing low fishing mortality, and excluding them *a priori* would mean sacrificing a great deal of valuable information. A second important complication is that fishing alters marine ecosystems in complex and pervasive ways that extend far beyond the direct mortality imposed on the target stock (Jennings and Kaiser 1998). For example, fishing may change the densities of predators, prey, and competitors, which may alter growth rates and age-specific mortality and thus influence maturation schedules (Kuparinen and Merila 2007). Notwithstanding these complexities, it is remarkable that simple models incorporating only recent, rough estimates of fishing intensity could explain 47-93% of the variation in the magnitude of change among stocks (for L50 and PMRNs).

Keeping the above caveats in mind, we now return to the question that motivated this analysis: to what extent are the changes in life histories observed in commercial fish stocks driven by fishing? We found significant correlations between fishing mortality and the rate of phenotypic change for two of the three traits examined, in a direction that was consistent with theoretical expectations for fisheries-induced evolution. These correlations explained a large portion of the variation in rates of change among populations, and were relatively robust to the types of metrics we used (i.e., years vs. generations, F categorical or continuous), or the different assumptions underlying our analysis (i.e., stocks vs. species as units of replication). Although correlations cannot prove that there is a causal link between fishing and phenotypic change, they support this hypothesis and corroborate other types of evidence showing that fishing can cause evolutionary changes in natural populations, including mathematical models and simulations (e.g., Ernande et al. 2004), field-based estimates of fisheries-induced selection (Carlson et al. 2007), and laboratory experiments (e.g., Conover et al. 2005; Conover and Baumann this issue). We conclude that the available evidence strongly points to exploitation as a major force driving life history change in commercial fish stocks. This reinforces the value of incorporating evolutionary thinking into fisheries management (e.g., Law and Grey 1989; Dunlop et al. this issue; Enberg et al. this issue; Okamoto et al. this issue).

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Table 1.1 Effect of fishing mortality on rates of change in length at 50% maturity (L_{50}).

"Fishing" is fishing mortality measured as a continuous variable, and "Fcat" is fishing mortality measured as a categorical variable. "Time" is the duration of the time series measured in years (log10-transformed); and "Gen" is the duration of the time series expressed in terms of the generation length of the species. Partial η^2 is a measure of effect size and was calculated as $SS_{effect}/(SS_{effect} + SS_{error})$. Significant p-values (<0.05) are indicated with an asterisk

Model	**Factor**	**F**	**df (factor, error)**	**p**	**partial η^2**
Stock-level analysis					
Fishing X Time (R^2=0.470)	Fishing	11.11	1, 14	0.005*	0.42
	Time	0.08	1, 14	0.784	0.01
	Fishing x Time	1.20	1,14	0.291	0.07
Fishing X Gen (R^2=0.659)	Fishing	15.12	1, 12	0.02*	0.56
	Gen	4.70	1, 12	0.051	0.28
	Fishing x Gen	3.35	1, 12	0.092	0.22
Fcat X Time (R^2=0.564)	Fcat	5.61	2, 12	0.019*	0.48
	Time	1.00	1, 12	0.337	0.08
	Fcat x Time	1.64	2,12	0.235	0.22
Fcat X Gen (R^2=0.673)	Fcat	6.34	2, 10	0.017*	0.56
	Gen	6.35	1, 10	0.03*	0.39
	Fcat x Gen	0.78	2, 10	0.484	0.14
Species-level analysis					
Fishing X Time (R^2=0.584)	Fishing	2.86	1,4	0.166	0.42
	Time	2.49	1,4	0.190	0.39
	Fishing x Time	0.26	1,4	0.634	0.07
Fishing X Gen (R^2=0.779)	Fishing	4.56	1, 3	0.122	0.60
	Gen	4.84	1, 3	0.115	0.62
	Fishing x Gen	1.20	1, 3	0.354	0.80
Fcat X Time (R^2=0.834)	Fcat	3.21	2,3	0.180	0.69
	Time	4.03	1,3	0.138	0.58
	Fcat x Time	4.65	1,3	0.120	0.42
Fcat X Gen (R^2=0.823)	Fcat	2.00	2,2	0.333	0.67
	Gen	3.37	1,2	0.208	0.63
	Fcat x Gen	1.93	1,2	0.300	0.50

Table 1.2 Effect of fishing mortality on rates of change in age at 50% maturity (A_{50})
In the species-level analysis, sample size was insufficient to fit models with fishing mortality as a categorical explanatory variable. For abbreviations and other conventions see note for Table 1.1.

Model	**Factor**	**F**	**df (factor, error)**	**p**	**partial η^2**
Stock-level analysis					
Fishing X Time (R^2=0.089)	Fishing	0.82	1, 21	0.375	0.04
	Time	1.11	1, 21	0.305	0.05
	Fishing x Time	0.13	1, 21	0.724	0.01
Fishing X Gen (R^2=0.025)	Fishing	0.01	1, 17	0.942	0.00
	Gen	0.22	1, 17	0.643	0.01
	Fishing x Gen	0.21	1, 17	0.643	0.01
Fcat X Time (R^2=0.393)	Fcat	6.57	2, 19	0.007*	0.41
	Time	0.00	1, 19	0.987	0.00
	Fcat x Time	2.42	2, 19	0.116	0.20
Fcat X Gen (R^2=0.469)	Fcat	4.47	2, 15	0.030*	0.37
	Gen	0.36	1, 15	0.557	0.02
	Fcat x Gen	1.96	2, 15	0.175	0.21
Species-level analysis					
Fishing + Time (R^2=0.351)	Fishing	1.28	1, 3	0.341	0.30
	Time	0.30	1, 3	0.620	0.09
	Fishing x Time	0.04	1, 3	0.856	0.02
Fishing + Gen (R^2=0.607)	Fishing	0.41	1, 1	0.638	0.33
	Gen	0.50	1, 1	0.608	0.33
	Fishing x Gen	0.63	1, 1	0.572	0.40

Table 1.3 Effect of fishing mortality on rates of change in probabilistic maturation reaction norm midpoints. The sample size was insufficient to fit models at the species level. For abbreviations and other conventions, see note for Table 1.1.

Model	**Factor**	**F**	**df (factor, error)**	**p**	**partial η^2**
Stock-level analysis					
Fishing X Time (R^2=0.930)	Fishing	62.83	1,7	<0.001*	0.90
	Time	12.89	1,7	0.009*	0.65
	Fishing x Time	17.16	1,7	0.004*	0.71
F X Gen (R^2=0.868)	Fishing	33.45	1,7	<0.001*	0.83
	Gen	1.16	1,7	0.318	0.14
	Fishing x Gen	11.57	1,7	0.011*	0.62
Fcat X Time (R^2=0.913)	Fcat	17.74	2,5	0.005*	0.88
	Time	7.63	1,5	0.040*	0.61
	Fcat x Time	4.57	2,5	0.074	0.65
Fcat X Gens (R^2=0.800)	Fcat	7.72	2,5	0.030*	0.94
	Gen	0.04	1,5	0.852	0.01
	Fcat x Gen	2.22	2,5	0.204	0.47

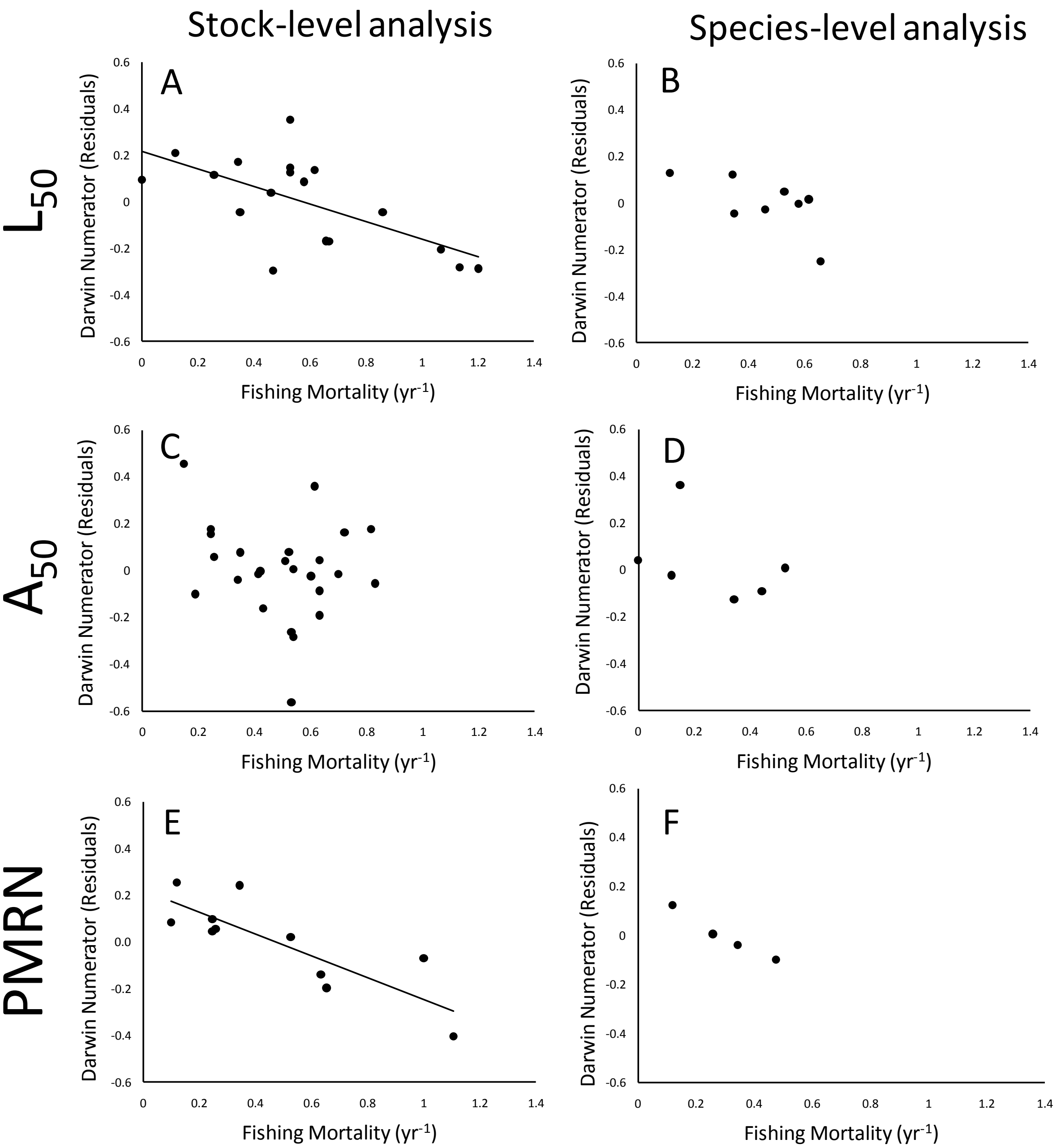

Fig. 1.1 Magnitude of phenotypic change in response to fishing mortality.

Phenotypic change is shown for length at 50% maturity (A, B), age at 50% maturity (C,D) and mid-points of probabilistic maturation reaction norms (PMRNs) (E,F). The Y axis shows residuals from a linear regression of darwin numerators ($[\ln(Z_1) - \ln(Z_0)]$) over time (log10 years); i.e., proportional phenotypic change after accounting for the effects of time. Fishing mortality is the average of yearly estimates of fishing mortality over the time period over which the phenotypic change was measured. Note that one data point (F=1.9) is not shown in panels C (x= 0.19, y = -0.10) and D (x = 0.19, y = -0.18) so as to match the scale in the other panels. Trendlines were fit only in cases where fishing mortality was found to be significant (at $P<0.05$).

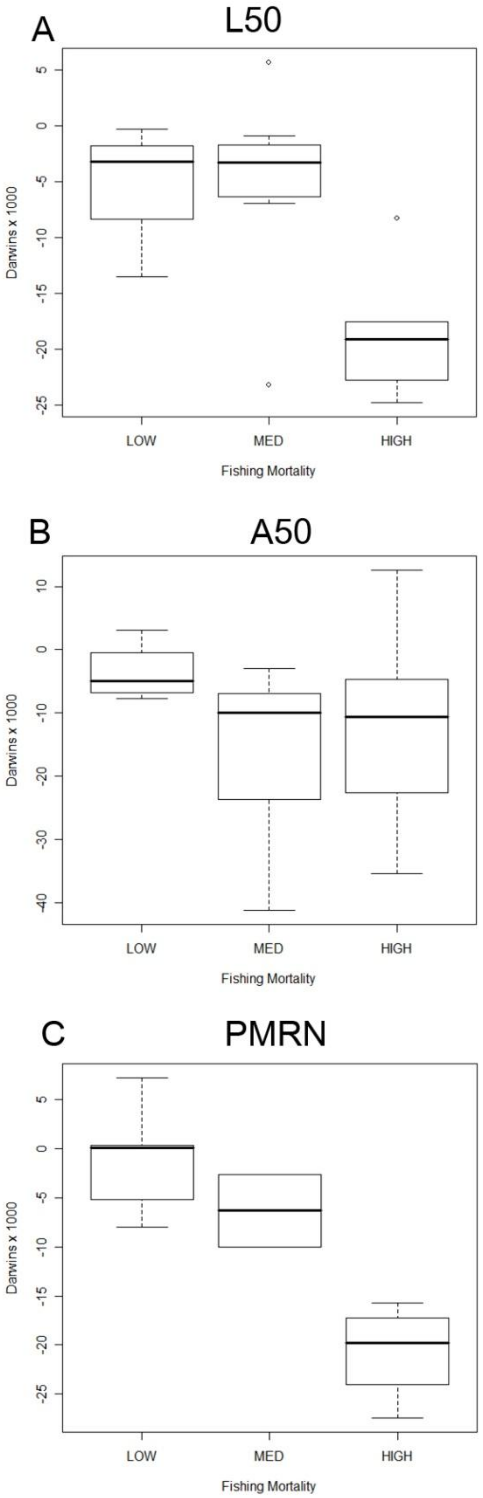

Fig. 1.2 Rates of phenotypic change for stocks experiencing low ($F<0.3$), medium ($0.3\leq F<0.6$) and high ($F\geq 0.6$) levels of fishing mortality (year^{-1}).

Rates are expressed in darwins (x 10^3) and are plotted separately for length at maturity (A), age at maturity (B) and midpoints of Probabilistic Maturation Reaction Norms (PMRNs) (C). The thick lines represent the median of each distribution, while the top and bottom of the boxes represent the 75th and 25th percentiles, respectively. The dashed error bars represent 1.5 times the interquartile range (approximately 2 standard deviations). Outliers are shown as separate data points.

PREFACE TO CHAPTER 2:

Broadening our understanding of fisheries-induced evolution: Evidence for fisheries-induced change in tropical inland waters?

In Chapter 1, I reviewed published time-series from 37 different commercial fish stocks, and I found consistent declines in length at maturity, age at maturity, and the mid-points of probabilistic maturation reaction norms (PMRNs). For length at maturity and PMRN mid-points, the rate of decline was significantly correlated with mean fishing mortality. These findings support the view that fishing pressure is driving widespread and rapid life history changes in commercial fish stocks, and that these changes may sometimes have a genetic basis. This review also highlighted some important gaps in the literature. Most notably, almost all published examples of fisheries-induced evolution come from a small number of temperate marine species. It is an open question whether fisheries-induced evolution may also be occurring in tropical inland fisheries, which tend to be multi-species, multi-gear fisheries with more complex and heterogeneous patterns of exploitation. I address this gap in the literature in the following chapter, where I test for fishing (and predator) induced life history change in *R. argentea* in one of the largest and most important inland tropical fisheries in the world: the Lake Victoria basin. Unlike many temperate marine fisheries that were exploited for centuries prior to the collection of phenotypic and ecological data, the development of the commercial *R. argentea* fishery in Uganda is very recent (1989). Thus, we have an almost unprecedented opportunity to track life history traits during the initial development and expansion of a fishery, and make inferences about the causal effects of fishing on life history traits.

CHAPTER 2

2 Life history change in response to fishing and an introduced predator in the East African cyprinid *Rastrineobola argentea*

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2.1 Abstract

Fishing and introduced species are among the most important stressors affecting freshwaters, and can be important selective agents. We examined the combined effects of commercial fishing and an introduced predator (Nile perch, *Lates niloticus*) on life history traits in an African cyprinid fish (*Rastrineobola argentea*) native to the Lake Victoria basin in East Africa. To understand whether these two stressors have driven shifts in life history traits of *R. argentea*, we tested for associations between life history phenotypes and the presence/absence of stressors both spatially (across 10 Ugandan lakes) and temporally (over 4 decades in Lake Victoria). Overall, introduced Nile perch and fishing tended to be associated with a suite of life history responses in *R. argentea*, including: decreased body size, maturation at smaller sizes, and increased reproductive effort (larger eggs; and higher relative fecundity, clutch volume, and ovary weight). This is one of the first well-documented examples of fisheries-induced phenotypic change in a tropical, freshwater stock; the magnitude of which raises some concerns for the long-term sustainability of this fishery, now the most important (by mass) in Lake Victoria.

Keywords

fisheries-induced evolution, invasive species, contemporary phenotypic change, life history evolution, mukene, dagaa, anthropogenic stressors

2.2 Introduction

A growing body of evidence suggests that anthropogenic stressors may be precipitating rapid phenotypic change as species struggle to adapt to human-dominated environments (Reznick and Ghalambor 2001; Stockwell et al. 2003; Hendry et al. 2008). However, much uncertainty remains regarding the rate, limits, and ubiquity of such responses, as well as the mechanisms that underlie them. This uncertainty compromises our ability to predict species' persistence in the face of continuing anthropogenic disturbance and to inform management decisions. In freshwater systems throughout the world, fishing and introduced species are among the most important stressors, with significant ecological and socio-economic impacts (Sala et al. 2000; Beeton 2002). In addition to their immediate ecological effects, they can also be important selective agents, with the potential to drive contemporary phenotypic change in native prey/harvested species (Palumbi 2001; Hendry et al. 2008; Darimont et al. 2009). The potential for fishing to drive evolutionary changes in the life histories of exploited fish populations has long been recognized, given that fisheries: (i) are often highly selective, (ii) frequently impose mortality much greater than natural mortality, and (iii) that many life history traits potentially under fisheries selection are heritable (Stokes and Law 2000; Heino and Godo 2002). In the past decade, several lines of evidence have helped guide an emerging consensus that fisheries-induced evolution is not only theoretically possible, but likely common in nature. These include: experimental evidence that artificial selection mimicking harvest can drive rapid evolution in life history traits (Conover and Munch 2002; Walsh et al. 2006); direct measurements of fisheries selection on wild populations (e.g., Carlson et al. 2007; Kendall et al. 2009; Olsen and Moland, 2010), and long-term field data from numerous commercial fish stocks showing phenotypic trends consistent with fisheries-induced evolution (reviewed in Trippel 1995; Law 2000; Hutchings and Baum 2005; Jorgensen et al. 2007; Sharpe and Hendry 2009). However, studies to date have been heavily biased towards a small number of temperate marine fishes (Sharpe and Hendry 2009), with none looking at fisheries-induced change in tropical, freshwater species. This is a critical research gap for several reasons. First, tropical fishes often have different life histories (e.g., several species breed throughout the year) and so might respond differently to harvest selection. Second, many inland tropical fisheries are artisanal, with different types of gear employed and little formal management, likely resulting in different and heterogeneous patterns and intensities of fishery selection. Third, inland tropical fisheries play an extremely important role in ensuring local food security, particularly in developing areas (Dugan et al. 2010), making it important to assess the prevalence of fisheries-induced evolution in these areas and determine how it can guide management practices.

Like fishing, biological invasions, particularly of predators, can be a potent form of novel selection. There is growing interest in understanding the extent to which selection pressures induced directly or indirectly by invasive species may be driving plastic and/or evolutionary changes in native prey (Mooney and Cleland 2001; Strauss et al. 2006; Carroll 2007). Native prey may adapt to introduced predators via the adoption of novel predator-avoidance behaviours (e.g., Kiesecker and Blaustein 1997; Losos et al. 2004), the evolution of morphological defences (e.g., Vermeij 1982), and/or altered life history tactics (e.g., Fisk et al. 2007). Beyond these few examples, however, we still know relatively little about the evolutionary consequences of biotic invasions (Strauss et al. 2006), especially in freshwaters, which are among the most heavily invaded ecosystems (Strayer, 2010).

In this study we examined the combined effects of fishing and an introduced predator on life history traits in the cyprinid fish, *Rastrineobola argentea*, native to the Lake Victoria basin in East Africa. Lake Victoria is the largest tropical lake in the world and Africa’s most important inland fishery. It has undergone multiple anthropogenic changes over the past century, including overfishing of native fish stocks, eutrophication, and the introduction of several non-native fishes in the 1950s and 60s, most notably the predatory Nile perch, *Lates niloticus* (see reviews by Kaufman 1992; Balirwa et al. 2003; Chapman et al. 2008). Together these stressors have led to the dramatic decline of many native fishes, and the extinction of hundreds of Lake Victoria’s endemic haplochromine cichlids (Ogutu-Ohwayo 1990; Witte et al. 1992; Seehausen et al. 1997; Goudswaard et al. 2008). However, one native fish species has not only persisted, but thrived through this period of ecological upheaval: the small pelagic cyprinid *Rastrineobola argentea*, known locally as mukene in Uganda, omena in Kenya, and dagaa in Tanzania.

Rastrineobola argentea has experienced increased mortality over the past half century from two major anthropogenic sources: predation from the introduced Nile perch and commercial fishing. Predation pressure from the Nile perch likely peaked in the mid 1980s when, after depleting its preferred prey, the haplochromine cichlids, the Nile perch began to prey on *R. argentea* throughout its invaded range (Hughes 1986; Ogutu-Ohwayo 1990b; Ogutu-Ohwayo 1993; Mbabazi 2004). Nile perch still prey on *R. argentea* today, although to a lesser extent (Budeba and Cowx 2007; Paterson and Chapman 2009). This likely reflects both an overall decline in the biomass of Nile perch, likely due to overfishing (Ogutu-Ohwayo 2004; Mkumbo et al. 2007; Muhoozi 2008), and a shift in the Nile perch diet back to the haplochromine cichlids, which appear to be undergoing a limited resurgence in some parts of Lake Victoria (Witte et al. 2000). Commercial fishing for *R. argentea* began in the late 1980s in Uganda, and landings have increased almost exponentially since then, making it now the most important fishery (by mass) in Lake Victoria (NaFIRRI, 2008). To test whether these two novel stressors have driven any shifts in life history traits of *R. argentea*, we used a combined approach, testing for associations between life history phenotypes and the presence/absence of stressors both spatially and temporally. For the spatial approach, we asked how life history traits of *R. argentea* varied across 10 lakes in Uganda that differ in the presence/absence of introduced Nile perch and *R. argentea* fisheries. For the temporal approach, we asked how life history traits of *R. argentea* have changed over the past four decades in Lake Victoria, following the introduction of the Nile perch and the onset of commercial fishing.

Classical life history theory predicts that increased mortality on adults will select for reduced age and size at maturation and increased reproductive effort, whereas increased mortality on juveniles should have the opposite effect. If mortality is uniformly distributed across age classes, no evolution is expected to occur (Gadgil and Bossert 1970; Law 1979; Michod 1979). However, more recent models of life history evolution argue that increased mortality, even if applied to both mature and immature individuals, will select for earlier maturation at smaller sizes (Law and Grey 1989; Abrams and Rowe 1996; Ernande et al., 2004). We suggest that this latter prediction is most likely to apply to *R. argentea*, as the commercial fishery targets a broad range of sizes that includes both mature and immature individuals (Wandera 1992; Taabu 2004; Sharpe and Chapman unpl. data). There have been no direct measurements of the size selectivity of Nile perch predation on *R. argentea*, but several lines of evidence suggest that both mature and immature *R. argentea* are regularly consumed by Nile perch after their ontogenetic dietary shift to piscivory (Ogutu-Ohwayo 1985; Ogutu-Ohwayo 2004; NaFIRRI 2004; Katunzi et al. 2006; but see Wanink 1998).

2.3 Materials and Methods

2.3.1 Study sites

Our study focussed on 10 different lakes located in three parts of the Lake Victoria basin in Uganda, East Africa (Fig. 2.1). These included Lake Victoria, 2 satellite lakes on the North-Western shore of Lake Victoria, and 7 lakes from the Kyoga lakes system, located approximately 150 km North of Lake Victoria. Our sampling covered all of *R. argentea*'s known distribution in Uganda, as well as uncovering six previously unknown populations. Lakes were classified into three perturbation levels based on Nile perch invasion history and the level of fishing pressure for *R. argentea* (Appendix D). The perturbation categories were: lakes without introduced Nile perch or fishing for *R. argentea* ('Unperturbed', n=3), lakes with introduced Nile perch but little or no fishing for *R. argentea* ('Nile Perch', n=5), and lakes with both introduced Nile perch and commercial *R. argentea* fisheries ('Nile Perch and Fishing', n=2). Some native fishes are also known to consume *R. argentea*, including the catfishes *Clarias gariepinus*, *Schilbe intermedius* and *Synodontis victoriae* and the mormyrid *Gnathonemus* *victoriae* (Mbabazi 2004). Although data on the distribution and diet of these species in our study lakes are sparse, the available evidence does not suggest that they constitute a major source of mortality for *R.argentea* in most of our study lakes (Appendix D). Several native birds are also known to feed on *R. argentea* in the Tanzanian portion of Lake Victoria, including the pied kingfisher *Ceryle rudis*, the great cormorant *Phalacrocorax carbo lucidus*, and the long-tailed cormorant *Phalacrocorax africanus* (Wanink and Goudswaard 1994; Wanink 1996). We do not know to what extent these avian predators may target *R. argentea* in Ugandan lakes.

2.3.2 Field collections

Rastrineobola argentea were collected from the 10 lakes described above during three field expeditions carried out during the dry season months of May-July in 2008, 2009, and 2010. A variety of fishing gears were used in order to capture as broad of a size range of fish as possible, although not all gears were successful in all lakes. In each lake, 2-4 sets of experimental gill-nets (nylon monofilament, ½"(12.7 mm) stretched mesh, 1.83 m deep x' 12.2 m long) were set overnight (approximately 16 hours) in the pelagic zone of the lake. We also attempted surface seining during the day time with a 5-mm mesh lampara net in the pelagic zone. On a few lakes (Nabugabo, Nawampasa, and Meito), we fished for *R. argentea* at night using the local fishing methods, which involves concentrating schools of *R. argentea* at the surface using light attraction from kerosene pressure lanterns, and then trapping them with a 5-mm mesh lampara net. On Lake Victoria, we collected *R. argentea* directly from fishers who were fishing at night on the Napoleon Gulf, about 1 km offshore from Kikondo (Fig. 1). After capture, fish were euthanized in either buffered MS-222 (2008 and 2009) or clove oil (2010), and immediately preserved in 10% formalin.

At each lake, we also collected environmental data at three replicate sites in the morning and in the afternoon. These data included water depth, water transparency (Secchi depth, m), and water temperature (°C) and dissolved oxygen (mg/L), measured with a Polaris dissolved oxygen meter.

2.3.3 Measurement of life history traits

Preserved *R. argentea* were measured (standard length to the nearest mm), weighed (to the nearest 0.01 g), and then dissected to determine sex and maturity status. Gonad maturity was macroscopically assessed based on a seven-point scale previously developed for *R. argentea* (S.B. Wandera, unpl. data). The ovaries of mature (Stage V and VI) females were removed and weighed (wet weight, to the nearest mg). Somatic weight was calculated by subtracting the ovary weight from the total body weight. Total fecundity was estimated using the gravimetric method (Hunter et al. 1985). We counted the number of yolked oocytes in three weighed subsamples taken from the centre, posterior, and anterior regions of the left ovary of mature (Stage V and VI) females. These counts were then extrapolated to the entire ovary by multiplying the average oocyte density by the total weight of the ovary.

Egg volume was estimated by measuring two perpendicular diameters on 20 randomly selected eggs from mature (Stage V and VI) females, using the image measurement software Motic (v. 2.0, 2003). We used the average of these two diameters (d) to estimate the volume of the egg, approximated as a sphere:

$$V = \frac{\pi d^3}{6}$$

These 20 measurements were then averaged to obtain one estimate of mean egg volume per female. Clutch volume was calculated as the product of mean egg volume and total fecundity. Finally, we also recorded the presence of intestinal parasites, as these are known to grow to such a large size as to partially or completely impair gonad development in *R. argentea* (Cowx et al. 2008). Nematode parasites were found in a moderate proportion of fish from Lake Kayanja (19%), and cestode parasites were found in a small proportion of *R. argentea* from Lakes Victoria (4.6%) and Kyoga (0.2%). *R. argentea* from all other lakes were found to be free of intestinal parasites. Parasitized females were excluded from all analyses on reproductive traits. We did not undertake an ageing study of *R. argentea*, although there is evidence for daily ring deposition in this species (Njiru et al., 2001), and this could be an important avenue for future work.

2.3.4 Statistical analysis

Spatial analysis

Body size

To examine variation in mean body size across lakes and perturbation levels, we compared the standard length of a random sample of fish caught in the least size-selective of our fishing gears (5-mm lampara net). This was done using a nested ANOVA, with lake as a fixed factor nested within perturbation category. Lake was considered as a fixed factor in all of our analyses because, to the best of our knowledge, our sampling covered the entirety of *R. argentea*'s range in Uganda. That is, lakes were not chosen randomly as examples of particular perturbation regimes; rather, we sampled all lakes known to contain *R. argentea* and then grouped them based on the stressors that they had been exposed to.

Two lakes (Kayanja and Nakuwa) were excluded from the body size analysis because we did not manage to catch *R. argentea* using the lampara net in these lakes. Five lakes were sampled with lampara nets in more than one year (Gigati, Bisina, Kyoga, Nawampasa, and Victoria); the rest were only sampled in 2010. For four of the five lakes that were sampled in multiple years, there were small, but statistically significant differences between years (results not shown). For this reason, we examined overall differences in body size across lakes in two ways: with sampling years considered separately and sampling years pooled.

Length at 50% maturity

To compare length at 50% maturity (L_{50}) across lakes and perturbation levels, we used fish collected in 2010, as this was the year with the most robust sample size, and the greatest number of lakes sampled. Two lakes were excluded from the analysis, one because of low sample size (Nakuwa), and the other because we could not detect a significant association between body size and the probability of maturation (Kayanja). Length at maturity was estimated for females only, as macroscopic staging of male gonads in such small fish is not very reliable.

To test for differences in L_{50}, we ran a nested generalized linear model (GLM) with maturity status (i.e., mature or immature) as a binomial response variable and the following as explanatory variables: perturbation level, lake nested within perturbation level, and standard length. We assumed a binomial error distribution and used a logit link function. We tested the significance of each effect by sequentially removing terms from the model, and testing whether such deletions caused a significant decrease in the log-likelihood of the model, using the likelihood ratio test. Lake-specific values of L_{50} were calculated by setting the probability of maturation to 0.5 in the regression equation for each lake, which simplifies to:

$$L50i = -\frac{(\alpha \mathrm{i})}{\beta \mathrm{i}}$$

where αi and β_i are the intercept and slope, respectively, for lake i. To test for pair-wise differences among specific perturbation levels, we performed an ANOVA on the lake-level estimates of L_{50}, followed by post-hoc Tukey tests. Since the assumptions of normality and homoscedasticity were not well met with so few data points, we also repeated the analysis using the non-parametric Kruskal-Wallis test.

Reproductive traits

We compared reproductive traits (fecundity, egg volume, clutch volume, and ovary weight) across lakes using nested ANCOVA, with lake as a fixed factor nested within perturbation level and somatic body weight as a covariate. Body weight data were missing for 5 fish in the dataset, and so were estimated for these individuals using lake-specific length-weight relationships derived from data for all other fish from that lake (R^2 values for these length-weight relationships were always > 0.98). When necessary, variables were log-transformed to improve normality and homogeneity of variances. For lakes that were sampled in multiple years, we pooled sampling years because visual inspection of the data showed that there were no major differences among years, and pooling improved sample size.

Across-lake trait co-variation

We tested for across-lake trait co-variation using Pearson correlation tests on size-standardized trait means. In particular, we were interested in testing for: (a) co-variation between mean length/L_{50} and size-adjusted reproductive effort (clutch volume and ovary weight adjusted to a common body mass), and (b) trade-offs between egg size and egg number.

Assessing the effect of environmental variables

We ran a separate series of tests to investigate how results from the models described above would be affected by inclusion of lake-specific environmental data (lake area, lake depth, temperature, dissolved oxygen, and water transparency). Several of these environmental variables were strongly inter-correlated, so we first performed a PCA on scaled, centered lake means in order to reduce dimensionality of the data. The first three principal components (PCs) explained 87% of the variance, so these were retained to be used as explanatory variables in our models. For each trait, we built a GLM that included perturbation level, environmental PCs 1 -3, and somatic body weight as covariate, where appropriate. Our interest here lay in testing whether any effects of perturbation level observed in the nested models above remained if we replaced lake with specific environmental data.

Temporal analysis

Historical data

We were able to obtain historical data and/or specimens of *R. argentea* from Lake Victoria for six different time periods spanning the past four decades (Appendix E). Data from 2000 and 2003 were pooled to increase sample size. All historical samples were collected from the Napoleon Gulf of Lake Victoria, which is where we carried out our contemporary (2008-2010) sampling as well. For Lake Kyoga, we were able to obtain historical data from 1991 (Table B1). These data were based on specimens collected at Bukungu Landing, about 50 km away from the Lyingo Landing of Lake Kyoga, where we carried out our contemporary (2008-2010) sampling. Using this combination of museum specimens and unpublished historical data, we were able to examine temporal changes in all life history traits, except for standard length, because different fishing gears were used to capture *R. argentea* in different years, so size distributions were not directly comparable.

Length at 50% maturity

To test for variation in length at maturity (L_{50}) across time periods in each lake, we used the same approach as for the spatial analysis outlined above. We first ran a generalized linear model (GLM) with maturity status (i.e., mature or immature) as a binomial response variable and the following as explanatory variables: standard length, year, and the interaction between SL and year. We then used the parameters from this model to estimate L_{50} for each year, as detailed above.

Reproductive traits

In Lake Victoria, we compared fecundity of *R. argentea* from three key time periods: (i) immediately following the Nile perch introduction into Lake Victoria but before its population boom (1966), (ii) post-Nile perch boom, but before the expansion of the *R. argentea* fishery (1992), and (iii) during the decline of the Nile perch population and large-scale development of the *R. argentea* fishery (2008-2010). In Lake Kyoga, we were only able to examine fecundity for two time periods, both post-Nile perch introduction, but one occurring before (1991) and one after the development of Lake Kyoga's *R. argentea* fishery (2008-2010). Variation in fecundity through time was explored using separate ANCOVAs for each lake, with log-transformed fecundity as the response variable, and year as a categorical explanatory factor. Only standard length was recorded across all time periods, so we used this as the body size covariate in our analyses. Analyses were restricted to mature (Stage V and VI), non-parasitized females.

Data on egg traits of *R. argentea* were only available from Lake Victoria, and only for two time periods: 1966 and 2008-2010. We compared egg traits (mean egg volume, clutch volume, and ovary weight) across years using ANCOVA, with year as a categorical explanatory factor, and somatic body weight as a covariate. We tested for interactions between year and somatic weight, but removed them when they were not significant in order to estimate adjusted means. When necessary, variables were log-transformed improve normality and homogeneity of variances. Because our historical data for egg traits were so limited, we included stage IV, V and VI females for this analysis in order to improve our sample size. Trends were very similar (although not always statistically significant) if we did restrict our analysis to stage V and VI females, as in other analyses.

Rates of phenotypic change

Rates of phenotypic change for each trait over time were calculated in Darwins as:

$$d = \frac{\ln(Z1) - \ln(Z0)}{\Delta \mathrm{T} \text{ x } 10 - 6}$$

where Z_0 and Z_1 are the trait values at the beginning and end of the time series, respectively, and ΔT is the amount of time elapsed, in years. While this metric was initially intended for measuring morphological changes in the fossil record, it has increasingly been applied to the study of contemporary phenotypic change (e.g., Hendry and Kinnison 1999), especially in anthropogenic contexts (Jorgensen et al. 2007; Sharpe and Hendry 2009; Darimont et al. 2009). Another widely-used rate metric is the haldane, which is scaled by the generation time of the species and thus more widely comparable across taxa (Hendry and Kinnison 1999). We did not calculate haldanes in our study, because there are no estimates of the generation time for the Ugandan populations of *R. argentea*, and there is also evidence (from studies carried out in the Tanzanian waters of Lake Victoria) that generation time may have changed dramatically over the time-frame in question (Wanink 1998).

2.4 Results

Spatial analysis

Body size

The mean standard length of *R. argentea* differed among lakes ($F_{5,2475}$ = 369.25, $p < 0.001$) and perturbation levels ($F_{2,2475}$ = 1614.12, $p < 0.001$), with *R. argentea* from unperturbed lakes being largest, those from lakes with Nile perch being intermediate, and those from lakes with Nile perch and fishing being smallest (Fig. 2.2). These patterns of among-lake variation were very consistent across sampling years, and results were virtually identical whether we looked at data from 2010 only or pooled data from all available sampling years for each lake (results not shown).

Length at 50% maturity

The probability of maturation of female *R. argentea* varied significantly across lakes and perturbation levels (Table 2.1). L_{50} was highest in the least perturbed lakes (Gigati, Omuno), intermediate in lakes with Nile perch and fishing (Kyoga and Victoria), and lowest in lakes with Nile perch only (Fig. 2.2). An ANOVA of the lake-level estimates of L_{50} confirmed the overall significance of perturbation level ($F_{2,5}$=9.03, p = 0.022), with post-hoc Tukey tests indicating that the only significant difference was between the unperturbed and nile perch categories. Although our sample size was substantially reduced in this latter analysis (since lake-level estimates were used), the model still had high explanatory power (R^2 = 0.70). When we repeated the analysis using the non-parametric Kruskal-Wallis test, perturbation remained significant (Kruskal Wallis $\chi^2_{0.05,2}$ = 6, p=0.050).

Reproductive traits

Somatic body weight was a significant covariate for fecundity, clutch volume, and ovary weight; but not for egg volume (Table 2.2). The former traits also varied significantly both across lakes and across perturbation levels (Table 2.2), being generally lowest in *R. argentea* from unperturbed lakes, intermediate in *R. argentea* from lakes with Nile perch, and greatest in *R. argentea* from lakes with Nile perch and fishing (

Fig. **2.3**). Egg volume differed among lakes, but not among perturbation levels (Table 2.2), *Rastrineobola argentea* from Lake Nakuwa exhibited noticeably higher fecundity, egg size, and ovary weight than all other lakes.

Across-lake trait co-variation

Mean standard length and L_{50} were positively correlated across lakes (r = 0.69, p = 0.06). *R. argentea* from unperturbed lakes tended to have both high mean body size and high L_{50}, whereas *R. argentea* from lakes with Nile perch had both lower mean body size and lower size at maturity (Fig. 2.4). There were indications of a negative relationship between body size and both metrics of total reproductive effort: size-adjusted clutch volume (r = -0.44, p = 0.28), and size-adjusted ovary weight (r = -0.52, p = 0.19). *R. argentea* from unperturbed lakes tended to have both larger mean body size and lower size-adjusted clutch volume/ovary weight; whereas populations from lakes with Nile perch and fishing tended to have lower mean body size and higher size-adjusted clutch volume/ovary weight (Fig. 2.4). There were no significant correlations between L_{50} and clutch volume (r = 0.27, p = 0.57) or ovary weight (r = -0.0003, p = 0.99). Finally, there was no evidence for a trade-off in egg size versus egg number of *R. argentea* across lakes (r = 0.18, p = 0.61).

Assessing the effect of environmental variables

Environmental variation across lakes was summarized by three major principal component axes, which together accounted for 87% of the variation (Appendix F). Inclusion of these three PCs in models of trait variation did not affect the qualitative or quantitative nature of the trends reported above. That is, perturbation remained statistically significant, and the differences between perturbation categories were conserved, regardless of whether we included lake as a nested factor (Table 2.2), or whether we explicitly modeled the effects of five environmental parameters that varied across those same lakes (Appendix G, Appendix H).

2.4.1 Temporal analysis

Length at 50% maturity

In Lake Victoria, the probability of maturation varied significantly across years (Table 2.1). The length at maturity of female *R. argentea* in Lake Victoria appears to have remained relatively steady at approximately 46 mm SL from 1966 until the 1990s, when it began to decline (Fig. 2.5). The rate of decline in L_{50} accelerated even further between 2000 and 2010, coinciding with intensification of the *R. argentea* fishery in the Ugandan waters of Lake Victoria. Overall, the length at maturity of female *R. argentea* has declined by about 16% in the past 44 years, which is equivalent to a phenotypic rate of change of -4.07×10^3 Darwins (Table 2.3) If we split the time-series in 1991, two years after the opening of the *R. argentea* fishery in the Napoleon Gulf (1989), we can roughly isolate the fisheries-induced portion of the decline. Looking at this latter part of the time-series, L_{50} has declined by about 16% in the 18 years since fishing began, which is equivalent to a rate of -10.15×10^3 Darwins.

Reproductive traits

In Lake Victoria, fecundity was positively correlated with body size for the 1992 and contemporary specimens (Table 2.4). For 1966; however, the range of body sizes of the available museum specimens was so narrow that the expected positive relationship between fecundity and standard length was not detectable. This resulted in a significant interaction between standard length and year, which we removed in order to compare adjusted means across years. Assuming a common relationship between fecundity and standard length across years, size-adjusted fecundity of *R. argentea* from Lake Victoria varied significantly across time periods ($F_{2,27} = 6.31$, $p = 0.006$), increasing from 1966 to 1992 and then declining again slightly between 1992 and 2008-2010 (Fig. 2.6). Overall, size-adjusted fecundity in Lake Victoria increased about 42% from 1966 to the present, which is equivalent to 8.14×10^3 Darwins (Table 2.3).

In Lake Kyoga, fecundity was also positively correlated with standard length, and there were no significant differences in the slope of this relationship between years (Table 2.4). Size-adjusted fecundity did not differ significantly before (1991) vs. after (2008-2010) the development of a commercial *R. argentea* fishery in Lake Kyoga ($F_{1,76}$ =0.006, p=0.939).

All egg traits (egg volume, clutch volume, and ovary weight) were significantly positively correlated with somatic body weight, and this relationship was consistent across time periods (Table 2.4). Size-adjusted egg volume, clutch volume, and ovary weight of *R. argentea* in the Napoleon Gulf of Lake Victoria all showed indications of an increase between 1966 and 2008-2010 (Fig. 2.6), and this increase was statistically significant for the first two traits (Table 2.4). Rates of increase for these traits varied between 6.98×10^3 and 15.81×10^3 Darwins (Table 2.3).

2.5 Discussion

We examined the joint effects of an introduced predator and fishing on life history traits in *R. argentea*, using both spatial (across-lake) and temporal comparisons. We found, first, that the mean length of *R. argentea* was significantly lower in invaded and fished lakes relative to unperturbed lakes, and that these differences were conserved across multiple sampling years. Length at 50% maturity was also significantly reduced in perturbed relative to unperturbed contexts. In the spatial analysis, L_{50} was lowest in lakes with Nile perch only, whereas in the temporal analysis, L_{50} was lowest in years with Nile perch and fishing. Size-specific fecundity generally increased in perturbed relative to unperturbed contexts. In the spatial analysis, the greatest increase in fecundity was observed in lakes with Nile perch and fishing; whereas in the temporal analysis, the greatest increase in fecundity was observed after the Nile perch introduction (1992) and there was no additional increase in fecundity after almost two decades of commercial fishing, either in Lake Victoria or Lake Kyoga. Egg volume did not differ across perturbation levels spatially; but did increase significantly over time. Size-adjusted clutch volume and ovary weight both increased in perturbed relative to unperturbed contexts; being greatest in contexts with introduced Nile perch and fishing, both across lakes and through time. Overall, introduced Nile perch and fishing tended to be associated with a suite of life history responses in

R. argentea, including: decreased body size, maturation at smaller sizes, and increased reproductive effort (larger eggs; and higher relative fecundity, clutch volume, and ovary weight).

Although it is not possible to conclusively infer causation from correlative, field-based studies, we believe that this study provides strong support for the hypothesis that the Nile perch introduction and commercial fishing are important drivers of contemporary life history change in *R. argentea*. First, we found that patterns of co-variation between life history phenotypes and the presence/absence of Nile perch and fishing were quite consistently replicated across both space and time. Such congruence would be unlikely if other unmeasured variables were the major drivers of life history change. Second, in the spatial analysis, we showed that our main findings (i.e., significant differences among perturbation categories) were robust to the inclusion of five important environmental variables (lake area, lake depth, water temperature, dissolved oxygen, and water transparency). It is important to note here that lake area is somewhat confounded with the effect of fishing, given that *R. argentea* fisheries have only been developed on the two largest lakes (Victoria and Kyoga). However, lake area tends to be positively correlated with body size and size at maturity in fish (e.g., Burr 1993; Chen and Harvey 1994; McDermid et al. 2010). If lake size were a major driver in our system, we would expect *R. argentea* in lakes Kyoga and Victoria to mature at larger sizes and be larger overall relative to *R. argentea* in smaller lakes; however, we observed the opposite. Third, the observed direction of change in life history traits is consistent with predictions from life history theory, i.e. that increased mortality will select for earlier maturation at smaller sizes (Law and Grey 1989; Abrams and Rowe 1996; Ernande et al., 2004).

2.5.1 R. argentea as a survivor in the highly perturbed Lake Victoria ecosystem

This study greatly expands our understanding of how *R. argentea* has adapted to novel stressors in Lake Victoria. Wanink (1998) was the first to suggest that *R. argentea* may have undergone rapid phenotypic changes as a result of the Nile perch introduction. He documented striking changes in life history traits of *R. argentea* in the Mwanza Gulf of Lake Victoria before (1983) versus after (1987-88) the Nile perch population boom, including declines in the mean size of ripe females, age and size at maturity, and absolute fecundity (Wanink 1998; Wanink and Witte 2000). By providing a longer-term historical context and covering a broader spatial scale, our data help to further elucidate the generality, timing, and potential drivers of these trends from the Tanzanian waters. For example, Wanink (1998) interpreted the decline in size at maturity of female *R. argentea* in the Mwanza Gulf between 1983 and 1988 primarily as a consequence of increased Nile perch predation. However, historical catch landings data show that this time period also coincided with the development of the *R. argentea* fishery in the Tanzanian waters (Wanink 1999). Interestingly, the difference in the timing of the decline in L_{50} of *R. argentea* across Lake Victoria is consistent with the difference in the timing of the development of the *R. argentea* fishery (both occurred about a decade earlier in the Mwanza Gulf relative to the Napoleon Gulf). Taken together, Wanink and Witte's data and our own show that a significant decline in L_{50} in *R. argentea* has occurred in at least two regions of Lake Victoria, and suggest that commercial fishing has likely played an equal, if not more important, role than Nile perch predation in driving these changes.

Because the *R. argentea* fishery is still so new, there has been little research prior to this study specifically examining its potential phenotypic impacts. Wandera (1992) found a small decline in the mean size of adult *R. argentea* during early years of expansion of the fishery in Ugandan waters. Further declines in the mean length of the Ugandan population were noted between the 1990s and 2006 (NaFIRRI, 2008). Taabu (2004) found that *R. argentea* in heavily fished inshore areas of Northern Lake Victoria were significantly smaller than *R. argentea* from offshore areas, consistent with our findings that populations are significantly smaller in fished versus unfished lakes. Previously published values for L_{50} of *R. argentea* from the Northern waters of Lake Victoria hint at a decline as well, from 43-44 mm SL in 1988 (Wandera, 1992), to 42 mm SL in 1996-97 (Wandera, 1999), 41 mm in 2001-2002 (Taabu, 2004), to 40 mm SL in 2004-2005 (NaFIRRI, 2005). Our study is consistent with, and extends, these early trends.

2.5.2 Underlying mechanisms for life history changes in R. argentea

What mechanisms might be underlying these observed shifts in life history traits in *R. argentea*? One possibility is that they represent a genetic (evolutionary) response to selection imposed by fishing and/or Nile perch predation. Genetic changes can be expected if mortality is high and non-random and the traits under selection are heritable. Artificial selection experiments and aquaculture studies have shown that life history traits are moderately heritable in many fishes (Gjedrem 1983; Law 2000), although this has not been tested in *R. argentea* specifically. We do know; however, that fishing mortality on *R. argentea* is high (1.22 - 1.98 yr^{-1}, Manyala and Ojuok 2007) and that this species has a short generation time (estimates from the Tanzanian waters of Lake Vitctoria: 0.3-0.9 yr, Wanink 1998), making contemporary evolutionary change a plausible hypothesis. A second possibility is that the observed shifts in life history traits represent plastic changes occurring as an indirect result of fishing and/or Nile perch predation. In theory, fishing and/or predation can lower the density of prey populations, thus increasing per capita food availability. This can result in increased individual growth rates, and associated plastic changes in life history traits, such as earlier maturation, larger size at maturity, and increased fecundity (e.g., Cardinale and Modin 1999; Cassoff et al. 2007; Walsh and Reznick 2008). In contrast to this expectation; however, there is evidence that the biomass of *R. argentea* in Lake Victoria has increased dramatically over the past three decades, potentially due to competitive release following the decline of the haplochromine cichlids in the 1980s (Wanink and Witte 2000). Experimental catch rates of *R. argentea* in the Mwanza Gulf increased 7-fold from 1981 to 1989 (Wanink 1999), and estimated lake-wide biomass more than quadrupled from 245,000 tons in 1999 to 1,055,600 tons in 2007 (NaFIRRI, 2008; Tumwebaze et al. 2007). There are few data on how availability of zooplankton (a primary food of *R. argentea*) has changed over time in Lake Victoria, but it may have increased as well, given that algal biomass has quintupled since the 1960s (Hecky et al. 2010), and that most of the lake’s other indigenous zooplanktivores have gone extinct or dramatically declined (Witte et al. 1992), although there is evidence of a limited, contemporary resurgence of some zooplanktivorous cichlids (Witte et al. 2000). Thus individual growth rates of *R. argentea* may conceivably have increased (if food availability has increased more rapidly than biomass), decreased (if the converse is true), or remained the same. Unfortunately, due to the difficulty of ageing tropical fish, there are no direct estimates of how individual growth rates of *R. argentea* vary through time or across lakes in the Lake Victoria basin. Length-frequency analysis has been used to derive growth estimates in two earlier studies (Wandera and Wanink 1995; Wanink 1998); however, interpretation of these data is challenging, and there is clearly a need for additional ageing studies,.

Our findings for L_{50} (lower L_{50} through time, and in invaded relative to uninvaded lakes) are consistent then with two possible mechanisms: (i) an evolutionary response to selection for smaller size at maturity, and/or (ii) a plastic effect, for example resulting from reduced per capita food availability. The observed pattern for reproductive effort (higher through time, and in fished vs. unfished contexts) would be also consistent with two possibilities: (i) an evolutionary response to selection for increased reproductive investment, and/or (ii) a plastic effect, for instance resulting from increased per capita food availability. Overall, the life history changes that we observed likely reflect some combination of evolutionary change and phenotypic plasticity, but our data do not yet allow us to determine the relative importance of these two mechanisms. Further research, such as common garden experiments rearing fish from invaded and uninvaded lakes at multiple resource levels is necessary to distinguish between these various possibilities.

We should note here that interpretations regarding the observed changes in L_{50} will depend on the form (shape) of the probabilistic maturation reaction norm (PMRN) for *R. argentea*. PMRNs describe the age and size-specific probabilities of reaching sexual maturation, independent of growth and mortality (Heino et al. 2002). Our interpretations above are based on the assumption that the PMRN for

R. argentea has a negative slope, i.e., that fish will have the same probability of maturing either by being large (at a young age), or by being old (at a smaller size). Of the species for which PMRNs have been calculated so far, almost all do indeed have negative slopes (e.g., North sea plaice (Grift et al. 2003; van Walraven et al. 2010), Northern cod (Olsen et al. 2004); American plaice (Barot et al. 2005); North sea sole (Mollet et al. 2007); and Icelandic cod (Pardoe et al. 2009)), making this a reasonable starting assumption for *R. argentea*. It should be pointed out too; however, that fishing can cause the slope of the PMRN itself to evolve, which has been highlighted in theoretical models (Ernande et al. 2004) and demonstrated empirically (Engelhard and Heino 2004). Elucidating the form of the PMRN for *R. argentea* and examining temporal and spatial variation in PMRNs will be an important direction for future research on fisheries-induced life history change in this species.

2.5.3 Fisheries-induced life history change

This study represents one of the first well-documented examples of fisheries-induced phenotypic change in a tropical, freshwater species. Our results corroborate trends observed in many other commercially harvested fish stocks, where declines in mean length and length at maturity have been widespread (reviewed in Hutchings and Baum 2005; Jorgensen et al. 2007; Sharpe and Hendry 2009). For *R. argentea*, we found a rate of fisheries-associated decline in L_{50} of -10.15 x 10^3 Darwins, which is very close to the average rate of decline for other commercial stocks (mean of 18 stocks: -10.6 +- 9.6 x 10^3 Darwins (Sharpe and Hendry 2009)). We should note; however, that the estimated generation time for *R. argentea* (0.3-0.9 yr, Wanink 1998) is much shorter than all other stocks in that meta-analysis, which should be kept in mind when comparing rates across taxa. Fewer studies have examined the long-term effects of fishing on fecundity or reproductive investment. Increases in size-specific fecundity following several decades of exploitation have been reported for inshore North Sea cod, *Gadus morhua* (Yoneda and Wright 2004), North Sea haddock, *Melanogrammus aeglefinus* (Wright et al. 2011), and Lake Constance whitefish, *Coregonus* *lavaretus* (Thomas et al. 2009), but were not conclusive for North Sea plaice, *Pleuronectes platessa* (Rijnsdorp et al. 2005; van Walraven et al. 2010).

The fact that the rate of fisheries-induced change in *R. argentea* is comparable to many heavily fished marine stocks is remarkable, for several reasons. First, the duration of exploitation for *R. argentea* has been quite short (about 20 years in the Ugandan waters), relative to many North Atlantic stocks that have been exploited for hundreds of years. Second, the *R. argentea* fishery in Ugandan waters is operated primarily from paddled craft, in contrast to many highly industrialized marine fisheries. Third, the *R. argentea* fishery targets a very broad range of sizes that includes both mature and immature individuals (Wandera 1992; Taabu 2004, Sharpe and Chapman, unpl. data) in contrast to many commercial marine fisheries that operate using highly size-selective gears. This last point is of particular interest, because age or size-selective mortality has long been thought to be an important pre-requisite for life history evolution in general (Gadgil and Bossert 1970; Law 1979; Michod 1979), and for fisheries-induced evolution in particular. However, recent models suggest that unselective predation (Abrams and Rowe 1996) or fishing (Law and Grey 1989; Heino 1998; Ernande et al. 2004) can also cause evolution in life history traits. Our work adds further empirical support to this body of theory; and suggests that strong size-selectivity may not be a necessary prerequisite for phenotypic change in life history traits in commercially fished stocks, so long as mortality is high.

2.5.4 Predator-induced life history change

This study is also one of the first to document contemporary life history change in native prey in response to an introduced predator. In a recent review of evolutionary responses of natives to introduced species, Strauss et al. (2006) compiled 11 known cases of phenotypic change in native prey in response to introduced predators: of these, six involved behavioural changes in the prey, and five involved changes in morphology; but there were none reporting changes in life history traits. To our knowledge, only a few other studies to date have found evidence for life history change in native prey following exposure to a novel predator (e.g., Fisk et al. 2007; Walsh and Reznick, 2010; Billman et al. 2011). As more examples like these accumulate, we will be better able to understand the conditions under which native prey adapt to novel predators rather than declining to extinction.

2.5.5 Implications for sustainability of the R. argentea fishery

Previous authors have argued that *R. argentea's* life history tactics and flexibility in other traits facilitated its success relative to other prey of the Nile perch, many of which went extinct (Wanink 1998; Wanink and Witte 2000). Indeed, *R. argentea* is a classic example of r-selected (*sensu* Pianka 1970) or opportunistic (*sensu* Winemiller and Rose 1992) species, which are expected to be resilient to uncertain environments and high mortality. This logic underlies the widespread assumption that short-lived, fast-growing pelagic fishes should be more resistant to overfishing than long-lived, late-maturing species. However, a recent meta-analysis showed that globally, fisheries targeting small, low trophic level species are just as likely to collapse as those targeting large, high trophic level fishes (Pinsky et al. 2011). Should we be concerned then about the long-term sustainability of the *R. argentea* fishery?

Based on our findings that (i) mean body size is 34% lower in invaded and fished lakes relative to unperturbed lakes; and (ii) L_{50} has declined by 16% since the Nile perch introduction and onset of fishing; we believe that there is now reason for concern for the future of the *R. argentea* fishery. Several researchers have suggested that rapid life history changes should be interpreted as a warning sign of impending stock decline, as they typically signal high levels of mortality (Trippel 1995; Olsen et al. 2004). Indeed, fishing mortality for *R. argentea* has been estimated to be as high as 1.22 – 1.98 yr^{-1} (Manyala and Ojuok, 2007). Furthermore, both theory and experiment suggest that fisheries-induced changes in life history traits can have negative implications for yield and the probability of population persistence (Edley and Law 1988; Heino 1998; Conover and Munch 2002; Walsh et al. 2006). In the case of *R. argentea*, the dramatic decline in body size and L_{50} over time and in perturbed relative to unperturbed lakes is of greatest concern, because fecundity (and hence recruitment) is positively correlated with the body size of spawners. Even though size-specific fecundity has increased, it may not be enough to counter-act the detrimental effects of the overall decline in body size, resulting in a net decline in per capita recruitment.

R. argentea is now the most important commercial fish stock by mass in Lake Victoria (NaFIRRI 2008), whose combined fisheries meet the fish consumption needs of an estimated 30 million East Africans (LVFO 2011). The Lake Victoria basin is also home to the fastest growing human population on the African continent (UNEP 2006), so ensuring food security in the coming decades will be a challenge. The *R. argentea* fishery is still in its infancy, yet already shows signs of potentially detrimental fisheries-induced phenotypic changes. Given the long history of overfishing and previous fisheries collapses in Lake Victoria, we urge that these early indications of fisheries-induced change in *R. argentea* be investigated further. We recommend continued monitoring of life history traits in *R. argentea*, as well as the implementation of a permanent lake-wide initiative to monitor basic stock characteristics. In order to reduce the probability of further fisheries-induced life history change in *R. argentea,* there are two avenues for managers to consider: (i) altering catch selectivity so as to reduce selection for early maturing genotypes, and/or (ii) lowering the overall rate of fishing mortality.

In the first instance, many authors have argued that the dome-shaped selectivity curves that characterize many fixed gears such as traps and gill-nets (those that target intermediate-sized fish and provide protection for both the smallest and largest individuals) are preferable in terms of avoiding fisheries-induced evolution (Conover and Munch 2002; Law 2007; Jørgensen et al. 2009; Hutchings 2009). In contrast, the knife-edged selectivity curves that characterize many active gears like trawls are most likely to generate strong selection for earlier maturation (Jørgensen et al. 2009; Hutchings 2009). Given that the *R. argentea* fishery currently relies on trawling with small-mesh gears exclusively, what options may be available to minimize the strong selection that this gear likely generates? Models indicate that fisheries-induced evolution imposed by knife-edged selectivity curves can be mitigated only by keeping F very low and confined to mature fish (Jørgensen et al. 2009), i.e. by setting the minimum size threshold above the maturation reaction norm (Ernande et al. 2004). In the case of *R. argentea,* this could be achieved by switching back to a 10 mm-mesh lampara net, which primarily targets individuals above 40 mm SL (just above the current size at maturation of *R. argentea* in Lake Victoria), and/or by encouraging fishers to move further offshore where there are fewer immature fish (Taabu 2004; Wanink 1999). In addition to reducing the probability of further fisheries-induced change, such practices would be consistent with the traditional fisheries management goal of preventing recruitment overfishing by reducing the high proportion of immature *R. argentea* in commercial catches (Wanink 1999; Taabu 2004; Tumwebaze et al. 2007). They would also help reduce by-catch of juveniles of other commercially-important species such as Nile perch and Nile tilapia (*Oreochromis niloticus)* (Taabu 2004).

A second avenue for avoiding fisheries-induced change irrespective of modifications to gear selectivity would be simply to lower the overall rate of fishing mortality (Hutchings 2009). Further research aimed at identifying the evolutionarily-sensitive threshold for this stock (i.e., the level of fishing mortality above which fisheries-induced evolution is expected to occur, F_{evol}, (Hutchings 2009)) would be useful for determining whether fishing effort should be curbed. In the Lake Victoria basin, this could be achieved by limiting the number of boats and/or lampara nets at each landing, although this would be challenging to implement in practice.

2.6 Data Archiving Statement:

Data deposited in the Dryad repository: doi:10.5061/dryad.1154dd89

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Table 2.1 Analysis of deviance from generalized linear models examining variation in maturation of female *R. argentea* across lakes (spatial analysis) and through time in Lake Victoria (temporal analysis).

Analysis	Effect removed	df	Deviance	Residual df	Residual deviance	p
Spatial	Perturbation	2	208.32	1001	1165.58	<0.0001
	Lake (Perturbation)	5	149.35	995	585.55	<0.0001
	SL	1	430.68	1000	734.90	<0.0001
Temporal	SL	1	1225.80	2887	2101.7	<0.0001
	Year	8	175.67	2879	1926.0	<0.0001
	Year x SL	8	129.45	2871	1796.5	<0.0001

Table 2.2 Results from nested ANCOVAs examining variation in reproductive traits of *R. argentea* across lakes and perturbation levels.

Trait	Effect	df	F	p	R^2
Log Fecundity	Perturbation	2	6.20	0.003	0.83
	Lake (Perturbation)	7	11.03	< 0.001	
	Log Somatic Weight	1	141.09	< 0.001	
	Residual	157			
Egg Volume	Perturbation	2	0.92	0.399	0.27
	Lake(Perturbation)	7	9.89	<0.001	
	Log Somatic Weight	1	0.11	0.739	
	Residual	151			
Log Clutch Volume	Perturbation	2	4.79	0.010	0.73
	Lake(Perturbation)	7	10.58	< 0.001	
	Log Somatic Weight	1	65.69	< 0.001	
	Residual	151			
Log Ovary Weight	Perturbation	2	11.12	< 0.001	0.82
	Lake(Perturbation)	7	14.37	< 0.001	
	Log Somatic Weight	1	164.02	< 0.001	
	Residual	209			

Table 2.3 Mean size-adjusted trait values for *R. argentea* from Lake Victoria at the beginning (Z_0) and end (Z_1) of the time-series, along with % change and rate of phenotypic change in Darwins. See text for equation for estimating Darwins.

Trait	Time Period	Z_0	Z_1	% Change	Rate (Darwins x 10^3)
L_{50} (overall)	1966 – 2008-10	46.54	39.07	-16.05	-4.07
L_{50} (fishing)	1991 – 2008-10	46.90	39.07	-16.70	-10.15
Relative fecundity	1966 – 2008-10	590	837	+41.91	8.14
Relative egg volume (mm^3)	1966 – 2008-10	0.046	0.078	+68.11	12.08
Relative clutch volume (mm^3)	1966 – 2008-10	26.05	51.42	+97.39	15.81
Relative ovary weight (mg)	1966 – 2008-10	74.44	100.48	+34.99	6.98

Table 2.4 Results from ANCOVAs examining variation in fecundity, egg volume, clutch volume, and ovary weight of *R. argentea* in the Napoleon Gulf of Lake Victoria from 1966 to 2008-2010; as well as variation in fecundity of *R. argentea* in Lake Kyoga from 1991 to 2008-2010.

Lake	Trait	Effect	df	F	p	R^2
Victoria	Log(Fecundity)	Year	2,27	3.19	0.057	0.44
		SL	1,27	0.99	0.330	
		Year x SL	2,27	3.91	0.032	
Victoria	Log(Egg Volume)	Year	1,33	15.80	< 0.001	0.29
		Somatic Weight	1,33	5.83	0.022	
Victoria	Log(Clutch Volume)	Year	1,33	6.70	0.014	0.19
		Somatic Weight	1,33	10.09	0.003	
Victoria	Log(Ovary Weight)	Year	1,34	2.27	0.141	0.44
		Somatic Weight	1,34	23.34	<0.001	
Kyoga	Log(Fecundity)	Year	1,76	0.006	0.939	0.86
		Log(SL)	1,76	154.25	<0.001	

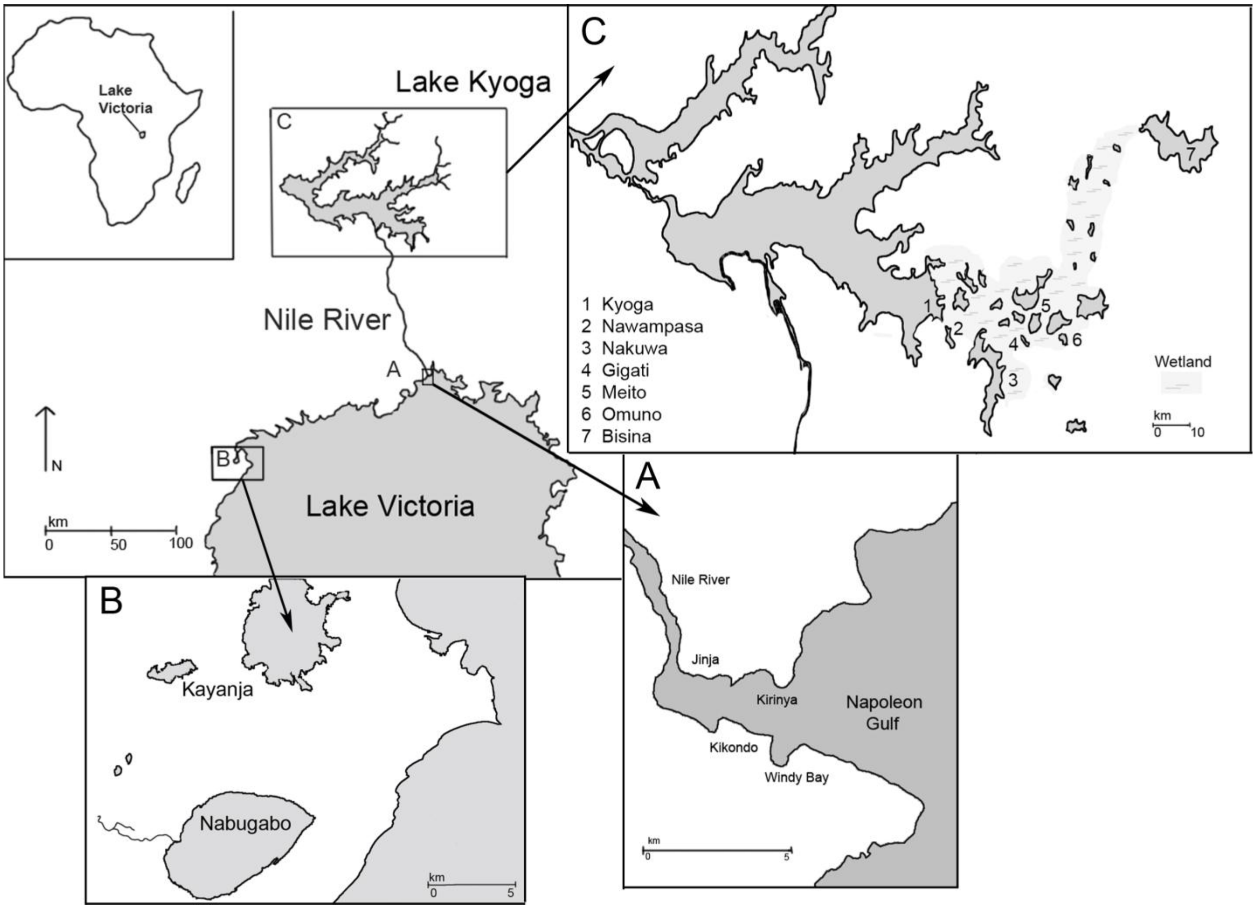

Fig. 2.1 Map of study sites within the Lake Victoria basin of East Africa, with sampling regions enlarged.

The 10 lakes sampled for this study were: Victoria (A), Nabugabo (B), Kayanja (B), Kyoga (C), Nawampasa (C), Nakuwa (C), Gigati (C), Meito (C), Omuno (C) and Bisina (C). All contemporary (2008-2010) and historical (1966-2000) sampling on Lake Victoria was carried out in the Napoleon Gulf (A), a large sheltered bay on the northern shore of Lake Victoria, just upstream of the source of the Victoria Nile. The catchment is densely populated (587 people/km^2) and encompasses Jinja, the second largest city in Uganda and a major national industrial centre. Lakes Nabugabo and Kayanja (B) are small satellite lakes on the Northwestern shore of Lake Victoria. The Lake Kyoga system (C) is comprised of over a dozen small, shallow lakes interconnected by extensive wetlands, which together span over 4700 km^2 across the Ugandan districts of Kamuli, Pallisa, Kumi, and Soroti. The wetlands of the Kyoga system are dominated by dense stands of papyrus, *Cyperus papyrus*, and are considered to be one of the remaining pristine wetland areas in Uganda, due to their remote location and relatively low population densities. The Kyoga system is characterized by strong seasonal flooding during the two rainy seasons, and so water levels and connectivity among lakes may shift over time.

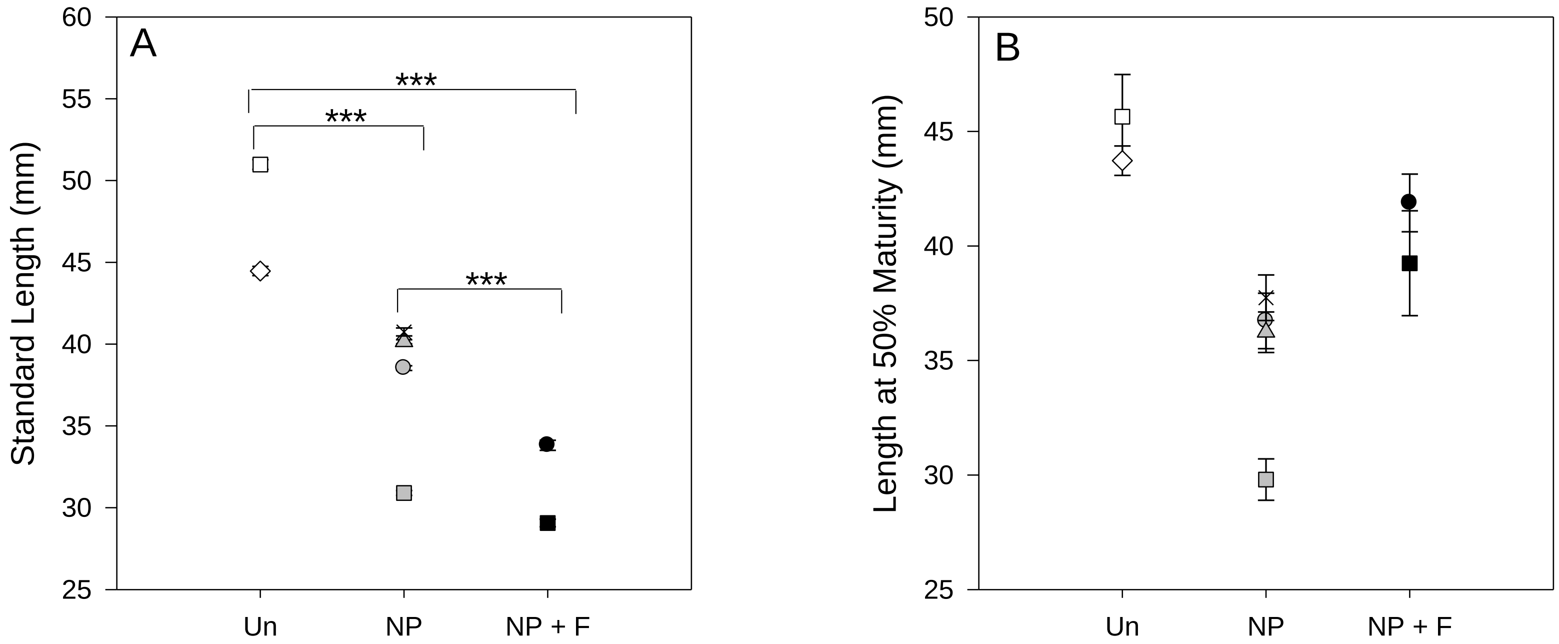

Fig. 2.2 Standard length and length at maturity of *R. argentea* across lakes.

Panel A shows the mean standard length (±1 SE) of *R. argentea* caught in 5-mm lampara nets in 2010. Panel B shows the length at 50% maturity (± 2 SE) of female *R. argentea* in 2010 . The colours represent unperturbed lakes (“Un”,white), lakes with Nile perch only (“NP”, grey), and lakes with Nile perch and commercial fishing (“NP + F”, black). The lakes are: Omuno (white square), Gigati (white diamond), Nawampasa (grey circle), Bisina (grey square), Meito (grey triangle), Nabugabo (grey cross), Kyoga (black circle), and Victoria (black square). For standard length, post-hoc Tukey tests showed that all group means were significantly different from one another ($p < 0.001$), indicated by ***. For length at maturity, post-hoc pair-wise comparisons were not conducted, since each estimate of L_{50} is a population-level estimate derived from parameters from the logistic regression. However, we have shown each mean ± 2 SE, which approximate 95% confidence intervals. Thus, pairs of lakes with non-overlapping error bars can be interpreted as being significantly different at the 0.05 significance level.

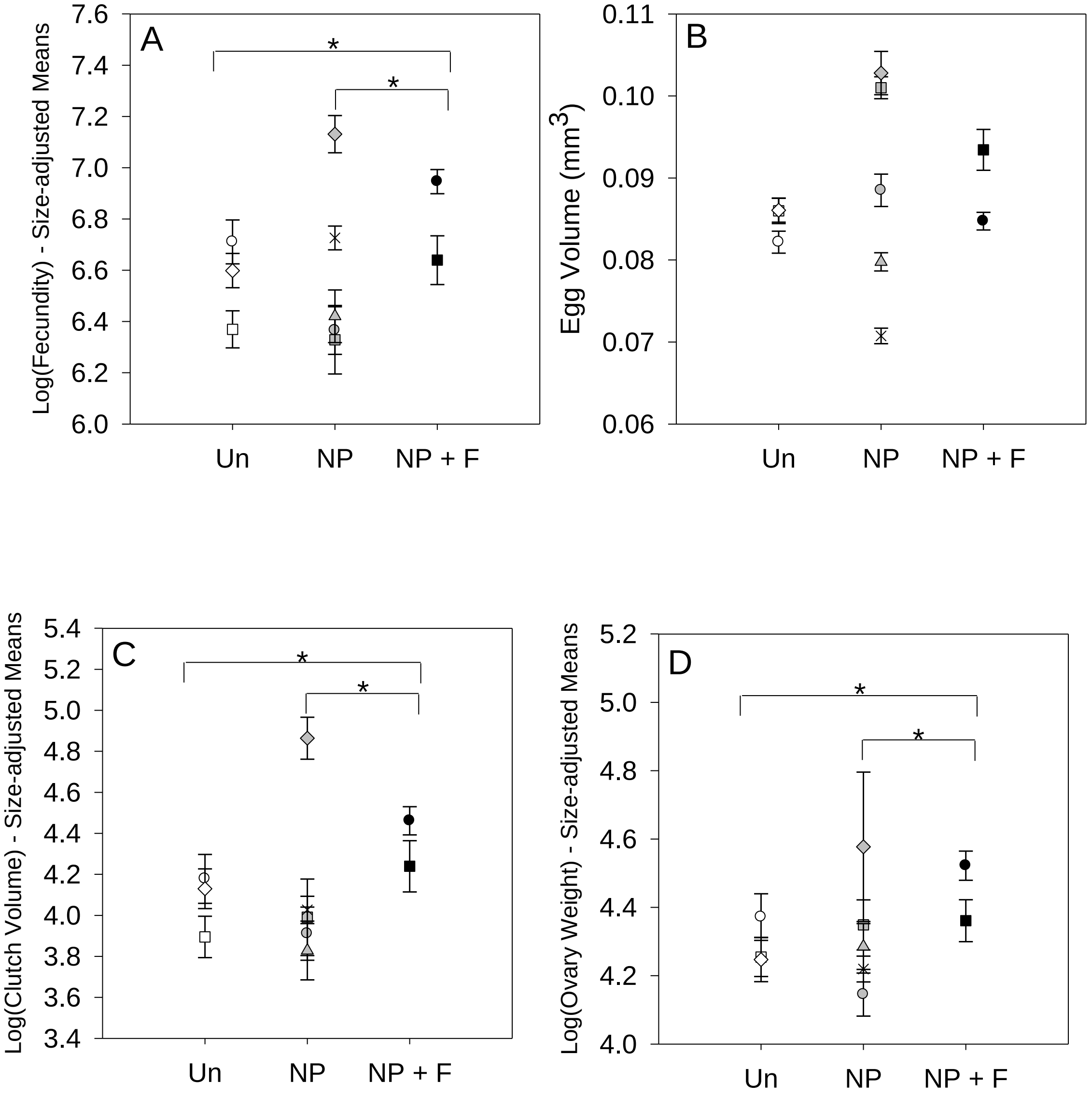

Fig. 2.3 Reproductive traits of *R. argentea* across lakes.
Size-adjusted means (± 1 SE) for (A) fecundity, (B) egg volume, (C) clutch volume, and (D) ovary weight of mature (Stage V and VI) female *R. argentea*. These are adjusted means from an ANCOVA with log(somatic body weight) as a covariate. The colours represent unperturbed lakes ("Un", white), lakes with Nile perch only ("NP", grey), and lakes with Nile perch and commercial fishing ("NP + F", black). The lakes are: Kayanja (white circle), Omuno (white square), Gigati (white diamond), Nawampasa (grey circle), Bisina (grey square), Nakuwa (grey diamond), Meito (grey triangle), Nabugabo (grey cross), Kyoga (black circle), and Victoria (black square). The * indicate significant ($p < 0.05$) differences between pairs of perturbation categories based on post-hoc Tukey tests.

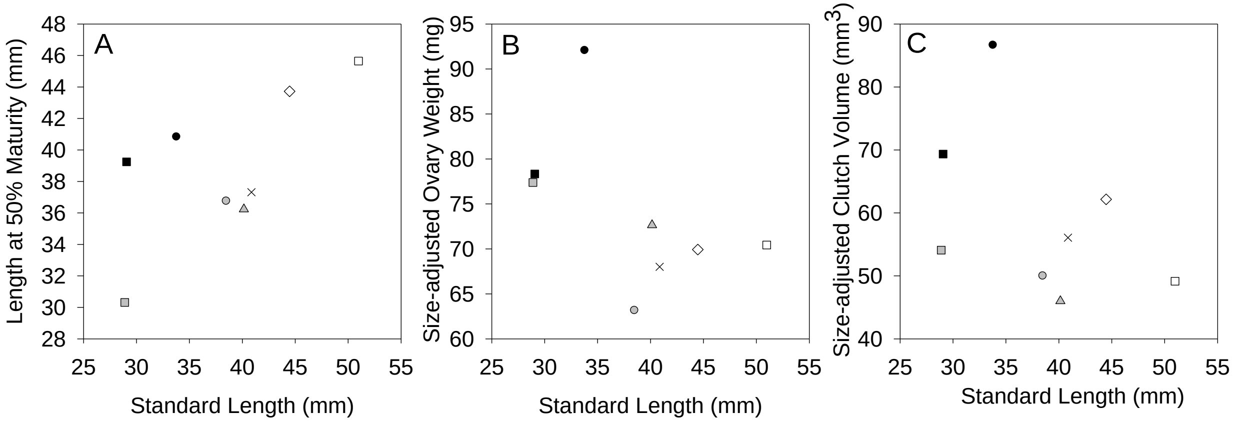

Fig. 2.4 Across-lake correlations between size-adjusted trait means.

The colours represent unperturbed lakes (white), lakes with Nile perch only (grey), and lakes with Nile perch and commercial fishing (black). The lakes are: Omuno (white square), Gigati (white diamond), Nawampasa (grey circle), Bisina (grey square), Meito (grey triangle), Nabugabo (grey cross), Kyoga (black circle), and Victoria (black square). Note that two lakes (Kayanja and Nakuwa) are not shown, because we did not have estimates of L_{50} and mean SL for these populations.

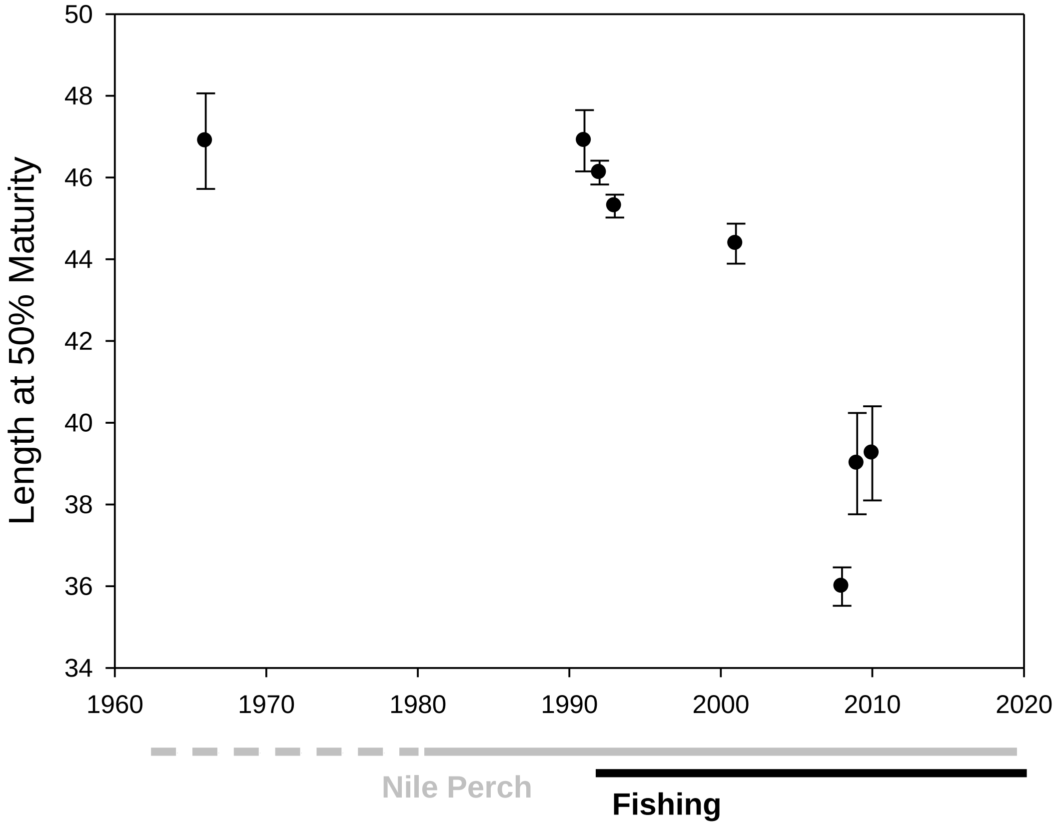

Fig. 2.5 Length at 50% maturity (± 1 SE) of female *R. argentea* from the Napoleon Gulf of Lake Victoria from 1966 to 2010.

The bars below the figure indicate the approximate timing of the population boom of the introduced Nile perch (grey) and the onset of commercial *R. argentea* fishing (black).

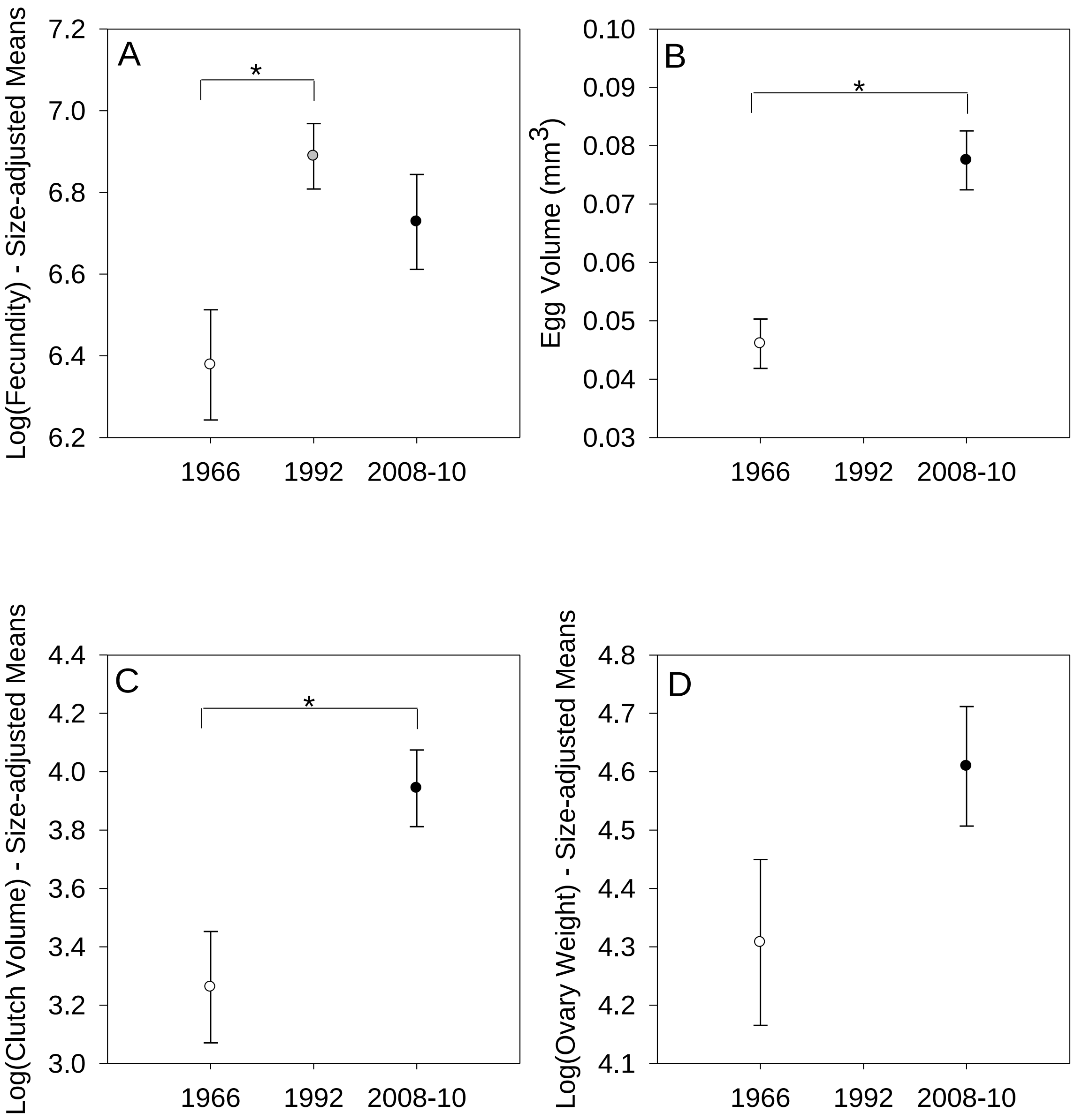

Fig. 2.6 Reproductive traits of *R. argentea* through time.
Size-adjusted means (± 1 SE) for (A) fecundity, (B) egg volume, (C) clutch volume, and (D) ovary weight for mature (Stage IV – VI) female *R. argentea* from the Napoleon Gulf of Lake Victoria. These are adjusted means from an ANCOVA model examining variation in each trait as a function of log(somatic weight) and year. The colours indicate the following time periods: pre-Nile perch boom/pre-commercial fishing (white), post-Nile perch boom/pre-commercial fishing (grey), and post-Nile perch boom/post-commercial fishing (black). The * indicate significantly different pairs based on post-hoc Tukey tests ($p < 0.05$).

PREFACE TO CHAPTER 3:

Morphological responses to an introduced predator?

In Chapter 2, I tested for the effects of two novel stressors (fishing and an introduced predator) on life history traits in *R. argentea*, using a combination of spatial and temporal comparisons. I found that, both through space and time, *R. argentea* populations that had been subjected to fishing and predation pressure generally showed reductions in mean body size and length at maturity, and increases in size-specific reproductive investment. These trends are consistent with expectations from life history theory, and match trends documented in many other global fish stocks (Chapter 1). In the following chapter, I shift the focus from life history traits to morphology, and ask whether predation from an introduced predator (the Nile perch) can select for changes in overall body morphology in native prey (*R. argentea*) on contemporary time scales. I use a similar approach (temporal and spatial comparisons between invaded and uninvaded populations) to test the prevailing ecomorphological paradigm that in fish, predation selects for increased allocation to the mid-body/caudal region, so as to improve escape swimming ability. This theory has good empirical support, but has not yet been examined in the context of biological invasions, and we do not yet have a good understanding of the extent to which rapid morphological adaptation might influence interactions between introduced predators and native prey.

CHAPTER 3

3 Evidence for rapid morphological change in a resilient endemic species in response to an introduced predator

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3.1 Abstract

Human activities, such as species introductions, are dramatically and rapidly altering natural ecological processes, and may result in novel selection regimes. To date, we still have a limited understanding of the extent to which such anthropogenic selection may be driving contemporary phenotypic change in natural populations. Here we test whether the introduction of the predatory Nile perch, *Lates niloticus*, into East Africa's Lake Victoria and nearby lakes resulted in morphological change in one resilient native prey species, *Rastrineobola argentea*. Drawing on prior eco-morphological research, we predicted that this novel predator would select for a deeper mid-body/caudal region in *R. argentea* to enhance burst swimming performance (and hence escape ability). To test this prediction, we compared body morphology of *R. argentea* across space (nine Ugandan lakes differing in Nile perch invasion history) and through time (before and after establishment of Nile perch in Lake Victoria). Spatial comparisons of contemporary populations supported our predictions, with *R. argentea* from invaded lakes generally having deeper mid-body/caudal regions and smaller heads compared to *R. argentea* from uninvaded lakes. We observed a more complex pattern through time in Lake Victoria, with *R. argentea* from inshore and offshore habitats showing different morphological changes. We conclude that predation from Nile perch has likely contributed to contemporary changes in body shape of *R. argentea*; however, other factors (such as habitat structure and changes in water quality) may also have influenced morphological outcomes in some lakes.

Keywords: contemporary evolution, predation, eco-morphology, geometric morphometrics, introduced species, predator-prey interactions, Lake Victoria, dagaa, mukene

3.2 Introduction

As humans continue to threaten biodiversity with a range of activities (e.g., species introductions, habitat modification, ecosystem fragmentation, overharvesting, and climate change), resilient organisms likely face marked shifts in selection regimes that may in turn lead to rapid phenotypic changes (Palumbi, 2001; Stockwell et al., 2003; Hendry et al., 2008). Understanding the magnitude, nature, and predictability of phenotypic change in response to anthropogenic modification can provide insights into basic evolutionary processes, and is also critically important for informing long-term conservation policies.

One common impact of humans is the introduction of non-native species. In particular, human-mediated predator introductions—whether accidental or purposeful—are widespread and provide a series of natural experiments that are well-suited to exploring in what ways (and how quickly) novel predators can drive phenotypic change in evolutionarily naïve prey. Predation represents an important agent of divergent selection, often driving intraspecific divergence in morphology (e.g., Nosil & Crespi, 2006), life history (e.g., Reznick & Endler, 1982), and behavior (e.g., Magurran, 1990b) in a variety of prey taxa (reviewed in Vamosi, 2005; Langerhans, 2006). Most previous studies of predator-induced diversification have employed a comparative approach, for example, contrasting phenotypes of prey populations naturally occurring with or without predators for significant periods of time. However, experimental manipulations that expose prey to novel predators in a natural setting provide a more direct and powerful means of testing for ecological and evolutionary consequences of predation. Some such experimental introductions have been carried out, and provide some of the strongest evidence that prey phenotypes can evolve dramatically and often rapidly in response to selection from predators. For example, natural populations of Trinidadian guppies (*Peocilia reticulata*) exposed to novel predation regimes through experimental introductions have undergone adaptive changes in life-history traits (Reznick & Bryga, 1987; Reznick et al., 1990; Gordon et al., 2009), male colouration (Endler, 1980; but see Karim et al., 2007), anti-predator behavior (Magurran et al., 1992), escape ability (O'Steen et al., 2002), and morphology (Palkovacs et al., 2011) in as little as 1-3 decades (reviewed in Reznick et al., 2008). In most ecosystems, the intentional introduction of predators for experimental purposes would not be permissible, and therefore the advantages of studying existing human-mediated predator introductions are clear.

Freshwaters are among the most heavily invaded systems in the world (Strayer, 2010), with widespread stocking of predatory fish in many regions, often resulting in negative consequences for native fishes (e.g., Chapman, 1996; Whittier et al., 1997; Findlay et al., 2000; Correa and Hendry *In Press*). Introduced predators may also drive phenotypic changes in prey taxa, but few empirical examples exist to date (Mooney & Cleland, 2001; Strauss et al., 2006; Carroll, 2007). For instance, *Daphnia melanica* in alpine lakes in California showed both plastic and genetic declines in age and size at maturity after the introduction of non-native salmonids (Fisk et al., 2007; Latta et al., 2007). Introduced fish predators might select for a suite of adaptations in their prey, including traits that decrease the probability of detection (e.g., crypsis), capture (e.g., improved escape ability), and/or successful handling (e.g., defensive armor).

Escape ability is of particular interest, because the biomechanics of fast-start swimming in fishes has been studied extensively, and the links between phenotype (morphology), performance (acceleration during fast-starts) and fitness (survival probability) are reasonably well-established (Blake, 2004; Langerhans & Reznick 2010). Most fish respond to predator strikes with a stereotyped burst of acceleration, called a “C-start”, which is highly conserved phylogenetically (Blake, 2004). C-start performance (e.g., acceleration, rotational velocity) strongly determines the probability of successfully evading a predator strike (Walker et al., 2005; Langerhans, 2009) and would therefore be expected to experience strong selection from predators. Biomechanical models indicate that C-start performance can be enhanced by increasing the area of the mid-body/caudal region, which is where the thrust for the propulsive stroke is generated. This can be achieved by deepening the caudal peduncle and posterior region of the body, moving the median fins posteriorally, and/or increasing the area of the caudal fin (Domenici & Blake, 1997; Walker, 1997; Weihs, 1989;

Webb, 1977; Webb, 1982). This predicted association between body morphology and fast-start performance has now been experimentally confirmed in a number of fishes (Langerhans, 2010). For example, in threespine stickleback, *Gasterosteus aculeatus*, deeper-bodied freshwater forms had superior burst-swimming performance than slender-bodied anadromous forms (Taylor & McPhail, 1986; Law & Blake, 1996). In the mosquitofishes *Gambusia affinis* and *Gambusia hubbsi*, individuals with larger caudal peduncles had faster burst swimming speeds, both within and across populations (Langerhans et al., 2004; Langerhans, 2009).

Based on the large body of work linking morphology to locomotor performance in fishes, Langerhans and colleagues (2004; 2010) have proposed a general ecomorphological paradigm for the evolution of body form in aquatic vertebrates in response to predation. Specifically, they propose that most fish face a trade-off between selection favoring steady-swimming abilities (e.g., cruising) in the absence of predation and selection favoring unsteady-swimming abilities (e.g., fast-starts, turning) in the presence of predation—two swimming modes optimized by different morphologies. Selection should favor steady-swimming performance in the absence of predation so as to minimize energy expenditure while foraging or searching for mates. Steady-swimming performance is generally enhanced with a streamlined body shape, i.e. a fusiform shape with the greatest depth near the anterior and the body tapering off near the caudal region. Conversely, selection should favor unsteady-swimming performance in the presence of predators so as to maximize acceleration during fast-starts. As mentioned above, burst-swimming performance is maximized by having a deeper mid-body/caudal region and smaller head/anterior region. In addition to its general role in escape locomotion, body depth may also be important for overcoming the gape limitation of certain predators. For example, predator-induced increases in body depth in the Crucian carp (*Carassius carassius*) decreased vulnerability to pike, which are gape-limited predators (Brönmark & Miner, 1992). These general predictions have now been tested, and supported, in several species, including threespine stickleback (Walker, 1997; Walker & Bell,

2000) and the live-bearing poecciliids *Brachyrhaphis rhabdophora*, *Gambusia affinis*, *Gambusia hubbsi*, and *Poecilia reticulata* (Langerhans et al., 2004; Langerhans & DeWitt, 2004; Langerhans et al., 2007; Langerhans & Reznick, 2010).

Here we test these ecomorphological predictions in an East-African cyprinid fish, *Rastrineobola argentea*, which is endemic to the Lake Victoria basin of East Africa. In the 1950s and 1960s, a large piscivore, the Nile perch (*Lates niloticus*), was introduced into Lake Victoria and neighbouring lakes to compensate for declining native fisheries. The Nile perch population exploded in the mid-1980s, forming the basis for a very productive and lucrative export-oriented fishery. The Nile perch boom coincided with the extinction or extirpation of roughly 40% of Lake Victoria's 400+ endemic haplochromine cichlids, likely due to a combination of overfishing, eutrophication and intense predation from the Nile perch (Kaufman, 1992; Balirwa et al., 2003; Chapman et al., 2008). Once its preferred prey base (the haplochromines) had been depleted, the Nile perch began preying on *R. argentea*. While *R. argentea* have always had native predators in the Lake Victoria basin (see below), the high densities of Nile perch observed in most invaded lakes, combined with the occurrence of *R. argentea* in Nile perch stomach contents, suggest that Nile perch introduction resulted in increased mortality rates for *R. argentea* (Hughes, 1986; Ogutu-Ohwayo, 1990;1993; 2004; Schofield & Chapman, 1999; Katunzi et al., 2006). Despite this novel predator, *R. argentea* increased dramatically in abundance during the 1980s and 90s (Wanink, 1999; Tumwebaze et al., 2007) and now supports the most important commercial fishery (by mass) in Lake Victoria (Mkumbo et al., 2007; NaFIRRI, 2008).

This system can provide several novel insights into both predation's role in shaping the body form of prey fishes and the broader question of how anthropogenic perturbations may drive rapid phenotypic changes in natural populations. First, most examples of predator-induced body shape evolution to date are from live-bearing fishes (Family Poeciliidae) from the neo-tropics. Thus, observed convergent responses to predation could partially reflect shared evolutionary histories or constraints in this group of fishes, with some distantly related fishes perhaps responding in alternative ways (Langerhans et al., 2004). To more broadly test this ecomorphological paradigm, we need to examine phylogenetically and geographically distinct taxa. Second, *R. argentea* is one of the few native fishes from Lake Victoria that has managed to thrive alongside the introduced Nile perch, and its apparent resilience may partially reflect adaptive phenotypic change. *Rastrineobola argentea* has undergone rapid life-history changes since the 1960s (Wanink, 1998; Sharpe et al., 2012) that are consistent with an adaptive response to increased mortality (from both Nile perch predation and fishing pressure). Testing whether any changes in morphology have also occurred will shed further light on *R. argentea*'s persistence within this highly anthropogenically-disturbed ecosystem.

We tested for morphological divergence in *R. argentea* in response to predation from the introduced Nile perch using two approaches. First, we compared body shape of contemporary populations from nine Ugandan lakes that differ in their history of Nile perch invasion. Second, using museum specimens, we compared body shape of *R. argentea* from before versus after the establishment of Nile perch in Lake Victoria. We predicted that, in Nile perch-free contexts (uninvaded lakes, and Lake Victoria pre-Nile perch establishment), *R. argentea* would have more streamlined bodies, reflecting selection for steady-swimming abilities. Conversely, in contexts with Nile perch (invaded lakes, and Lake Victoria post-Nile perch establishment), *R. argentea* should have deeper mid-body/caudal regions and smaller heads, reflecting selection for increased fast-start escape ability. Selection to overcome the gape limitation of Nile perch seems improbable in this case due to the large difference in size between predator and prey: Nile perch switch to piscivory at approximately 30cm TL (Schofield & Chapman 1999) and can reach lengths of up to 2m, whereas *R. argentea* rarely exceed 6-7cm.

3.3 Methods

3.3.1 *Study sites*

Our study focussed on nine lakes located in the Lake Victoria basin in Uganda, East Africa (Fig. 3.1, Table 3.1), which together account for all of *R. argentea*'s known distribution in Uganda, and are described in detail in our previous work (Sharpe et al., 2012). The lakes differed in their Nile perch invasion history, with three being uninvaded, four having established Nile perch populations, and two (Bisina and Nawampasa) having experienced a transient Nile perch presence. Lake Bisina was stocked with Nile perch in the early 1970s and sustained a Nile perch fishery for a time (Mbabazi, 2004). However, the Nile perch population has since collapsed and repeated surveys in 2001-2003 (Mbabazi, 2004) and 2009-2010 (Sharpe & Chapman, unpl. data) did not uncover any Nile perch in the lake. Lake Nawampasa was free of Nile perch until 1998, when extensive flooding due to El Niño appeared to facilitate dispersal of Nile perch individuals into the lake (Wandera, S.B., unpl. data). It is not known whether these individuals have managed to persist, although our sampling in 2009 and 2010 did not uncover any Nile perch (Sharpe & Chapman, unpl. data).

While the Nile perch is likely the most important predator on *R. argentea* in the Lake Victoria basin, several native fishes may also consume *R. argentea*, including the catfishes *Clarias gariepinus*, *Schilbe intermedius*, and *Synodontis victoriae* (Mbabazi, 2004). Known avian predators include the pied kingfisher *Ceryle rudis,* the great cormorant *Phalacrocorax carbo lucidus,* and the long-tailed cormorant *Phalacrocorax africanus* (Wanink & Goudswaard, 1994; Wanink, 1996). However, the available evidence suggests that mortality from these other sources is not likely to differ systematically between lakes with or without Nile perch, and so should not confound our analysis (Appendix I).

We collected the following environmental data at each lake: water depth (m), water transparency (Secchi depth, m), water temperature (°C) and dissolved oxygen concentration (mg/L), measured with a Polaris dissolved oxygen meter. These data were collected at three replicate sites in the pelagic zone of each lake, both in the morning and in the afternoon. Although all fish were collected in 2010, environmental measurements were repeated over multiple years (2008, 2009, and 2010) for some lakes, and were averaged over time in these cases. We estimated lake surface area (km^2) from satellite images downloaded from Google Earth. Although all of these parameters varied across individual lakes (Appendix I), there were no consistent and significant differences between invasion categories for any of the environmental variables (lake area: $F_{2,7} = 2.11$, $p = 0.192$, lake depth: $F_{2,7} = 1.34$, $p = 0.323$, Secchi depth: $F_{2,7} = 1.35$, $p = 0.319$, temperature: $F_{2,7} = 0.12$, $p=0.893$, dissolved oxygen: $F_{2,7} = 0.22$, $p=0.812$).

3.3.2 Fish collections

Rastrineobola argentea were collected from the nine lakes described above in 2010 (Fig. 3.1), during the dry season (May-June). Fish were captured with a 5 mm-mesh lampara net (the local commercial fishing gear), which was operated as a surface seine in the pelagic zone of each lake. In two lakes, this method of fishing was unsuccessful, so *R. argentea* were collected using other gears (a 5-mm mesh beach seine in Lake Kayanja, and a 5 mm-mesh pelagic trawl in Lake Victoria). We retained approximately 30 individuals per lake (randomly selected from the largest quartile), which were euthanized with clove oil and immediately preserved in 10% formalin for morphological analyses (Table 3.1).

For the temporal analysis, we used a combination of preserved museum specimens and collections made by our team over the past decade (Table 3.2). Museum specimens were photographed, with permission, from collections at the Biodiversity Museum of the National Fisheries Resources Research Institute (NaFIRRI) in Jinja, Uganda, and included *R. argentea* from 1966, 1974, 1997 and 2003. Nile perch were introduced into Lake Victoria sometime in the early 1960s, but did not begin appearing regularly in catches until the early 1980s, hence we consider 1966 and 1974 to largely reflect pre-invasion conditions. Our team collected *R. argentea* from Lake Victoria in 2010, as described above. All specimens were preserved in 10% formalin. For the most part, historical specimens originated from the Northern waters of Lake Victoria – exact locations are given in Table 3.2.

3.3.3 Morphological analyses

Variation in the overall body shape of *R. argentea* was examined using geometric morphometric methods, a powerful approach that uses information from spatial co-ordinates (landmarks) to describe, visualize and analyse shape variation (Rohlf & Marcus, 1993; Adams et al., 2004). Preserved *R. argentea* were photographed in the laboratory using a Canon Powershot digital camera. We digitized 12 homologous landmarks on the lateral body profile of images (Fig. 3.2) using TPSDig software (Rohlf 2006). Landmarks comprised: (1) most anterior point of the premaxilla, (2) indentation at the posterodorsal end of the head, (3) anterior insertion point of the dorsal fin, (4) posterior insertion point of the dorsal fin, (5) dorsal insertion point of the caudal fin, (6) ventral insertion point of the caudal fin, (7) posterior-most point where the anal fin meets the body, (8) anterior insertion point of the anal fin, (9) insertion point of the pelvic fin, (10) dorsal insertion point of the pectoral fin, (11) intersection of the operculum and body profile, and (12) centre of the eye orbit.

Photographs were landmarked by two individuals (E. Low-Decarie and D. Sharpe), but all landmarks were individually doubled-checked by D. Sharpe before analyses were conducted. To quantify any potential inter-observer bias, we randomly selected 20 photos for digitization by both observers. Repeatability was estimated as the intraclass correlation coefficient, calculated for each landmark co-ordinate separately (Lessels & Boag, 1987), and was generally high (mean: 0.85, all $p < 0.01$).

Landmark configurations were scaled to a common size, and aligned using generalized Procustes analysis (Rohlf & Slice, 1990) in TPSRelw (Rohlf, 2010). Deviations of each fish from the consensus (mean) configuration were quantified in terms of affine (uniform) and non-affine (partial warp) components (Zelditch et al., 2004), which together represent changes in multivariate body shape, and were used as dependent variables in subsequent analyses. TPSRelw was also used to calculate centroid size – a metric of body size commonly employed in geometric morphometrics, which is the square root of the sum of the squared distances from each landmark to the centroid of the landmark configuration.

In addition to these geometric morphometrics analyses that explored changes in overall body shape, we also calculated the following univariate measurements, which captured key traits in the caudal region that we expected a priori might vary across invasion contexts. These were: (i) lateral mid-body/caudal area, calculated using a minimum convex polygon drawn between landmarks 3, 4, 5, 6, 7, 8, and 9 (shaded area on Fig. 3.2), and (ii) anal fin length, calculated as the Euclidean distance between landmarks 7 and 8. Both were calculated in R (R Development Core Team, 2012) from the raw landmark data. For all contemporary specimens, we measured standard length (mm) and total wet body mass (mg). Both variables were both highly correlated with centroid size (standard length: $r = 0.99$, $p < 0.001$, weight: $r = 0.96$, $p < 0.001$) and so centroid size was used as the body size covariate in all geometric morphometric analyses. Relative body condition (K) was quantified in order to assess how much variation in overall body shape might be due to variation in condition. For example, heavier, more well-fed individuals would be expected to be deeper-bodied than starved individuals, irrespective of predator-regime. K was calculated as: $K = wi/a*slib$, where wi is the weight of individual i (in mg), sli is the standard length of individual i (in mm), and a and b are parameters derived from a linear regression of log-transformed weight vs. log-transformed length for all individuals in the data-set (a is the back-transformed intercept (0.009), and b is the slope from the linear regression (3.09)).

After the photographs had been taken, we dissected each fish to check for intestinal macro-parasites, which can distend the abdomens of infected individuals and so potentially distort overall body shape. We also determined the sex and maturity status of each fish, using a seven-point scale previously developed for *R. argentea* (Wandera, *unpl data*, Sharpe et al., 2012). We were not able to dissect the museum specimens, but we did measure standard length (in mm) for each fish, which we then used to roughly estimate maturity, based on previously-published values for length at 50% maturity (L_{50}) for *R. argentea* from Lake Victoria over this particular time period (Sharpe et al., 2012). Using this approach, 9 individuals (out of 179) fell below the L_{50} threshold for the year in question, and were therefore assumed to be immature. We ran the analysis both including and excluding these putatively immature individuals, and the results were unaffected, so we present results only from the first analysis including all individuals.

3.3.4 Statistical analysis

To test for variation in body morphology of *R. argentea* associated with the Nile perch introduction, we performed the following three analyses, applied separately to both spatial and temporal data-sets. First, to test for differences in body shape across Nile-perch invaded and uninvaded lakes, we performed a nested MANCOVA with the 18 partial warps and 2 uniform components as dependent shape variables, and the following as independent variables: Nile perch category, lake nested within Nile perch category, sex, and body condition and centroid size as covariates. We treated lake as a fixed nested factor in our analyses because: (i) we sampled the entire known distribution of *R. argentea* in Uganda (i.e., our samples are not a subset of a larger theoretical population), and (ii) we were interested in making specific inferences about the lakes in our study. To test for differences in body shape through time, we used a MANCOVA with year as a fixed factor and centroid size as a covariate (sex and body condition were not included in this model because these data were not available for museum specimens). This initial analysis of the historical data suggested that there were consistent differences in body shape between *R. argentea* collected from inshore versus offshore habitats, so we subsequently performed separate MANCOVAs for each habitat. In all models, we tested for heterogeneity of slopes across Nile perch categories (or years), and removed any non-significant terms and interactions from our final model. Multivariate effect size in these MANCOVA models was quantified using Wilks' partial η2 (Langerhans & DeWitt, 2004). Body shape variation associated with our factor of interest (Nile perch or year) was then examined using the canonical variates (CVs) for that factor derived from our

MANCOVA model, which were visualized by generating thin-plate spline deformation grids using TPSRegr (Rohlf, 2009). For MANCOVAs that generated multiple CVs, we focused our interpretations on those cumulatively explaining at least 75% of the variation for that factor (usually CV1 and CV2). Many geometric morphometrics studies also explore shape variation using principal components analysis (also known as "relative warp analysis"), rather than, or in addition to, MANCOVA. We also performed a relative warp analysis, but the results were generally quite similar to those of the MANCOVA, so we do not include them here (but see Appendix J for full details).

Second, we performed a discriminant function analysis (DFA) using leave-one-out cross-validation to determine how well individuals could be assigned to Nile perch categories (or years) based on their multivariate body shape (partial warps, uniform components and centroid size). Finally, we tested for variation in the two univariate traits of interest (mid-body/caudal area and anal fin length) across invasion categories using an ANCOVA, with lake nested as a fixed effect within Nile perch category. Total lateral body area was used a covariate for mid-body/caudal area, and standard length was used as a covariate for anal fin length. For the historical analysis, we examined variation in these same two traits through time using an ANCOVA with year, the appropriate body size covariate, and the interaction between the two as explanatory variables. All variables were log-transformed to improve normality. All analyses were done in R, except for the MANCOVAs, which were done using JMP (v. 5.1.2, © 2004, SAS).

3.4 Results

3.4.1 Spatial: body shape variation across lakes

MANCOVA revealed significant differences in multivariate body shape across lakes and invasion categories, with the greatest amount of partial variance explained by Nile perch invasion category (Table 3.3). Sex, centroid size and body condition were not significant ($p > 0.05$), as were interactions between covariates and Nile perch category, and so all were removed from the final model.

Variation along the first canonical variate for the Nile perch factor (CV1) indicated that *R. argentea* from invaded lakes tended to have deeper bodies, particularly in the mid-body/caudal region, shorter anal fins, narrower/smaller heads, and more ventrally-located eyes and pectoral fins (Fig. 3.3). The DFA showed that *R. argentea* were correctly classified into the appropriate Nile perch category most of the time (74% correctly assigned for invaded lakes, 61% for uninvaded lakes, and 73% for transiently invaded lakes, $n = 270$, $p < 0.0001$).

Our direct univariate measure of mid-body/caudal area differed between some lakes (lake: $F_{6,260} = 17.62$, $p < 0.001$), but did not differ significantly across Nile perch invasion categories (Nile perch: $F_{2,260} = 0.90$, $p = 0.409$). On the other hand, anal fin length differed significantly both across lakes ($F_{6,260} = 51.94$, $p < 0.001$), and Nile perch categories ($F_{2,260} = 38.40$, $p < 0.001$). *R. argentea* from invaded lakes had shorter anal fins on average than populations from uninvaded or transiently invaded lakes, although this was largely driven by one population, lake Victoria (Appendix K).

Our dissections indicated that the majority of photographed specimens (83%) were sexually mature, and free of intestinal macro-parasites (94%). Excluding immature or parasitized individuals from the geometric morphometric analysis did not alter our results in any way (not shown). Body condition varied significantly across invasion categories ($F_{2,266} = 34.441$, $p < 0.001$), being greatest in uninvaded lakes, and lowest in transiently invaded lakes. However, as mentioned above, body condition was not a significant covariate in the MANCOVA examining overall variation in body shape. Across all lakes, body shape (CV1) was not correlated with lake area ($r = -0.29$, $p = 0.450$), lake depth ($r = -0.33$, $p = 0.382$), Secchi depth ($r = -0.21$, $p = 0.595$), temperature ($r = 0.27$, $p = 0.482$), or dissolved oxygen concentration ($r = 0.073$, $p = 0.852$).

3.4.2 Temporal: body shape variation through time

The MANCOVA found that the multivariate body shape of *R. argentea* varied significantly through time in Lake Victoria (Year: $F_{100,755.96} = 3.76$, $p < 0.0001$). Centroid size, and the interaction between centroid size and year were non-significant ($p > 0.05$), and so were removed from the final model. The first canonical variate for the year term in the MANOVA was primarily related to changes in the shape of the mid-body/caudal region (Fig. 3.4A). Along CV1, *R. argentea* from 1997 and 2003 (the offshore sample) had shallower caudal regions, shorter anal fins, and smaller heads than individuals from all other years. Body shape variation along CV1 was not clearly related to Nile perch presence, but seemed to be at least partially related to collection site (inshore vs. offshore) in 2003. The second canonical variate more clearly discriminated our time periods of interest, with *R. argentea* from contemporary (post-Nile perch) years tending to have higher scores than those from earlier (pre-Nile perch) years. Along CV2, contemporary (post-Nile perch) populations tended to have: longer dorsal fins, shorter anal fins, smaller mid-body/caudal regions, more terminal (rather than upturned) mouths, ventrally-displaced eyes, larger heads, and posteriorally-displaced pelvic fins (Fig. 3.4B). A planned contrast comparing pre (1966, 74) vs. post (1997, 2003, 10) Nile perch years indicated that this difference in body shape was significant ($F_{20,154} = 154$, $p < 0.001$).

Analyzing inshore and offshore samples separately more clearly revealed the habitat-specific trends suggested by the MANCOVA above. The body shape of inshore *R. argentea* differed significantly across years (1966 vs. 2003ins, $F_{20,40} = 2.318$, $p = 0.012$), but there was no significant effect of centroid size ($p > 0.05$). Contemporary (post Nile perch) *R. argentea* from inshore habitats were deeper-bodied overall, and had deeper mid-body/caudal regions, longer dorsal fins, more posteriorally-positioned pectoral fins, larger heads, and more ventrally-displaced eyes relative to historical (pre-Nile perch) *R. argentea* (Fig. 3.5). The body shape of offshore *R. argentea* also varied significantly across years (1974, 1977, 2003off, 2010, $F_{60,284.26} = 4.355$, $p < 0.001$), but not with centroid size ($p > 0.05$). For offshore habitats, the first canonical variate for the year effect seemed to be driven by one sample (1997), which had a shallower mid-body/caudal region, smaller head, and more up-turned mouth relative to other years (Fig. 3.6A). The second canonical variate seemed to better capture temporal variation, with contemporary (post Nile perch) *R. argentea* having shallower mid-body/caudal regions, longer dorsal fins, shorter anal fins, bigger heads, ventrally-displaced pectoral fins, and more ventrally-positioned eyes than historical (pre Nile perch) *R. argentea* (Fig. 3.6B).

The DFA correctly assigned *R. argentea* to the year of collection at a moderately high rate (1966: 80%, 1974: 94%, 1997: 68%, 2003 (inshore): 71%, 2003 (offshore): 59%, 2010: 90%, $p < 0.0001$). A separate DFA correctly assigned *R. argentea* to pre vs. post Nile perch context at a very high rate (pre-Nile perch: 90%, post-Nile perch: 96%, $p < 0.0001$). Our univariate analysis showed that size-adjusted mid-body/caudal area varied significantly across years ($F_{5,172} = 1813$, $p < 0.001$), declining from 1966 to 2010 (Appendix K). Anal fin length also differed across years ($F_{5,172} = 211.16$, $p < 0.001$), being greatest in 1974 (pre-Nile perch boom), and lowest in 1997 and 2010 (Appendix K).

3.5 Discussion:

We set out to test the hypothesis that predators can drive rapid and predictable morphological change in natural prey populations, using replicate introductions of the predatory Nile perch in the Lake Victoria basin as a natural experiment. We tested this hypothesis using two complimentary approaches: examining body shape variation across space (invaded vs. uninvaded lakes), and through time (before vs. after the establishment of Nile perch in Lake Victoria). We predicted that populations of *R. argentea* that co-occurred with Nile perch would exhibit morphologies associated with burst-swimming performance; specifically an increase in the relative area of the mid-body/caudal region. Parallel patterns of phenotypic change through space and time (i.e., similar patterns of co-variation between body shape phenotypes and the presence/absence of Nile perch across both axes) would be strong evidence that the Nile perch is an important driver of body shape variation in *R. argentea*. Although we did find evidence of significant morphological variation in *R. argentea*, spatial and temporal patterns were not congruent, and the observed differences were not consistently in the direction predicted. We now discuss each analysis in turn, and then provide a set of potential scenarios to reconcile disparate results.

3.5.1 Variation in body shape across lakes:

In the spatial analysis, our multivariate analysis (MANCOVA) suggested that *R. argentea* from invaded lakes tended to have deeper mid-body/caudal regions, smaller heads, shorter anal fins, and more ventrally-displaced eyes and pectoral fins, relative to *R. argentea* from uninvaded or transiently invaded lakes. Our direct univariate analyses supported these trends for anal fin length, but not for mid-body/caudal area.

The shift in allocation of body depth towards the caudal region suggested by the MANCOVA is consistent with our a priori ecomorphological predictions, and closely parallels predator-associated morphological changes documented in poecilid fishes (Langerhans & DeWitt, 2004; Langerhans et al., 2004; Langerhans et al., 2007). The magnitude of body shape variation observed in *R. argentea* in our study is, however, much less pronounced than that documented previously (see for example Fig. 3 in Langerhans & DeWitt, 2004). The ventral shift in the position of the eye in *R. argentea* in invaded lakes is also consistent with this prior work, and may enhance predator detection. Nile perch have a demersal distribution in Lake Victoria (Getabu et al., 2003), while *R. argentea* are pelagic (Tumwebaze et al., 2007) so it is likely that the majority of predator strikes come from below. Indeed, laboratory trials have shown that Nile perch tended to lurk at the bottom of tanks and attack surface-swimming *R. argentea* from below (Hamblyn, 1966). Therefore, a more ventrally-placed eye in *R. argentea* would presumably allow earlier and more effective detection of an approaching Nile perch.

Although we found a significant association across lakes between the body shape *R. argentea* and the presence/absence of Nile perch, this pattern may also reflect the influence of other factors. Fish body shape is known to vary with a number of physical and ecological variables, including water flow (e.g., Langerhans, 2008), dissolved oxygen (e.g., Langerhans et al., 2007, Crispo & Chapman, 2011), temperature (e.g., Marcil et al., 2006), relative littoral area (Walker, 1997), and diet/habitat use (e.g., Sharpe et al., 2008). We did not measure water flow in our study; however, all populations were from lentic systems (lakes), so this is unlikely to be an important source of variation. Dissolved oxygen and temperature did not vary significantly across invasion categories, and the range of variation across lakes was relatively small, so these are also unlikely explanations for the observed patterns of spatial variation in body shape in our study. Relative littoral area (RLA, defined as the relative area in a lake that is shallower than the euphotic zone) affects body shape in threespine stickleback, with fish from small, shallow lakes (high RLA) having deeper bodies, and fish from large, deep lakes (low RLA) being more streamlined (Walker, 1997; Walker & Bell, 2000). We did not calculate RLA in our study, but we did consider the effects of lake surface area and depth. Neither were significantly different among invasion categories, and neither were correlated with body shape across lakes. While we did not have sufficient spatial replication to statistically partition out the relative importance of lake area and invasion history (due to the limited geographic range of *R. argentea*), there is some reason to believe that they may interact in this system, a possibility we will return to below. Finally, diet and habitat use have been shown to influence body morphology in a number of fishes. A commonly-observed polymorphism in lacustrine fishes is that benthic or littoral-dwelling fish that feed on benthic macro-invertebrates in structurally-complex habitats tend to be deeper-bodied than pelagic-dwelling fish that feed on zooplankton in open habitats (e.g., Malmquist, 1992; Schluter & Mcphail, 1992; Robinson et al., 1993; Svanbäck & Eklöv, 2002; see also review by Robinson & Wilson, 1994). We sought to avoid this potentially confounding variation by exclusively sampling *R. argentea* from the pelagic zone, and focusing primarily on mature individuals (thus avoiding the possibility of any ontogenetic dietary shifts). In a parallel study, we have examined the diet of *R. argentea* across a subset of these same lakes. We found that the diet of *R. argentea* varied considerably across lakes, but there were no consistent differences in diet between invaded versus uninvaded lakes (Sharpe & Chapman, in prep), so diet is also not a likely driver of the body shape differences that we observed across lakes. Overall, it seems unlikely that some unmeasured feature of these lakes other than the Nile perch invasion history could be the primary driver of the observed patterns of body shape variation between lakes.

3.5.2 Variation in body shape through time:

In the temporal analysis, we observed a more complex pattern of body shape variation that seemed to reflect the influence of habitat as well as Nile perch presence or absence. When inshore samples from Lake Victoria were analyzed separately, we observed an increase in the depth of the mid-body/caudal region from 1966 to 2003, consistent with the pattern observed across lakes, and with our a priori ecomorphological predictions. In contrast, when offshore samples were analyzed separately, we found that *R. argentea* from contemporary (post-Nile perch) years tended to have smaller mid-body/caudal regions, larger heads, shorter anal fins, and longer dorsal fins relative to *R. argentea* from earlier (pre-Nile perch) years. *Rastrineobola argentea* thus appear to have become more streamlined following the introduction of Nile perch in offshore waters of Lake Victoria; but deeper-bodied in inshore areas of Lake Victoria. In both habitats, we observed a ventral shift in the position of the eye in *R. argentea* in post-Nile perch years. This paralleled the shift in eye position observed in *R. argentea* in invaded lakes, and may similarly reflect selection to improve detection of predator strikes from below.

One possible explanation for the divergent trend in mid-body/caudal depth across habitats is that the response to Nile perch predation in offshore waters of Lake Victoria has been functionally different than that in inshore bays of Lake Victoria and in other smaller invaded lakes. Lake Victoria is by far the largest lake in our study (with a surface area of approximately 68,000km^2), and *R. argentea* in this lake are truly pelagic, making use of both inshore and offshore waters (Tumwebaze et al., 2007), although we do not know to what extent inshore and offshore populations may mix. Although *R.argentea*'s behaviour has never been studied explicitly, they have often been observed swimming in large schools in Lake Victoria (e.g., Kaufman & Ochumba, 1993; Tumwebaze et al., 2007). Schooling is a common anti-predator behaviour in fish, and is thought to significantly improve prey survival in the face of predation (Magurran, 1990a). In some species, there is evidence for heritable intraspecific variation in schooling behaviour, with prey populations that have co-evolved with predators being more prone to school relative to naive conspecifics (e.g., in Trinandian guppies, *Peocilia reticulata* (Seghers, 1974; Huizinga et al., 2009) and European minnow, *Phoxinus phoxinus* (Magurran, 1990b). One hypothesis is that *R. argentea* in offshore waters of Lake Victoria have responded behaviourally to the Nile perch introduction by forming larger and more cohesive schools and/or schooling more frequently, which may select for increased steady-swimming performance. This hypothesis remains to be tested, but might explain the observed morphological shift towards greater streamlining over time observed in offshore waters only.

More generally, we hypothesize that *R. argentea*'s response to Nile perch predation may be contingent on lake size. In the open waters of larger invaded lakes, *R. argentea* may attempt to evade Nile perch through increased schooling behaviour, which would favour increased steady swimming performance, and thus more streamlined bodies. Conversely, in smaller invaded lakes, manoeuvrability and improved burst-swimming performance (hence deeper caudal regions) may be more important for predator evasion. Indeed, if we revisit the correlation between body shape (CV1) and lake area, there was no significant correlation across all lakes; but, if we consider only the lakes where Nile perch became established, there is some indication of a positive relationship, despite the very small sample size (Fig. 3.7, r = 0.80, p = 0.20, n = 4). That is, *R. argentea* from the smallest invaded lakes (Meito and Nabugabo) were the deepest bodied, whereas *R. argentea* from the largest invaded lakes (Victoria and Kyoga) were more streamlined.

Finally, it is important to consider that the observed changes in the body shape of *R. argentea* over time in Lake Victoria may also reflect the influence of factors other than predation from the introduced Nile perch. Three such factors that have also varied over time in Lake Victoria are: (i) dissolved oxygen, (ii) the diet of *R. argentea*, and (iii) fishing pressure on *R. argentea*. Rapid human population growth in the catchment over the past century has led to the eutrophication of Lake Victoria, and dramatic changes in a number of limnological parameters. Algal biomass has quintupled since the 1960s, and the severity and frequency of hypolimnetic hypoxia has increased significantly (Hecky et al., 1994; Hecky et al., 2010). There is some evidence for long-term changes in gill morphology in *R. argentea* in Lake Victoria, likely as a response to increasing hypoxia. Wanink and Witte (2000) found an increase in the number of gill filaments on the first gill arch in *R. argentea* from the Mwanza Gulf of Lake Victoria between 1983 and 1988. Preliminary data from the Ugandan waters of Lake Victoria suggest an increase in length-adjusted gill filament number, total gill filament length, gill hemibranch area, and hemibranch perimeter (all calculated from the first gill arch) between 1966 and 2010 (Sharpe & Chapman, unpl. data). Head size might be expected to increase in order to accommodate larger gills, and indeed this has been observed in several other fishes from low-oxygen environments in the Lake Victoria basin, including for example *Pseudocrenilabrus multicolor victoriae* (Crispo & Chapman, 2010) and *Barbus neumayeri* (Langerhans et al., 2007). It is possible therefore that the increased head size of *R. argentea* over time observed here may partially reflect accommodation for larger gills.

As discussed earlier, body shape in fishes is often correlated with their feeding mode. There is evidence that the diet of *R. argentea* has shifted over time in Lake Victoria, from a specialized zooplankton diet in the 1960s to a broader contemporary diet that includes insect larvae as well as emergent aquatic insects (Sharpe et al., in prep). One potential morphological correlate of feeding on emerging aquatic insects would be an upturned/dorsally-oriented mouth (Watson & Balon, 1984; Wikramanayake, 1990; Hugueny & Pouilly, 1999); however, we observed the opposite pattern. That is, *R. argentea* from later years (which included insects in their diet) had more terminal mouths than *R. argentea* from earlier years (which were zooplankton specialists). It seems then that temporal changes in the diet of *R. argentea* are an unlikely explanation for the observed morphological changes.

Third, commercial fishing of *R. argentea* began in Ugandan waters in the late 1980s (Wandera, 1999) and has expanded dramatically since (NaFIRRI, 2008; Muhoozi, 2008). While fishing is known to exert selection on numerous traits of harvested species, including body size, life history traits and behaviour (reviewed in Heino & Godo, 2002); there has been less emphasis on the extent to which different gear types might also select on body shape. Much of the work on shape to date has focussed on key linear measurements, such as girth, which can affect escape probabilities in both trawls (e.g., Tosunoglu et al., 2003) and gill-nets (reviewed by Hamley, 1975). Layman et al. (2005) examined the effects of gill-net fishing on body shape across a community of riverine fishes, but found no evidence for effects on body shape. In the case of the *R. argentea*, fisheries selection on body shape also seems unlikely, because of the relatively unselective gears employed in this fishery. Rastrineobola argentea are concentrated by light attraction at night, and then scooped up in extremely fish-meshed (3mm – 5mm) "lampara" nets, leaving little opportunity for escape for even the smallest or more slender individuals (pers. obs.). Overall, Nile perch predation (and potentially changes in dissolved oxygen) seem the most likely drivers of the observed changes in body shape of *R. argentea* over time in Lake Victoria.

3.5.3 Underlying basis of phenotypic changes:

What mechanisms might be underlying the observed phenotypic divergence in body shape between *R. argentea* in invaded versus uninvaded contexts? Some fishes are capable of very rapid, phenotypically-plastic changes in body shape in response to the presence of predators, including for example Crucian carp (Brönmark and Pettersson 1994) and juvenile perch and roach (Eklöv and Jonsson 2007). Conversely, in other species, intra-specific variation in body shape has been shown to be heritable, reflecting evolution in response to divergent natural selection (e.g., Langerhans et al. 2004). Although these heritable differences may often take thousands of years to evolve, in some cases, genetic differences in body shape seem to have evolved quite rapidly (e.g., less than 150 years in *Gambusia affinis*, Langerhans 2009). Finally, in many cases, intraspecific variation in body shape may reflect both plastic and genetic components of variation (e.g., Sharpe et al. 2008). Assuming that adaptive plasticity is generally costly to maintain (Dewitt et al. 1998), we would expect fishes to evolve plasticity in body shape only when they are intermittently but repeatedly exposed to predation. For example, Crucian carp can survive in shallow ponds in which piscivorous fish are periodically completely eliminated due to hypoxic events; and this fluctuation in predation regime is what is thought to have driven the evolution of adaptive plasticity in body shape in this species (Brönmark and Pettersson 1994). Conversely, we would expect that species that are exposed to a stable predation regime would evolve a more genetically canalized morphology. In the case of *R. argentea*, we do not at present have any data on the heritability of body shape (or the temporal stability of past predation regimes), and so we do not know to what extent the apparent contemporary morphological response to Nile perch may reflect plasticity and/or heritable change. Given the very short generation time of *R. argentea* (03.-0.9 years, Wanink 1998), genetic change is a realistic possibility in this system. Common-garden rearing of individuals from invaded versus univaded lakes, with and without predator cues, would be a good way to determine the extent to which across-lake variation in body shape may reflect genetic differences, phenotypic plasticity, or a combination of the two.

3.5.4 Conclusions and implications

Our results lend partial support to the ecomorphological paradigm of body shape evolution in fishes advanced by Langerhans et al. (2004, 2010). The qualitative nature of morphological change in *R. argentea* across invaded vs. uninvaded lakes, and over time in inshore waters of Lake Victoria, closely matched that seen in the New World poeciliids, which is noteworthy given that *R. argentea* is phylogenetically and geographically distinct from this group. The magnitude of shape variation that we observed was much more subtle, however, and patterns were only partially consistent through time and space. Our results from the temporal analysis (more streamlined bodies over time) may reflect divergent outcomes in offshore habitats of larger lakes (for example due to selection for increased schooling rather than fast-start escape ability), and/or the influence of other factors, such an increasing hypoxia over time.

As human impacts on the natural world intensify, evolutionary biologists have become increasingly interested in understanding the extent to which adaptation may be able to buffer natural populations against anthropogenic stressors. Only a few studies to date have documented adaptive phenotypic responses in native prey to introduced predators, the majority involving the adoption of novel anti-predator behaviour (Strauss et al., 2006). Morphological adaptations have been observed in a few taxa, including for example the thickening of shells of marine molluscs in response to the introduced green crab (Vermeij, 1982), and body shape changes in yellow perch in response to the re-colonization of previously extirpated piscivores (Lippert et al., 2007). Rastrineobola argentea provide a particularly interesting case study for understanding the role of phenotypic adaptation in buffering anthropogenic change. We have previously shown that *R. argentea* have undergone rapid changes in life history traits in response to the Nile perch introduction and fishing pressure (Sharpe et al., 2012), and our current study indicates that some morphological changes may be occurring as well. Owing in large part to their remarkable persistence, *R. argentea* have now emerged as the most important commercial fish stock in Lake Victoria, outstripping even Nile perch in terms of catch landings (NaFIRRI, 2008). They now play a major role in the food-web of Lake Victoria (accounting for approximately 60% of the fish biomass of the lake, NaFIRRI, 2008), and are critical for food security in the region. Understanding phenotypic responses in *R. argentea* to ongoing anthropogenic stressors in the Lake Victoria region will be very important for the management of this fishery, and the ecosystem as a whole.

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Table 3.1 Summary of *R. argentea* populations included in the spatial analysis of body shape, ordered by Nile perch invasion history.

Bisina and Nawampasa are special cases, because Nile perch were introduced, but seem to have failed to establish (see text for details). Sample sizes (n) and the mean (± SE) standard length of each population of *R. argentea* included in the geometric morphometric analysis are indicated.

Lake	Nile perch	n	Standard length (mm)
Kayanja	Absent	30	37.23 ± 2.66
Omuno	Absent	30	50.77 ± 2.46
Gigati	Absent	30	47.40 ± 2.61
Bisina	Transient (1970s – 1990s?)	30	37.90 ± 2.66
Nawampasa	Transient (1998 – Present?)	30	39.87 ± 2.13
Meito	Established	30	40.40 ± 1.50
Nabugabo	Established (1960 - Present)	30	44.03 ± 2.04
Kyoga	Established (1955 - Present)	31	45.13 ± 4.14
Victoria	Established (1950s/1960s - Present)	29	41.17 ± 1.91

Table 3.2 Summary of *R. argentea* populations included in the historical analysis of body shape.

Nile perch were introduced into Lake Victoria sometime in the 1950s/1960s, but did not begin appearing regularly in catches until the early 1980s. Sample sizes (n) refer to the number of individuals included in the final analysis. Standard lengths are given as means ± SE. The precise location for the 1974 sample was not recorded; however, consultation with NaFIRRI scientists indicated that this sample almost certainly came from offshore waters and not the Napoleon Gulf (Wandera, S.B. *pers. comm.*).

Year	Nile Perch	n	Standard Length	Collectors	Location
1966	Rare	30	55.29 ± 0.77	NaFIRRI	Napoleon Gulf (Inshore)
1974	Rare	33	65.86 ± 0.50	NaFIRRI	Lake Victoria (Offshore)
1997	Established	22	48.73 ± 0.75	NaFIRRI	Buvuma Channel (Offshore)
2003in	Established	31	44.27 ± 0.62	NaFIRRI	Napoleon Gulf (Inshore)
2003off	Established	34	50.68 ± 0.51	NaFIRRI	Nkata (Offshore)
2010	Established	29	41.17 ± 0.35	Sharpe and Chapman	Buvuma Channel (Offshore)

Table 3.3. Nested multivariate analysis of covariance (MANCOVA) examining variation in body shape of *R. argentea* (partial warps and uniform components) across invaded and uninvaded lakes.

F-ratios were approximated using Wilks' λ. Partial variance was estimated based on Wilks' partial η^2 (Langerhans and DeWitt 2004). Note that centroid size, sex and body condition were non-significant and so were all removed from the final model.

Effect	df	F	p	Partial variance
Nile perch	40,482	6.12	<0.0001	0.34
Lake(Nile perch)	120,1400.3	6.13	<0.0001	0.26

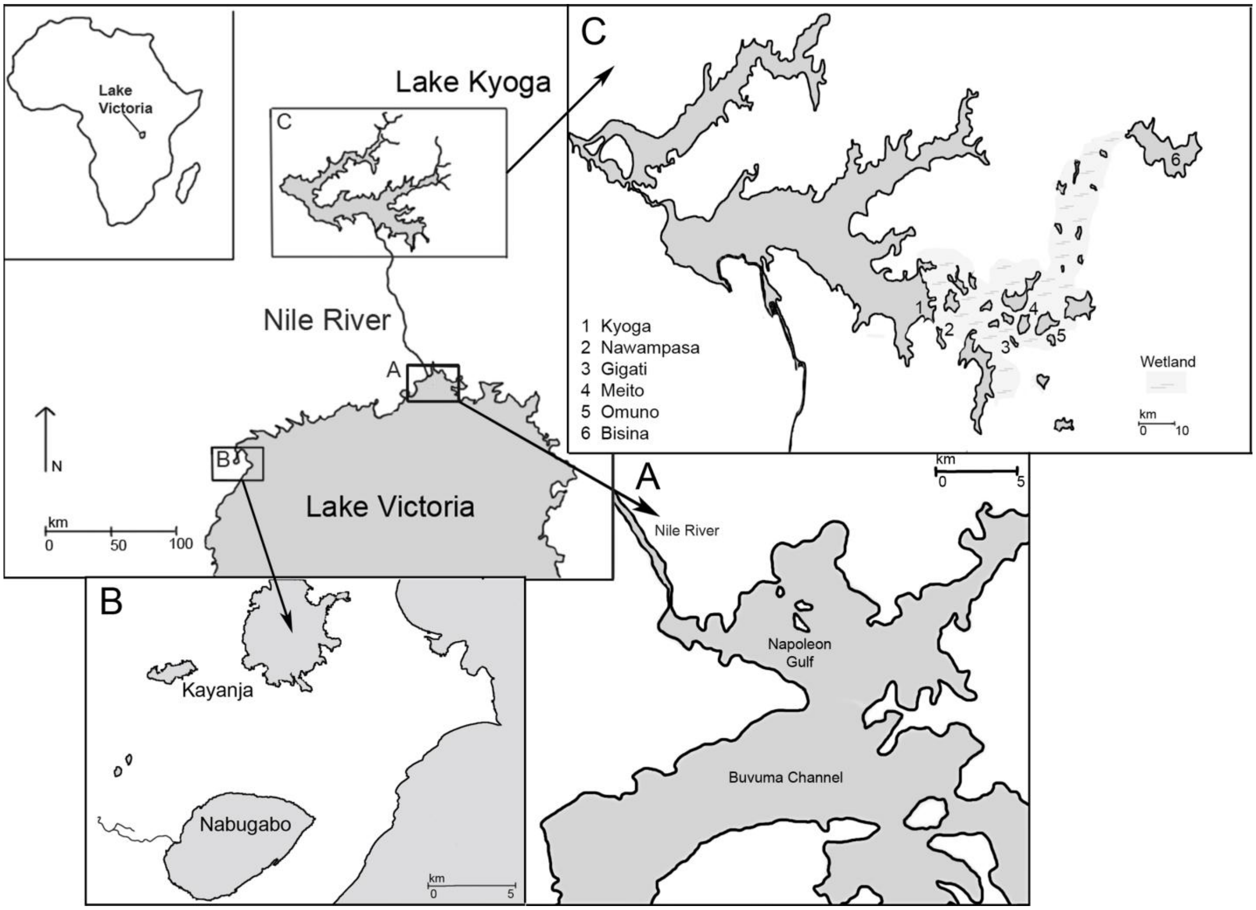

Fig. 3.1 Map of study sites within the Lake Victoria basin of East Africa (modified from Sharpe et al. 2012).

The lakes that we sampled included three lakes with no history of Nile perch invasion (Kayanja, Gigati and Omuno), two lakes which experienced a transient Nile perch presence (Bisina and Nawampasa), and four lakes with established Nile perch populations (Kyoga, Meito, Nabugabo and Victoria).

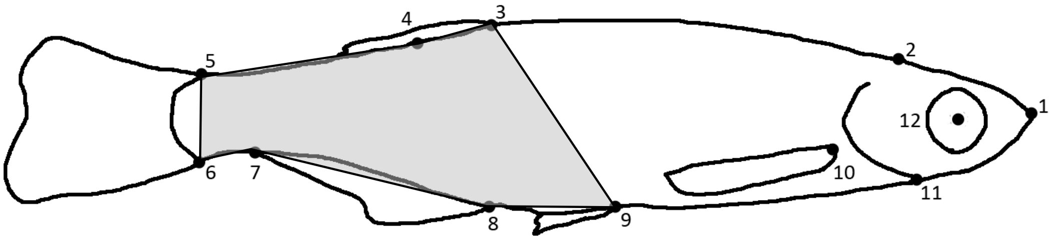

Fig. 3.2 Landmarks used to quantify body shape variation (see text for details). The shaded area is the minimum convex polygon used to estimate the lateral area of the mid-body/caudal region.

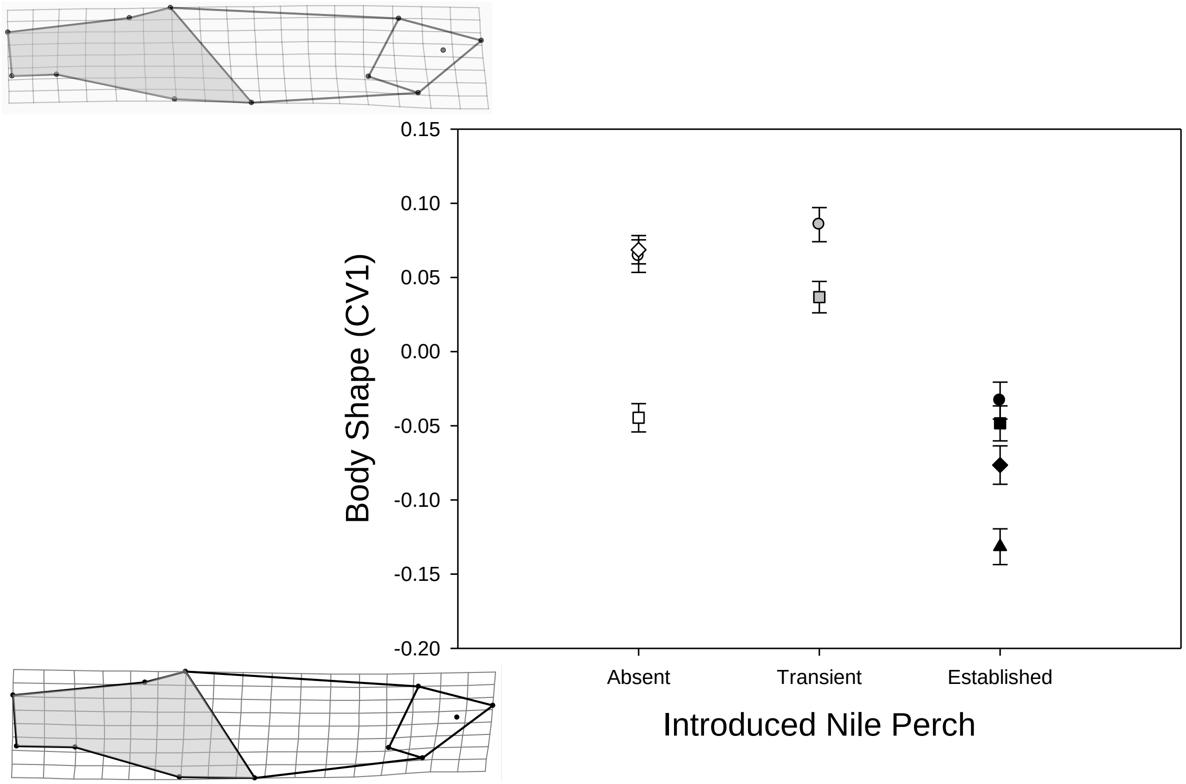

Fig. 3.3 Variation in overall body morphology of *R. argentea* between lakes with either no, transient, or established populations of the introduced predator, the Nile perch.

Data are mean scores (± 1 SE) along the first canonical variate for the Nile perch effect from MANCOVA. Body shape variation along this axis has been visualized using thin-plate spline transformation grids, which represent the positive and negative extremes of this axis and have been magnified by 3 to better illustrate the differences among groups. The colours indicate lakes in which Nile perch were either established (black), transiently present (grey), or absent (white). The lakes shown are: Kayanja (white circle), Omuno (white square), Gigati (white diamond), Nawampasa (grey circle), Bisina (grey square), Meito (black triangle), Nabugabo (black diamond), Kyoga (black circle), and Victoria (black square).

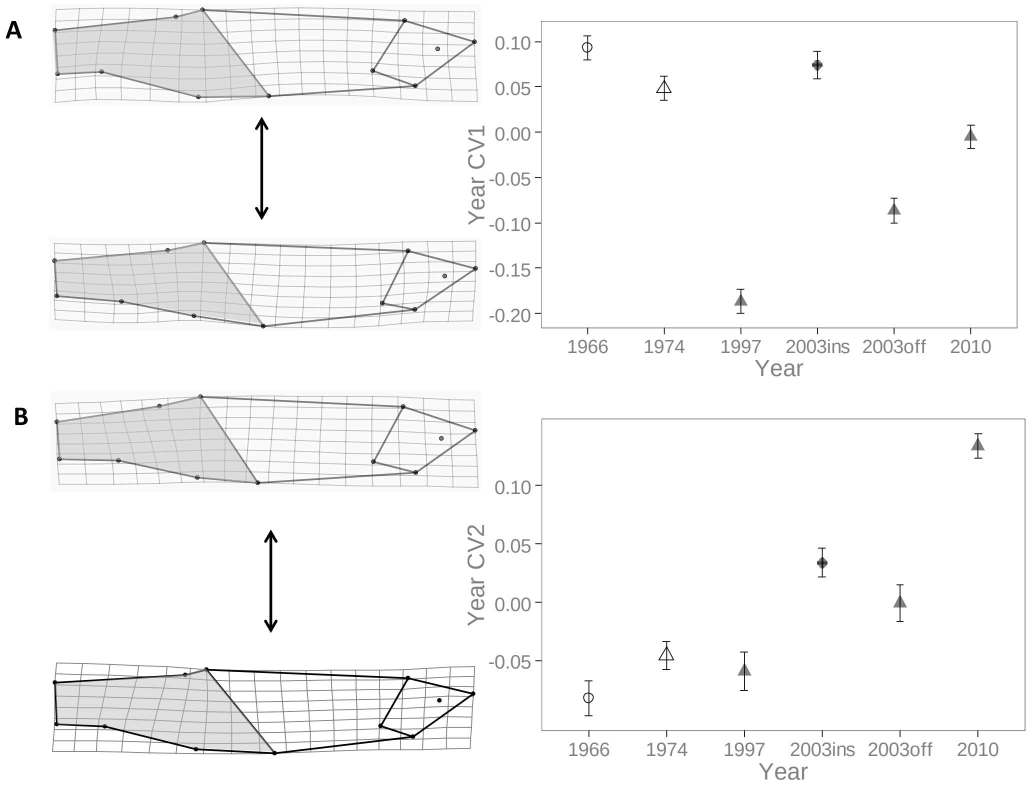

Fig. 3.4 Variation in overall body morphology of *R. argentea* over time in Lake Victoria.

Data are plotted along the first (Panel A) and second (Panel B) canonical variates for the year effect from MANCOVA. Body shape variation along each CV has been visualized using thin-plate spline transformation grids, which represent the positive and negative extremes of each axis and have been magnified 3 times. The colours represent years before (white) vs. after (black) the Nile perch population boom in Lake Victoria. The symbols represent collections from inshore (circles) vs. offshore (triangles) waters in Lake Victoria.

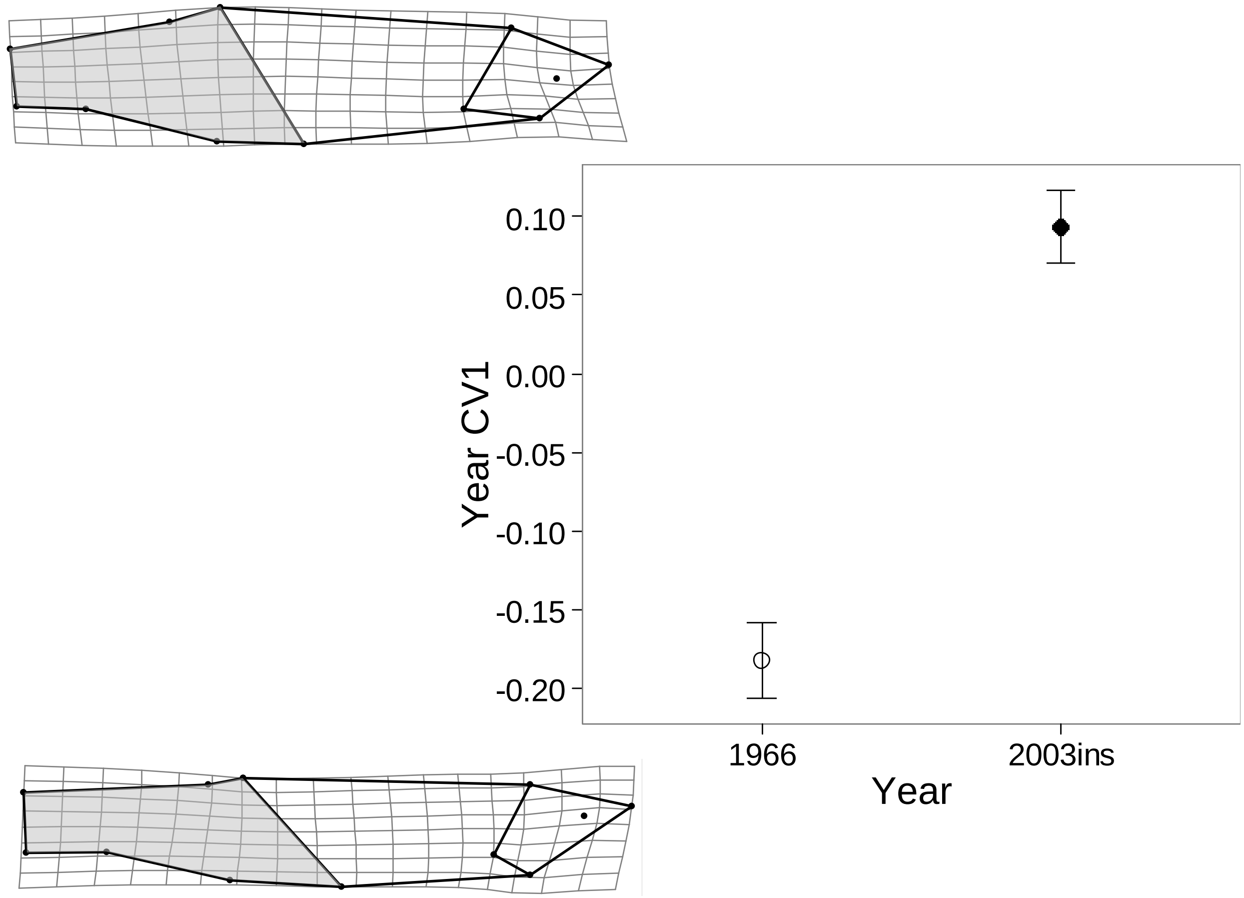

Fig. 3.5 Variation in overall body morphology of *R. argentea* over time in Lake Victoria, for *inshore* habitats only.

Data are plotted along the first canonical variate for the year effect from MANCOVA. Body shape variation along CV1 has been visualized using thin-plate spline transformation grids, which represent the positive and negative extremes of each axis and have been magnified 3 times. The colours represent years before (white) versus after (black) the Nile perch population boom in Lake Victoria.

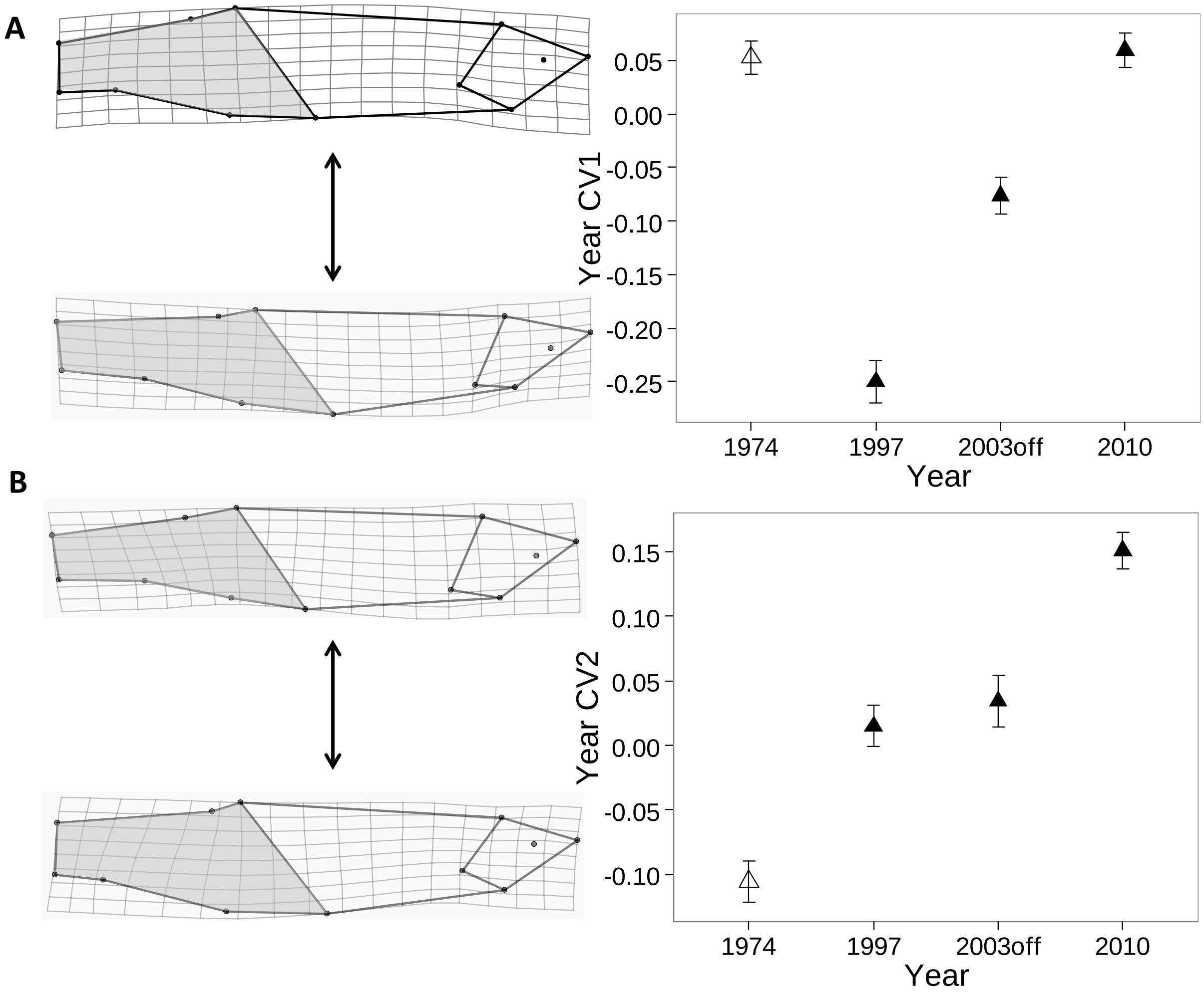

Fig. 3.6 Variation in overall body morphology of *R. argentea* over time in Lake Victoria, for *offshore* habitats only.

Data are plotted along the first (Panel A) and second (Panel B) canonical variate for the year effect from MANCOVA. Body shape variation along each CV has been visualized using thin-plate spline transformation grids, which represent the positive and negative extremes of each axis and have been magnified 3 times. The colours represent years before (white) versus after (black) the Nile perch population boom in Lake Victoria.

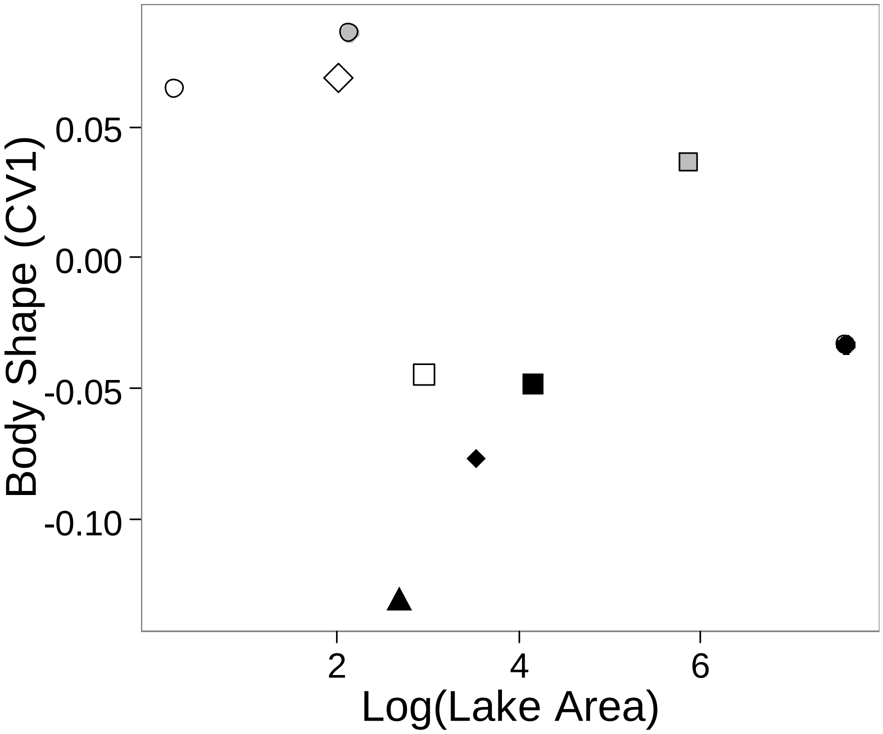

Fig. 3.7 Relationship between body shape (CV1 for the Nile perch factor from the MANCOVA) and log-transformed lake surface area (km^2), across lakes.

Negative scores along CV1 represent deeper-bodied fish with deeper caudal regions, and positive scores represent more streamlined fish (see Fig. 3.3 for visualization of CV1). For an explanation of symbols, please the caption for Fig. 3.3.

PREFACE TO CHAPTER 4:

From direct to indirect ecological and phenotypic impacts of introduced predators

The previous two chapters explored potentialdirect effects of Nile perch predation on the life history traits (Chapter 2) and body morphology (Chapter 3) of *R. argentea*. In Chapter 3, I found mixed support for the hypothesis that Nile perch predation would select for increased allocation to the mid-body/caudal region, which is associated with improved burst swimming speed and higher escape probability in other fishes. *R. argentea* from invaded lakes did have deeper mid-body/caudal regions than *R. argentea* from uninvaded lakes (as predicted); but the pattern of morphological change Lake Victoria through time appeared to be habitat-dependent. Thus, the effects of Nile perch predation on body shape in *R. argentea* are not straight-forward, and other factors (including the importance of habitat shifts and schooling behavior) should be considered in future work. In the following chapter, I consider potential *indirect* effects of the Nile perch introduction on the trophic ecology and morphology of *R. argentea*, mediated through changes in community composition in Lake Victoria. Specifically, I ask whether the dramatic decline in abundance and diversity of haplochromine cichlids following the Nile perch introduction released *R. argentea* from competition, thus allowing for niche expansion, and associated morphological changes. I use this natural experiment to test various hypotheses related to competitive release, including the role that individual specialization plays in population niche expansion, and the relationship between population niche breadth and morphological variance.

CHAPTER 4

4 Niche expansion and morphological change in a resilient endemic species following introduction of a novel top predator?

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4.1 Abstract

Introduced species can have profound direct ecological and evolutionary impacts on native species; yet their potential *indirect* effects remain relatively unexplored. For instance, introduced predators may directly impact some native species via predation, which may in turn have indirect consequences for other natives, for example, by releasing them from competition. We explore this possibility in East Africa’s Lake Victoria basin, where introduction of the predatory Nile perch in the 1950s and 60s contributed to the extinction or extirpation of hundreds of native fishes in the 1980s. We ask whether this dramatic change in community composition has led to competitive release and niche expansion in *Rastrineobola argentea*, a resilient native cyprinid fish that has thrived in this highly perturbed ecosystem. To address this question, we compare the trophic ecology and morphology of *R. argentea* before (1966) versus after (2011) the introduction of the Nile perch in Lake Victoria; and across 10 lakes that differ in their Nile perch invasion history. Using this combination of spatial and temporal comparisons, we test for (i) increases in dietary niche breadth (niche expansion), (ii) changes in the level of individual specialization, (iii) changes in trophic position, and/or (iv) changes in trophic morphology of *R. argentea* in invaded versus uninvaded contexts. In our historical comparison, we find good evidence for dietary niche expansion, an increase in inter-individual diet variation, and an increase in morphological variance in *R. argentea* following the Nile perch introduction in Lake Victoria. Across lakes; however, strong bottom-up effects (i.e., variation in prey availability) appear to obscure any potential top-down effects of the Nile perch introduction on the trophic ecology of *R. argentea*. Understanding both the direct and indirect impacts of introduced species is challenging, but important for successful long-term management of human-altered ecosystems.

Keywords: contemporary evolution, niche expansion, competitive release, individual specialization, character release, competition, introduced species, Lake Victoria, dagaa

4.2 Introduction

Introduced species can have dramatic ecological and evolutionary impacts on the communities that they invade, and are often cited as one of major drivers of contemporary biodiversity loss (Wilcove et al. 1998; Sala et al. 2000; Clavero and Garciá 2005, but see Gurevitch and Padilla 2004). Much of the literature to-date has focused on the *direct* consequences of introduced species for native biodiversity, including extinctions, extirpations, and declines in native species due to predation (e.g., Barel et al. 1985; Blackburn et al. 2004), competitive exclusion (e.g., Bøhn et al. 2007), and parasitism/disease (e.g., Brasier 2001). In recent years, there has also been increased interest in understanding the evolutionary consequences of ecological interactions between introduced and native species (Carroll 2007; Strauss et al. 2006). In contrast, the *indirect* effects of non-indigenous species, and their potential evolutionary consequences, have received less attention. By indirect effects, we refer to changes in the abundance, distribution, or other biological traits of native species that occur as an indirect result of community or ecosystem-level changes following a biological invasion, such as alterations to community composition, food-web structure, nutrient cycling, habitat structure, etc… One potentially important indirect effect is competitive release, which can occur when an invader reduces the abundance of competitively-dominant native species (for example via predation), allowing competitively-inferior native species to flourish. For example, the introduced predatory European green crab, *Carcinus meanas*, significantly reduced the abundance of several species of native clams and shore crabs in a Californian coastal ecosystem, which simultaneously resulted in increases in three other invertebrate taxa, most likely as a result of competitive release (Grosholz et al. 2000).

What might be some potential ecological and evolutionary consequences of “invader-mediated” competitive release for resilient native species? Theory suggests that competitive release can lead to niche expansion resulting from the combination of ecological opportunity provided by the reduction or disappearance of competitors, and/or disruptive selection imposed by increasing intra-specific competition as population density increases (Van Valen 1965; Roughgarden 1972). This hypothesis is supported by the observation that natural populations found in depauperate habitats tend to have broader ecological niches, as seen for example in birds (Diamond 1970) and lizards (Lister 1976) on oceanic islands, and freshwater fishes in species-poor temperate lakes (Robinson and Wilson 1994). In addition, several recent experiments have shown that manipulating levels of intra- or inter-specific competition can lead to niche expansion in the lab (Bolnick 2001), in enclosure experiments (Svanbäck and Bolnick 2007; Bolnick et al. 2010), and in bio-manipulated lakes (Persson and Hansson 1999; Syväranta and Jones 2008).

An increase in niche breadth can occur in several ways, each with different implications for individual resource use and phenotypic variation. One possibility is that, following competitive release, individual niche width remains constant, but variation in resource use among individuals increases, resulting in an increase in overall niche breadth of the population. Thus, the population would be composed of individual specialists, each exploiting a distinct, but relatively narrow, portion of the total resource spectrum (Bolnick et al. 2003; 2007). In this case, we would also potentially expect an increase in phenotypic variation among individuals ("The Niche Variation Hypothesis", Van Valen 1965), but only if phenotype is correlated to resource use (Bolnick et al. 2007). Alternatively, individual niche width may increase, while variation among individuals remains constant; and the population would be instead composed of individual generalists, each exploiting the entire range of available resources (e.g., Lister 1976). Here, we might expect a shift in the mean phenotype towards a generalist morphology that can exploit a broader range of resources, but no change in phenotypic variance. Finally, individuals might simply modify their behavior so as to exploit a wider niche (e.g., Werner and Sherry 1987), in which case niche expansion could occur with no change in phenotype. Of course, we might also expect some combination of the above, but these provide a useful framework for predicting potential phenotypic consequences of increased niche breadth.

The introduction of the predatory Nile perch, *Lates niloticus*, into Lake Victoria, East Africa in the 1950s and 1960s (Pringle 2005) contributed to a drastic reduction the lake's fish fauna, and thus provides a compelling natural experiment to test for competitive release, niche expansion, and morphological change in resilient native species (Wanink 1998; Wanink and Witte 2000b). Lake Victoria was transformed from a diverse community of over 500 fish species in the early 1980s to one now dominated by only three species: the native cyprinid *Rastrineobola argentea,* the introduced Nile perch, and the introduced Nile tilapia, *Oreochromis niloticus* (Kaufman 1992; Balirwa et al. 2003; Chapman et al. 2008). The once-abundant endemic haplochromine cichlid fishes, which previously accounted for over 80% of the biomass of Lake Victoria (Kudhongania and Cordone 1974), virtually disappeared from the deepwater regions of Lake Victoria in the mid- to late 1980s, with approximately 40% of the 500+ species of haplchromine cichlids believed to have been extirpated or gone extinct (Witte et al. 1992; Seehausen et al. 1997). Many other native species also suffered serious declines during this time period, including the African lungfish, *Protopterus aethiopicus* (Goudswaard et al. 2002), the native tilapiines *Oreochromis variabilis* and *Oreochromis esculentus* (Goudswaard et al. 2002), and several native catfishes, including *Bagrus docmak, Clarias gariepinus, Synodontis afrofishceri*, and *Synodontis victoriae* (Goudswaard and Witte 1997). As a result, a once diverse and complex community composed of numerous trophic specialists was replaced by a much simpler community dominated by only a handful of more generalist and omnivorous species (Ojwang et al. 2010; Downing et al. 2012). Similar faunal changes occurred in other lakes in the region where the Nile perch were introduced, including in Lake Kyoga (Mbabazi et al. 2004), and Lake Nabugabo (Ogutu-Ohwayo 1993; Chapman et al. 2003). With Nile perch populations themselves now in apparent decline (Getabu et al. 2003; Mkumbo et al. 2007; NaFIRRI 2008), there is evidence for a limited recovery of a small subset of the basin fauna (Chapman et al. 2003; Witte et al. 2000, 2007), but the food-web as a whole remains drastically simplified compared to what it was at the turn of the century.

In this paper, we explore the ecological and phenotypic consequences of these dramatic changes in community composition on the resilient native zooplanktivore, *R. argentea*. Contrary to the declines observed for most other native fishes, *R. argentea* increased dramatically in abundance in the 1980s (Wanink 1999), and this species now dominates the biomass of Lake Victoria, accounting for approximately 57% of the total fish biomass of the lake (NaFIRRI 2008). *R. argentea* is also now the most important commercial species (by weight) in Lake Victoria, and is thus a critical resource for the approximately 22 million people that depend on Lake Victoria's fisheries for their livelihoods and nutrition (NaFIRRI 2008; LVFO 2011). Several authors have speculated that *R. argentea's* success in Lake Victoria may, among other things, reflect competitive release following the decline of the haplochromine cichlids. This group included more than 20 species of zooplanktivores, which *R. argentea* has effectively "replaced" (Goldschmidt et al. 1993; Ojwang et al. 2010; Wanink 1998; Wanink and Witte 2000). The only direct empirical support for this competitive release hypothesis so far comes from a series of studies by Wanink and Witte (1998, 2000), who reported shifts in the habitat and diet of *R. argentea* from the Mwanza Gulf (Tanzanian waters) of Lake Victoria shortly after the disappearance of the haplochromine cichlids from that part of the lake.

Here, we expand on this previous work by examining multiple aspects of the trophic ecology of morphology of *R. argentea* in a broader spatial and temporal context. We use a combination of historical and contemporary data from 10 Ugandan lakes to address the following questions. First, did the Nile perch introduction, and the subsequent simplification of aquatic food webs in lakes throughout the Lake Victoria basin, lead to an expansion of the dietary niche of *R. argentea*? *R. argentea* has been previously described as a zooplanktivore specialist (Corbet 1961), but data from the Mwanza Gulf suggest that benthic prey became incorporated into the diet shortly after the disappearance of many haplochromine cichlids (Wanink 1998). Did these diet changes occur generally throughout Lake Victoria, and in other invaded lakes in the basin? Second, are increases in dietary niche breadth (if they occur) due to increases in individual diet breadth (i.e., increased variation *within* individuals), or to increases in individual specialization (i.e., increased variation *among* individuals)? Third, have there been changes in the overall trophic position of *R. argentea*? Finally, have the mean and/or variance of trophic morphology (gill rakers) changed in tandem with diet breadth?

To address these questions, we use a combined approach, comparing diet and morphology of *R. argentea* across 10 lakes that differ in Nile perch invasion history, and before versus after the establishment of Nile perch in one region of the most heavily-impacted lake (Lake Victoria). We quantify diet, trophic niche breadth, and trophic position using a combination of traditional gut contents data (which provide a detailed "snapshot" of diet at the time of sampling) and stable isotope data (which provide a more indirect, but time-integrated representation of feeding patterns). For trophic morphology, we focus on gill rakers, which are often correlated with diet in planktivorous fishes (Robinson and Wilson 1994).

4.3 Methods

4.3.1 Study Sites:

Our sampling covered all of *R. argentea'*s known distribution in the Lake Victoria basin in Uganda, East Africa (Fig. 4.1,Table 4.1). Of the 10 lakes we sampled, three lakes (Kayanja, Omuno, and Gigati) had never been stocked with Nile perch, and still have intact native fish communities dominated by haplochromine cichlids. Two lakes (Bisina and Nawampasa) were transiently invaded by Nile perch, but also still support relatively intact native fish communities. Lake Bisina was stocked with Nile perch in the 1970s and supported a Nile perch fishery in the 1980s (Mbabazi 2004). However, the fishery has since collapsed, and Nile perch not have been caught commercially or in experimental surveys since the early 2000s (Mbabazi 2004; Sharpe and Chapman, *unpl. data*). Nile perch gained access to Lake Nawampasa during the El Niño floods of 1998 (Wandera, S.B. *unpl. data*), but it is not known whether they have managed to persist since then. The remaining five lakes in our study were stocked with Nile perch between the 1950s and 1970s, and dramatic declines in native taxa, particularly the haplochromine cichlids, followed in lakes Nabugabo (Ogutu-Ohwayo 1993), Kyoga (Mbabazi et al. 2004), and Victoria (Witte et al. 1992), and presumably in the other invaded lakes (Meito and Nakuwa) as well, although detailed historical data for the latter are lacking. Increasing fishing pressure on Nile perch has coincided with a limited resurgence in a subset of native taxa in recent years, in Lake Nabugabo (Chapman et al. 2003) and in Lake Victoria (Witte et al. 2000).

4.3.2 Gut contents analysis:

Fish collections:

Because our study of inter-lake variation in diet would have to rely on point-in-time sampling (due to logistical constraints), we first sought to quantify seasonal variation in the diet of *R. argentea* in one of our most accessible study lakes, Lake Nabugabo, in order to assess potential biases and limitations associated with making inferences about diet from one sampling event. For this seasonal study, *R. argentea* were caught in ½” mono-filament gill-nets set at the surface for 1-3 hours in the mid-afternoon, approximately 100m offshore. Nets were set in the same three locations each month, corresponding to the three major habitat types that characterize the shoreline of Lake Nabugabo: forest edge, hippo grass wetland, and *Miscanthidium* wetland. Fish from the three sampling locations were pooled in the final analysis (due to small sample sizes), but this design ensured a representative sampling of the lake’s habitats. Sampling was repeated in four wet season months (May, October, November, and December) and two dry season months (January and February) during 2008-2009 (Table 4.2). All fish were euthanized in clove oil and preserved in 10% formalin.

To examine diet variation across lakes, *R. argentea* were sampled from 10 Ugandan lakes in June 2010 (Fig. 4.1). The diet of *R. argentea* is known to vary diurnally, and with the lunar cycle (Wandera 1992; Wanink 1998); so we collected all samples at the same time of day (mid-afternoon), and within the same 10 day period (June 9th to 20th 2010, which corresponded to the new moon). *R. argentea* were targeted using 5mm-mesh surface seines operated in the pelagic zone of each lake, but this gear was ineffective in 3 out of the 10 lakes (Nabugabo, Nakuwa and Meito), where we caught few or no individuals even after repeated attempts. For Nabugabo, we therefore relied on diet data collected during our earlier seasonal study (using the May sample, as it was closest to June). For Meito and Nakuwa, we had too few individuals for gut contents analysis, but we did have a sufficient sample size to include these lakes in the stable isotope analysis (see below). In Lake Victoria (Napoleon Gulf), almost all of the over 200 stomachs that we examined from June 2010 were empty, so we returned in August 2011 (also during the new moon portion of the lunar cycle) to collect additional samples (Table 4.2).

To examine diet variation through time in Lake Victoria, we compared museum specimens of *R. argentea* caught in the Napoleon Gulf in 1966 to *R. argentea* caught in the Napoleon Gulf in 2011 (Table 4.1). The historical specimens were obtained with permission from the Biodiveristy Museum of the National Fisheries Resources Research Institute (NaFIRRI), in Jinja, Uganda.

Laboratory analysis:

In each population, we restricted our analysis to the largest 30 individuals, so as to minimize variation due to potential ontogenetic diet shifts, which was not the focus of our study. Individuals were measured for standard length (mm) and dissected. Sex and maturity status (based on macroscopic examination of the gonads following a scale previously developed for *R. argentea;* Wandera, *unpl. data*, Sharpe et al. 2012) were recorded, as well as the presence of any macroparasites in the abdominal cavity (Table 4.2).

R. argentea do not have a true stomach; instead their digestive system consists of an intestine with three distinctive loops. For consistency, and to avoid uncertainties associated with analyzing overly digested material, we focused exclusively on contents of the first (most anterior) loop of the intestine. Gut fullness was scored on a scale of 0 to 4, with 0 representing a completely empty intestine segment, and 4 representing a completely full intestine segment. Prey were identified and grouped into one of the following nine categories: Copepoda, Cladocera, Rotifera, emerging insects, chironomid larvae, *Chaoborus* pupae, *Chaoborus* larvae, plant matter, and other. Emerging insects included adult stages of aquatic insects, but most were too digested to reliably identify to a lower taxonomic level (although the majority were dipterans). The category "other" included fish scales, fish eggs, and a few other infrequently-occurring and/or unidentifiable items. It was not clear whether the latter items were intentionally consumed, or merely accidentally ingested with other prey.

The relative importance of different prey types was estimated using the *points method* (reviewd by Hynes 1950; Hyslop 1980). Although this method can be quite subjective (Marrero and Lopez-Rojas 1995), it is appropriate for small fish which consume prey items that cannot easily be enumerated in the gut, either because they are macerated, not discrete (e.g. plant matter), or because direct counts may be biased by prey taxa that have multiple parts (e.g., insect legs, wings). Furthermore, this method has been widely used in recent fish diet literature (e.g., Bwanika et al. 2006; Binning et al. 2009). We attempted to reduce potential biases associated with the points method by adopting the following protocols: (i) all stomachs were scored by the same person, (ii) stomachs were examined in a random order, and (iii) all stomachs were double-checked by a second person at the end of the study.

Following the points method, we visually estimated the proportional importance of each prey item based on the relative volume it occupied in the intestine. These proportions were then weighted by the fullness of the gut to yield a "points" estimate for each prey item (j) in each individual (i):

$$\text{Points}_{ij} = F_j \cdot q_{ij}$$

where F_i is the fullness of the gut (intestine segment) of individual i (0 – 4), and q_{ij} is the proportion of prey taxon j in the gut of individual i. The relative importance of each prey type at the population level (p_j) was calculated as the sum of points attributed to prey type j across all n individuals in that population, divided by the total points attributed to all R prey taxa in the population:

$$p_j = \frac{\sum_{i=1}^{n} (\text{Points}_{ji})}{\sum_{j=1}^{R} \sum_{i=1}^{n} (\text{Points}_{ji})}$$

We also calculated the frequency of occurrence (FO) of each prey type in each population as the proportion of individuals in that population with non-empty stomachs whose guts contained that prey type.

Statistical analysis:

Seasonal variation in the diet of *R. argentea* in Lake Nabugabo was examined by plotting the relative importance (p_j) of prey items across sampling months. The degree of pairwise overlap between months was quantified using the percent similarity index, PSI (Schoener 1970):

$$\text{PSI} = 1 - 0.5\sum_{j=1}^{R} |p_{xj} - p_{yj}|$$

where p_{xj} is the proportion of prey taxon j in the diet of *R. argentea* during month x and p_{yj} is the proportion of prey taxon j in the diet of *R. argentea* during month y. PSI ranges from 0 to 1, with 0 indicating that the two populations share no dietary resources; and 1 indicating that they have an identical diet.

Variation in diet across lakes, and across years in fish collected in the Naploleon Gulf of Lake Victoria, was first examined qualitatively using the measures of relative importance described above (p_j and FO).

Dietary niche breadth was quantified using two indices proposed by Levins (1968): the Shannon-Weiner diversity index (H), and the inverse of the Simpson index, often now referred to as Levin's index (B_n):

$$H = -\sum_{j=1}^{R} p_j \cdot \ln(p_j)$$

and

$$B_n = \frac{1}{R \cdot \sum_{j=1}^{R} p_j^2}$$

where p_j is the proportion of prey type j in the population's diet (calculated from the points as outlined above), and R is the number of prey types (9 in our case). For Levin's index, we used the normalized version, B_n, which varies from 1/R (when the population uses one resource exclusively) to 1, when the population uses all resources in equal proportions (Feinsinger et al. 1981). Similarly, H is maximized when the population uses all resources proportionally (Colwell and Futuyma 1971). Both indices were calculated in R. The raw data (p_{ij} values) were then re-sampled 1000 times in order to calculate boot-strapped 95% confidence intervals around H and B_n, using the boot package in R. We tested for differences in H and B_n across Nile perch invasion categories using the Kruskal-Wallis test.

Individual specialization was quantified using PS_i, as proposed by Bolnick et al. (2002). PS_i is analogous to Schoener's index, except that in this case, the index calculates pairwise overlap between each individual and the population as a whole. PS_i is calculated as:

$$PSi = 1 - 0.5\sum_{j=1}^{R} |p_{ij} - q_i|$$

where p_{ij} is the proportion of prey type j in the diet of individual i, and q_i is the proportion of prey type j in the population as a whole. PS_i can be calculated by either including or excluding i from the calculation of q_i. In our case, the results were almost identical using both approaches, so we present only the latter case. The overall prevalence of individual specialization in the population (IS) is the mean of individual PS_i scores. IS has a maximum value of 1 (when all individuals consume resources in direct proportion to the population as a whole), with lower values indicated higher individual specialization (Bolnick et al. 2002). We tested for differences in IS across Nile perch invasion categories using the Kruskal-Wallis test. We also calculated *mean pairwise overlap*, which is the mean percent similarity (PSI) between all pairwise combinations of individuals in the population. Another widely used metric of individual specialization is the ratio of within-individual niche variation to total niche width (WIC/TWN). However, WIC/TWN can be strongly biased when individuals are monophagous (Bolnick et al. 2002). Since monophagy was quite was common in our data-set, we chose not to calculate this index. All individual specialization calculations were carried out in IndSpec (© Bolnick, 2012).

4.3.3 Across lake variation in prey availability:

Because diet is constrained by the availability of potential prey, we sought to quantify the relative abundance of potential prey across our study lakes. We focused on zooplankton, because *R. argentea* are most often described as zooplanktivorous in the literature. We sampled zooplankton using a 80μm plankton net, which was towed vertically through the entire water column at four randomly-selected sites in the pelagic zone of each lake. Samples were preserved in 10% formalin, and enumerated under a dissecting microscope in the laboratory. Zooplankton densities were corrected by dividing the sample density by mean lake depth (calculated as the mean of three replicate depth measures per lake, see Table 4.1 for values). Adjusted zooplankton densities were then compared across lakes using ANOVA. We tested for correlations between the relative abundance of zooplankton in the diet of *R. argentea* (sum of points attributed to Cladocera, Copepoda, and Rotifera), and the density of zooplankton in the environment (sum of mean densities of Cladocera, Copepoda, copepod nauplii, and Rotifera in each lake) using a Pearson correlation.

4.3.4 Stable isotopes:

Collection and sample preparation:

We collected adult *R. argentea* from the 10 lakes as described above for gut contents, and then dissected out a small piece of dorsal muscle tissue (removing all scales and bones), from approximately 10 individuals per lake. In fish, white muscle tissue is the best tissue type for stable isotope studies because it contains the lowest amounts of lipids and inorganic carbonates, which can otherwise alter the isotopic signature (Pinnegar and Polunin 1999). We focused on adult individuals (35 to 56 SL mm), to minimize any variation due to potential ontogenetic shifts in diet. Snails (and clams whenever possible) were collected in order to establish the isotopic baseline in each lake (see below for details). Snails and clams were collected by hand from submerged shoreline vegetation, nets, or dredges, broken open, and the soft tissue was retained for analysis. All tissue samples were sun-dried in the field (following Mbabazi et al. 2009) using a home-made solar oven (at approximately 50°C for 2-5 hours), and then packaged and shipped back to our laboratory at McGill University, where they were dried again in a drying oven at 60°C for approximately 24 hours. Tissue samples were then ground into a fine powder using a mortar and pestle, weighed, and packaged into 5x9mm tin capsules. Samples were analyzed for carbon and nitrogen stable isotope ratios using a PDZ Europa ANCA-GSL elemental analyzer and PDZ Europa 20-20 isotope ratio mass spectrometer at the Stable Isotope Facility at UC Davis. Samples were run with replicated laboratory standards in order to calibrate the stable isotope ratios of the samples, and to estimate the standard deviation of the measurements, which was approximately 0.3‰ for δN and 0.2‰ for δC. Stable isotope ratios are expressed using the delta notation, which compares the ratio of carbon ($^{13}C/^{12}C$) or nitrogen isotopes ($^{15}N/^{14}N$) in a sample relative to those in an international standard:

$$\delta N \text{ or } \delta C = [(R_{sample}/R_{standard}) - 1] \times 10^3 \qquad \text{(Peterson and Fry 1987)}$$

The standards used were V-PDB (Vienna PeeDee Belemnite), and atmospheric nitrogen, for carbon and nitrogen respectively (UC Davis, 2012)

Statistical analysis:

Stable isotope signatures can be used to infer trophic position in food webs because $\delta^{15}N$ becomes enriched in a predictable, step-wise manner as one moves up a food chain, generally being 3.4‰ greater in the tissues of consumers relative to their prey (Peterson and Fry 1987). However, because the isotopic signatures at the base of food webs can vary considerably across space, it is important to quantify this variation in primary producers and use it to calibrate one's estimates of the trophic position of consumers in different habitats. Sampling primary producers directly can be challenging, but several studies have shown that long-lived primary consumers can be used as reliable proxies of the isotopic baseline

(Cabana and Rasmussen 1996;Vander Zanden and Rasmussen 1999; Post 2002). In aquatic systems, bivalves have been shown to be representative of the base of the pelagic food web, while snails are good indicators of the base of the littoral food web. In our study lakes, bivalves were harder to find, so we used snails to calibrate our isotopic baselines. However, in the three lakes where we did manage to find clams, they grouped closely with snails in isotopic space (Fig. 4.10), suggesting that use of snails exclusively may be a reasonable first approximation in our system. Following Post et al. (2000), we calculated the trophic position of *R. argentea* in each lake as:

$$TP_{Ra} = 2 + [\delta^{15}N_{Ra} - \delta^{15}N_{snails}]/\Delta N$$

where 2 is the trophic position of snails, $\delta^{15}N_{Ra}$ is the mean $\delta^{15}N$ value for *R. argentea*, $\delta^{15}N_{snails}$ is the mean $\delta^{15}N$ value for snails, and ΔN is the trophic fractionation rate, estimated as 3.4‰ (Peterson and Fry 1987; Post 2002).

In recent years, several authors have suggested that intrapopulation variability in stable isotopic signatures could be used to infer trophic niche width, based on the premise that a population of consumers that feeds on multiple and diverse prey types will have more variable isotopic signatures than a population of consumers that feeds on only a few prey types. Bearhop et al. (2004) therefore proposed that the variance in stable isotope ratios ($\delta^{15}N$ and $\delta^{13}C$) could be used to approximate dietary niche width. This approach has been supported by laboratory experiments with *Daphnia* that confirmed that populations with more generalist diets showed greater variance in isotopic signatures (Fink et al. 2012). However, in another study, mathematical simulations showed that isotopic data may yield very deceptive estimates of niche width under certain circumstances, for example if consumers forage in multiple habitats (Flaherty and Ben-David 2010); implying caution in inferences drawn. A conceptually similar approach to that of Bearhop et al. is to estimate population niche width as the total area encompassed by the smallest convex polygon containing all individuals in a population isotopic space (*convex hull method*, Layman 2007). We calculated all three indices of isotopic niche width (variance in δ^{15}N and δ^{13}C, and the convex hull area) for *R.argentea*. The convex hull area was approximated as the area of convex polygons traced on the isotopic biplots of each lake in ImageJ (v 1.45). We tested for differences in these three indices across Nile perch invasion categories using separate Kruskal-Wallis tests.

4.3.5 Gill raker morphology:

To examine variation in gill raker morphology across lakes, we used the same individuals as for the gut contents analysis above, as well as additional specimens from 2008 and 2009 for a subset of these same lakes. To examine variation in gill raker morphology in Lake Victoria through time, we compared museum specimens from 1966 and 2000 to contemporary specimens from 2008, 2009, and 2010. We dissected out the first gill arch from the left side of each fish, and counted the number of rakers on both the upper and lower arch under a dissecting microscope. We then photographed each first gill arch, and used Motic (v. 1.3, 2000) to measure gill raker length, width, and inter-raker space. These measurements were repeated on the 2nd, 3rd and 4th rakers of the lower arch, and the mean of the three measurements was used in the analysis.

Gill raker number was uncorrelated with standard length (r = -0.03, p = 0.49), but gill raker length, width, and spacing were all positively correlated with standard length. The latter traits were therefore size-standardized to a common body length using the following allometric equation:

$$Z_{std} = Z_o[44.49/SL_o)^b$$

where Z_{std} is the size-standardized trait value, Z_o is the observed trait value, 44.49 is the mean standard length of all individuals in the data-set, SL_o is the observed standard length, and b is the slope from a regression of $\log(Z_o)\sim\log(SL_o)$ for each trait.

Sample sizes ranged from 21-42 individuals per lake, per year. Contemporary years (2008-2010) were pooled after visual inspection of the data showed no major differences across years within lakes. Total sample sizes were 488 individuals for the across-lake analysis, and 137 for the historical analysis.

We performed a principal components analysis (PCA) on the size-standardized gill raker traits in order to visualize variation in gill raker morphology. To test for the morphological variation across lakes, and across years in Lake Victoria, we performed a MANCOVA, followed by separate ANCOVAs on each trait to examine specific differences in more detail. In each model, lake (or year) was treated as a fixed factor, and standard length was included as a covariate. We tested for differences in the variance of size-standardized gill raker traits across lakes, and across years in Lake Victoria, using Bartlett's test of homogeneity of variances.

Finally, we tested for correlations between gill raker morphology and diet using the subset of individuals for which we had data on both gill raker morphology and gut contents (147 fish from 6 lakes). We tested for associations between morphology and diet using Pearson correlations between the first two morphological principal components (gill raker PC1 and PC2), and 5 major diet variables that we expected *a priori* might influence raker morphology: the proportion of Cladocera in the gut, the proportion of Copepoda in the gut, the total proportion of zooplankton in the gut (Cladocera, Copepoda, and Rotifera), the proportion of insects in the gut, and the proportion of large benthic prey in the gut (chironomid larvae, *Chaoborus* larvae, and *Chaoborus* pupae). Lakes were pooled in this analysis; i.e., we did not test for differences in the slopes and intercepts of different lakes. Since 20 correlations were carried out, we present our results with and without the Bonferroni correction. All statistical analyses were conducted in R (2012), unless otherwise indicated.

4.4 Results

4.4.1 Trophic ecology of R. argentea in Lake Victoria before vs. after the Nile perch introduction:

Diet composition:

The diet of *R. argentea* in 1966 was dominated (based on the proportion of points, p_j) by zooplankton, primarily copepods (87%; Fig. 4.2). In contrast, the diet of *R. argentea* in 2011 included a wider variety of prey types, including Cladocera (34%), emerging insects (22%), and *Chaoborus* larvae (34%). Copepods were extremely rare in the stomachs of contemporary samples (<0.01%). The frequency of occurrence data largely confirmed these results (Appendix L). Overall, the gut contents analysis suggested a marked shift in diet composition of *R. argentea* between 1966 and 2011.

Dietary niche breadth and individual specialization:

Both Levin's index of niche breadth and the Shannon diversity index were significantly greater for contemporary (2011) relative to historical (1966) populations, indicating an increase in dietary niche breadth over time (Fig. 4.3). The prevalence of individual specialization was also significantly different across time periods (Wilcoxon rank sum test: W=836, $p < 0.001$), with lower IS values in 2011 (mean ± SE: 0.38 ± 0.02) than in 1966 (0.89 ± 0.02), indicating increased individual specialization over time. Mean pairwise overlap among individuals declined from 86% in 1966 to 30% in 2011.

Trophic morphology:

Overall, gill raker morphology differed significantly across years in Lake Victoria (MANCOVA: $F_{16,373.35} = 2.29$, $p = 0.003$). Separate AN(C)OVAs revealed that these differences were significant for raker length ($F_{4,127} = 3.02$, $p = 0.020$) and spacing ($F_{4,127} = 3.14$, $p = 0.017$), but not for raker width or number. Contemporary (2009) populations of *R. argentea* had shorter and more tightly-packed gill rakers than *R. argentea* from 1966 (Table 4.3). There was a significance increase in the variance of gill raker width over time (Bartlett's K^2= 11.31, $p = 0.02$; Appendix M), but there was no change in the variance of the other three traits. The increase in variance in gill raker width between 1966 and 2010 paralleled the increase in niche width between 1966 and 2011 (Fig. 4.3).

4.4.2 Trophic ecology of *R. argentea* across invaded vs. univaded lakes:

Diet composition:

Seasonal variation in diet in Lake Nabugabo:

Both the proportion of points and frequency of occurrence of prey types indicated that zooplankton (Cladocera and Copepoda) dominated the diet of *R. argentea* in Nabugabo throughout the year, although more so in the dry season (January and February) than in the wet season (Fig. 4.4, Appendix N). Chironomid and chaoborid larvae were also consumed throughout the year, but comprised a greater proportional of the diet in the wet season months, particularly November and December. Although the relative importance of prey types varied somewhat throughout the year, no novel prey type appeared in any month, and no major prey type was absent from any month. Percent similarity in diet was 89% between dry season months, 76% among wet season months, and 66% across all months (Appendix O).

Variation in diet across lakes:

Gut contents analysis suggested that there was considerable variability in the diet of *R. argentea* across the eight study lakes where stomach contents could be evaluated (Fig. 4.5, Appendix P). *R. argentea* from lakes Kayanja and Bisina were primarily insectivorous, feeding mainly on emerging aquatic insects. *R. argentea* from lakes Gigati and Kyoga were zooplanktivorous, feeding predominately on Cladocera. *R. argentea* from lakes Omuno, Nawampasa, Nabugabo, and Victoria had more diverse diets, feeding on both zooplankton and various stages of aquatic insects. The population of *R. argentea* from Nawampasa was the only one observed to be feeding on plant matter: their guts were full of green material and what appeared to be water lily seeds (the entire surface area of Lake Nawampasa was covered in water lilies during our 2010 sampling). In Lake Victoria, we observed a blue-green “fluff” in almost all stomachs, which may have been cyanobacteria that were ingested along with other prey. However, because we could not identify it with certainly, it was not included in our quantitative analyses of diet. Fragments of synthetic fishing line were found in 34% of the 220 non-empty stomachs examined. Although there was substantial variation in diet across lakes, there were no consistent differences in diet composition across Nile perch invasion categories (Fig. 4.5).

Spatial variation in prey availability:

Zooplankton densities varied significantly across lakes (ANOVA: $F_{9,30}$ = 95.90, $p < 0.001$), being highest in lakes Kyoga and Nakuwa, and lowest in lakes Bisina and Kayanja (Appendix Q). The relative abundance of zooplankton in the diet of *R. argentea* was positively correlated with the density of zooplankton across lakes (r = 0.70, p = 0.054, df = 6). That is, *R. argentea* from lakes that were richest in zooplankton also tended to feed most heavily on zooplankton (Fig. 4.6A). The ratio of Cladocera to Copepoda was much higher in the diet of *R. argentea* than in the environment, indicating a strong preference for Cladocera (Fig. 4.6B).

Dietary niche breadth and individual specialization:

There was substantial variation in dietary niche breadth among populations of *R. argentea* (Fig. 4.7). Both Levin's index and the Shannon Diversity index showed a similar pattern, with *R. argentea* from lakes Omuno, Nawampasa, Nabugabo and Victoria having the broadest niches. As can be inferred from the spread of bootstrapped 95% confidence intervals plotted in Fig. 4.7; the niche breadths of many lakes were significantly different from one another. However, dietary niche width did not differ across invasion categories, either for Levin's index (Kruskal-Wallis test: χ^2 = 1.89, p = 0.40) or for the Shannon Index (Kruskal-Wallis test: χ^2 = 1.36, p = 0.51).

The prevalence of individual specialization varied significantly across lakes (Kruskal-Wallis test: χ^2 = 157.59, $p < 0.001$), being greatest in lakes Omuno, Nawampasa, Nabugabo and Victoria (Fig. 4.7). Similarly, mean pairwise overlap between individuals was lowest in these same four lakes (30 – 45%), and highest in Lake Kayanja (93%; Table 4.4). The overall degree of individual specialization did not differ among Nile perch invasion categories (Kruskal-Wallis test: χ^2 = 2.25, p = 0.325). Dietary niche breadth and individual specialization were negatively correlated across lakes (Pearson correlations for Levin's index: r = -0.89, p = 0.003, df =6; and Shannon index: r = -0.92, p = 0.001, df =6). That is, lakes with broader dietary niches at the population level also showed higher levels of individual specialization, and vice-versa (Fig. 4.8).

Dietary niche breadth was also estimated from the stable isotope data, based on the variance in $\delta^{15}N$, variance in $\delta^{13}C$, and the convex hull area (Appendix R). The three indices each painted a somewhat different picture of variation in niche breadth across lakes (Fig. 4.9), but three lakes consistently emerged as having broad "isotopic niches": Kayanja and Nawampasa, and to a lesser extent, Victoria. Overall, however, there were no significant differences in isotopic niche width across invasion categories, either for variance in $\delta^{15}N$ (Kruskal-Wallis test: $\chi^2 = 0.30$, $p = 0.86$), variance in $\delta^{13}C$ (Kruskal-Wallis test: $\chi^2 = 1.87$, $p = 0.39$), or for the convex hull area (Kruskal-Wallis test: $\chi^2 = 0.37$, $p=0.83$).

Trophic position:

The mean stable isotope composition of *R. argentea* muscle tissue from the 10 lakes surveyed varied from 4.82‰ to 8.18‰ for $\delta^{15}N$, and -25.22‰ to -10.09‰ for $\delta^{13}C$ (Fig. 4.10, Table 4.5). Stable-isotope derived estimates of trophic position ranged from 2.24 (Gigati) to 4.34 (Nabugabo; Appendix R). Trophic position tended to be higher in invaded relative to uninvaded lakes (Fig. 4.11), although this trend was not statistically significant (Kruskal-Wallis test: $\chi^2 = 2.33$, $p = 0.31$).

Trophic morphology:

Gill raker morphology differed significantly across lakes (MANCOVA: $F_{32,1572.6} = 23.69$, $p < 0.001$). A PCA on size-standardized gill raker traits (Table 4.6) revealed three major groupings among the lakes (Fig. 4.12). The first group was distinguished by *R. argentea* having longer, thinner, more numerous and more tightly-packed gill rakers, and included lakes Nakuwa and Bisina. The second group was distinguished by *R. argentea* that had fewer, shorter, thicker, more widely-spaced rakers, and included Lake Kayanja only. Almost all the other lakes showed an intermediate, and overlapping gill raker morphology; although of these, Nawampasa and Victoria stood out slightly from the others, having slightly longer rakers.

Across individuals, variation in PC1 was negatively correlated with the proportion of Cladocera in the gut ($r = - 0.18$, $p = 0.029$, $df = 145$; Fig. 4.13) but not significantly related to the proportion of Copepoda, or zooplankton as a whole. That is, individuals with more Cladocera in their gut tended to have thinner, more numerous, more tightly-packed rakers than individuals who had consumed fewer Cladocera. Variation in PC2 was negatively correlated with the proportion of Cladocera ($r = -0.37$, $p < 0.001$, df = 145) and zooplankton as a whole ($r = -0.27$, $p = 0.001$, df = 145); and positively correlated with the proportion of insects in the gut ($r = 0.18$, $p = 0.026$, df = 145). That is, individuals with more zooplankton, and fewer insects in their gut tended to have shorter gill rakers, while individuals with less zooplankton and more insects tended to have longer gill rakers. Applying the Bonferonni correction, of the correlations reported above, only those where $p < 0.005$ should be considered significant.

There were significant differences across invasion categories in the variance of raker width (Bartlett's $K^2 = 15.40$, $p < 0.001$), but not for the number, length, or spacing of rakers. Variance in gill raker width was highest in lakes with established Nile perch populations (Appendix S). However, variance in gill raker width was not significantly related to niche width, either based on gut contents analysis (Pearson correlation with Levin's index: $r = 0.13$, $p = 0.75$, df = 6), or stable isotope data (Pearson correlation with convex hull area: $r = - 0.26$, $p = 0.54$, df =6). In other words, populations with broader niches were not significantly more morphologically variable than populations with narrower niches.

4.5 Discussion

We set out to explore the potential indirect effects of the introduction of the predatory Nile perch into the Lake Victoria basin on the trophic ecology and morphology of the resilient native cyprinid, *R. argentea*. Specifically, we tested for: (i) increases in dietary niche breadth (niche expansion), (ii) changes in the level of individual specialization, (iii) changes in trophic position, and/or (iv) changes in trophic morphology of *R. argentea* in invaded versus uninvaded contexts. To do this, we compared populations of *R. argentea* before (1966) versus after (2011) the introduction of the Nile perch in Lake Victoria; and across 10 lakes that differ in their Nile perch invasion history. We now discuss the major findings of each of these analyses in turn, before drawing some general conclusions.

4.5.1 Trophic ecology of R. argentea in Lake Victoria before vs. after the Nile perch introduction:

We found that the diet of *R. argentea* in Northern Lake Victoria in 1966 was dominated by zooplankton, primarily copepods. This is consistent with historical accounts from Lake Victoria (Corbet 1961), as well as a similar analysis by Mwebaza-Ndawula (1998), who examined 30 adult *R. argentea* from the same 1966 museum collection that we sampled, and also found strong dominance by copepods (which accounted for approximately 65% of the diet, by weight). Our contemporary (2011) data suggest that two important dietary shifts have occurred in *R. argentea* since 1966. First, we observed the appearance of several apparently novel prey items in the day-time diet of contemporary *R. argentea*, including emerging insects and *Chaoborus* larvae and pupae. The appearance of insect and macro-invertebrate prey in the day-time diet of *R. argentea* has been observed in several other studies since the late 1980s, including: in *R. argentea* from the Napoleon Gulf in 1992 (with insects accounting for approximately 20% of the day-time stomach contents; Wandera 1992); in Northern Lake Victoria in 1994-95 (with emerging insects and *Chaoborus* (larvae and pupae) each accounting for approximately 10-15% of the diet by weight, Mwebaza-Ndawula 1998); in the

Mwanza Gulf in 1987 (Wanink 1998), and in the Tanzanian waters of Lake Victoria in 1999-2002 (with *Chaoborus*, Chironomid larvae, and insects accounting for approximately 31%, 5%, and 3% of the diet, respectively; Budeba and Cowx 2007). The presence of benthic macro-invertebrates in the diet is also supported by stable isotope data from the Napoleon Gulf (Campbell et al. 2003; but see Ojwang et al. 2004). Taken together, these data suggest a lake-wide increase in the importance of insect and macro-inverterbate prey in the diet of *R. argentea* since the late 1980s. An interesting regional pattern emerges as well, with the detritivorous Nile shrimp *Caridina nilotica* appearing in the diet of *R. argentea* from Tanzanian waters (Wanink 1998; Budeba and Cowx 2007); but not in Ugandan waters (Mwebaza-Ndawula 1998; Wandera 1992; current study).

Second, we observed a dramatic reversal in the zooplankton composition of the diet of *R. argentea* over time, with Copepoda dominating over Cladocera in 1966 (87% vs. 12%); but Cladocera strongly dominating over Copepoda in 2011 (34% vs. less than 1%). This pattern contrasts with observations from the Tanzanian waters in 1999-2002, where Copepoda were more important than Cladocera in the diet (36% vs. 17%; Budeba and Cowx 2007). Similarily, Mwebala-Ndawula (1998) found that Copepoda strongly dominated the diet of *R. argentea* in Northern Lake Victoria in 1994-95 (> 70%), whereas Cladocera comprised a negligible portion of the diet (< 5%). The almost complete absence of Copepoda in the stomachs we examined may partially reflect the limited nature of our sampling, as all individuals were caught at the same site, and on the same day. Nevertheless, our sample size was robust (30 individuals), and the difference that we observed was dramatic: we caught multiple individuals that had between 200 and 400 Cladocera in their stomachs, and not a single copepod. Assuming that the observed increase in the importance of Cladocera in the diet of *R. argentea* is not an artifact of our sampling, this may indicate an important ecological shift. Cladocera are generally favored by planktivorous fishes, both because they are larger (and thus more energetically rich) and more conspicuous to visual predators (Brooks and Dodson 1965; Lazzaro 1987). However, the relative abundance of Cladocera appears to have declined substantially over time in Lake Victoria, from

39% of the zooplankton community in 1931 to less than 1% in 1990 (Mwebaza-Ndawula 1994). This suggests that *R. argentea* today are even more successful in capturing and consuming this increasingly rare resource than they were historically. Indeed, we found that the ratio of Cladocera:Copepoda was 10.4 times higher in the contemporary diet of *R. argentea* from Lake Victoria than in the water column. This suggests both a very strong preference for Cladocera, and, perhaps, an absence of competition from other zooplanktivorous fish species that would otherwise be competing for this favoured resource.

That being said, there is evidence that some zooplanktivorous cichlids are now recovering in the Tanzanian waters of Lake Victoria (Witte et al. 2000; 2007). It is still unknown to what extent this recovery may be occurring in other parts of Lake Victoria, and in other invaded lakes. It is also unclear to what extent this most recent shift in community composition might result in increased levels of competition for *R. argentea*. A stable isotope study conducted in the Kenyan waters of Lake Victoria found a high degree of isotopic overlap between *R. argentea* and two resilient pelagic cichlids, suggesting that they have very similar diets (Ojwang et al. 2004). In contrast, Campbell et al. (2003) found little overlap in $\delta^{13}C$ signatures of *R. argentea* and the cichlid *Y. laparograma* from the Napoleon Gulf, and proposed that the two species coexist by occupying different diet/habitat niches. Addressing these uncertainties will be an important avenue for research in this very dynamic ecosystem. We would predict that a continued resurgence of zooplanktivorous haplochromines will lead to a decrease in the consumption of potentially preferred cladoceran prey in *R. argentea*.

We observed a significant increase in the dietary niche breadth of *R. argentea* in Napoleon Gulf between 1966 and 2011, consistent with findings from the Mwanza Gulf (Wanink 1998), and supportive of the hypothesis of “invader-mediated” competitive release. Dietary shifts and/or expansion have been observed in several other native fishes in Lake Victoria post-invasion, including in the characid *Brycinus sadleri* (Wanink and Joordens 2007), several species of benthivorous cichlids (Kishe-Machumu et al. 2008), the zooplanktivorous cichlid *Haplochromis pyrrhocephalus* (Katunzi et al. 2003), two catfishes (Olowo and

Chapman 1999); as well as in the introduced Nile tilapia, *Oreochromis niloticus* (Njiru et al. 2004; Bwanika et al. 2006). Niche expansion therefore appears to be a relatively common feature of the post-Nile perch icthyofauna of Lake Victoria; suggesting an important role for competitive release in the restructuring of this invaded community, and/or other environmental changes that alter the costs and benefits of alternative prey. In *R. argentea*, this increase in dietary niche breadth was accompanied by a significant increase in the prevalence of individual specialization; indicating that the generalism that we observed at the population level was the result of individuals specializing on different parts of a broader resource spectrum; rather than all individuals becoming more generalist. To our knowledge, this is the first study to examine the individual-level mechanisms underlying population niche expansion in Lake Victoria.

We detected changes in both the mean and variance of trophic morphology over time, with contemporary *R. argentea* having significantly shorter and more tightly-packed rakers; and also greater inter-individual variation in raker width, relative to the 1966 population. The latter observation is consistent with predictions of the Niche Variation Hypothesis that populations with broader niches will be more morphologically variable (Van Valen 1965). The direction of change in mean raker morphology is somewhat surprising; however, given that contemporary *R. argentea* were more omnivorous and consumed larger prey; yet had smaller inter-raker spaces than the historical, highly zooplanktivorous population.

One potential explanation for this apparent ecomorphological mismatch is that some other factor is constraining gill raker morphology. Lake Victoria has become progressively more eutrophic over the past century, with significant increases in the frequency and severity of hypolimnetic hypoxia, (Hecky et al. 1994; 2010) and fishes that feed on bottom-dwelling insects may encounter hypoxia more frequently than zooplanktivores. Many other fishes in the basin are known to respond to increasing hypoxia via plastic increases in gill surface area (Chapman et al. 2000; 2007, 2008; Crispo and Chapman 2010); and this may cause crowding for other nearby structures, such as the gill rakers. Studies of three other fish species that occur in the lake basin have demonstrated indirect effects of hypoxia on the size and shape of the head, supporting tradeoffs between gill proliferation and adjacent structures (Langerhans et al. 2007; Binning et al. 2010; Crispo and Chapman 2011). We hypothesize therefore that the observed decline in inter-raker spacing in *R. argentea* over time may reflect crowding due to simultaneous increases in gill area in response to increasing hypoxia in the lake. To test this idea, we returned to the same specimens for which gill raker traits were measured, and measured several gill metrics on first gill arch, including total hemibranch area, gill perimeter, and average gill filament length (Sharpe, Mitrofanov, and Chapman, *unpl. data*). We found evidence for significant increases in length-adjusted hemibranch area ($F_{1,50} = 423.1$, $p < 0.001$), perimeter ($F_{1,50} = 512.5$, $p < 0.001$), and average filament length ($F_{1,50} = 189.0$, $p < 0.001$) between 1966 and 2010. These preliminary findings support those of Wanink and Witte (2000a), who found an increase in the number of gill filaments in *R. argentea* from the Mwanza Gulf between 1983 and 1988, which they also linked to hypoxia. Temporal changes in the trophic morphology in *R. argentea* in Lake Victoria may therefore reflect a trade-off between accommodating larger prey, but also larger gills – a hypothesis that we will be exploring further in future work.

Overall, the results of our historical analysis are consistent with the hypothesis that the Nile perch introduction released *R. argentea* from competition, allowing for exploitation of novel prey, an increase in dietary niche breadth, increased individual specialization, increased exploitation of preferred prey (Cladocera), and an increase in morphological variance. Nevertheless, as our study is correlative, other hypotheses cannot be ruled out. For example, Olowo (1998) proposed that a shift to a broader diet by the characid *Brycinus sadleri* in the presence of Nile perch was the result of flexibility in diel feeding patterns that minimized overlap with Nile perch and therefore minimized predation risk. Wanink and Joordens (2007) suggested that increased omnivory over time in other resilient Lake Victoria fishes may reflect that the fact that eutrophication has led to declines in water transparency (Seehausen et al. 1997; Hecky et al. 2010), resulting in decreased encounter rates with preferred prey and therefore broader diets. Alternatively, strong temporal changes in the abundance of different prey types may be influencing the patterns of diet variation over time. For example, it is widely believed that the abundance of snails and lake flies (*Chaoborus*) has increased in Lake Victoria over the past few decades. However, this is based on anecdotal observations (Kaufman 1992); and unfortunately, there are no long-term, quantitative data on the abundance of zooplankton or macro-invertebrates in Lake Victoria with which to critically evaluate the relationship between prey availability and diet over time.

4.5.2 Trophic ecology of R. argentea across invaded vs. univaded lakes:

We found that there was some seasonal variation in the diet of *R. argentea*, but that it was not dramatic. This is consistent with previous work (Budeba and Cowx 2007; Mwebaza-Ndawula 1998), and suggests that the point-in-time sampling that we used to compare diets across lakes, and to estimate niche breath and the extent of individual specialization, should be reasonably representative.

There was considerable variation in the diet of *R. argentea* across lakes, which appeared to be driven primarily by variation in the availability of prey (zooplankton) across lakes. This is consistent with earlier work by Wanink (1998), who found that the abundance of macro-invertebrate prey in the stomachs of *R. argentea* from the Mwanza Gulf was significantly correlated with their abundance in the water column. Our data confirm thus Wanink's characterization of *R. argentea* as opportunistic feeders (Wanink 1998), although we did find evidence for a preference for Cladocera (relative to Copepoda); as the former were significantly more concentrated in stomachs than in the water column. Interestingly, this preference was most pronounced in the two lakes that have been most strongly impacted by the Nile perch introduction: lakes Victoria and Kyoga. Overall; however, resource availability (and not the presence or absence of Nile perch) appeared to be the dominant driver of diet variation in *R. argentea* across lakes.

There was no evidence for dietary niche expansion in Nile-perch invaded lakes, using niche breadth indices derived either from gut contents analysis, or stable isotopes. Nevertheless, there was considerable variation in dietary niche breadth across lakes, with four lakes (Omuno, Nawampasa, Nabugabo and Victoria) having significantly broader dietary niches than the others. Broader niches in these lakes might in theory reflect lower levels of interspecific competition (Syväranta and Jones 2008), although this seems an unlikely explanation for at least two of the lakes, given that Omuno was uninvaded by Nile perch, and Nawampasa has an intact and diverse fish fauna (Mbabazi 2004). Alternatively, broader niches in these four lakes could be due to higher levels of intraspecific competition (e.g., Svanbäck and Bolnick 2007). More detailed data on the biomass of *R. argentea*, and its potential competitors, are needed to explore these hypotheses further.

The prevalence of individual specialization ranged from very high in some lakes (e.g., Victoria, Nabugabo), to extremely low in others (e.g., Kayanja, Gigati). Our IS values for 9 populations of *R. argentea* covered quite a broad range (0.38 – 0.93); comparable to that spanned by several dozen studies of individual specialization in fishes (range covered by 52 studies on fishes: 0.20 – 0.90; Araújo et al. 2011). The mean IS in our study (mean ± SD: 0.68 ± 0.21, n = 8) was slightly higher than the literature average for fishes (approximately 0.5; Araújo et al. 2011, Fig. 2d), and for other taxa for which IS has been quantified to-date (0.47 ± 0.20, n = 142, Araújo et al. 2011). Our data support the emerging view that individual specialization is a relatively common and important feature of natural populations (Bolnick et al. 2003; Araújo et al. 2011).

We found a very strong correlation between population niche breadth and the prevalence of individual specialization across lakes, consistent with the pattern observed through time in Lake Victoria, and with predictions from the Niche Variation Hypothesis (Van Valen 1965). This correlation suggests that population-level generalism was repeatedly achieved in the same way across our study populations; with individuals specializing on different parts of a broader resource spectrum, but not broadening their individual niches. Similar correlations between population niche breath and inter-individual diet variation have been found in several other taxa, including threespine stickleback, *Gasterosteus aculeatus*, Eurasian perch, *Perca fluviatilis*, Whelk *Nucella spp*., Brazilian savannah frogs, and the lizard *Anolis sagrei* (Bolnick et al. 2007). Increased individual specialization as the population niche width increases implies the existence of functional constraints or trade-offs that prevent individuals from broadening their niches (Bolnick et al. 2003). Such trade-offs might be morphological (e.g., Svanbäck and Eklöv, 2003, 2004), behavourial/cognitive (e.g., Werner et al. 1981), or both (e.g., Ehlinger 1990; Robinson 2000). In our case, we found significant correlations between individual trophic morphology and some components of the diet (see below), suggesting that in *R. argentea*, morphology may be one of the factors constraining individual niche breadth.

The majority of populations that we examined had similar mean trophic morphology (i.e., overlapping scores along gill raker PC1), with the exception of three particularly divergent populations (Kayanja, Nakuwa, and Bisina). Across lakes, mean trophic morphology was not consistently related to the average population diet. For example, *R. argentea* from Lake Bisina had a more zooplanktivorous morphology on average (longer, thinner, more numerous and more tightly-packed gill rakers); yet gut contents analysis showed a diet composed exclusively of insects. In contrast, on the individual level, there were significant correlations between individual trophic morphology and individual gut contents. *R. argentea* that fed on zooplankton (and particularly on Cladocera) tended to have thinner, more numerous and more tightly-packed rakers (lower scores on PC1), consistent with patterns of intraspecific eco-morphological variation documented in other planktivorous fishes, such as stickleback, *Gasterosteus aculeatus* (Schluter and Mcphail 1992), whitefish, *Coregonus spp*. (Lindsey 1981; Amundsen et al. 2004), and Arctic charr, *Salvelius alpinu*s (Malmquist et al. 1992; Snorrason et al. 1994). However, zooplanktivorous *R. argentea* also tended to have shorter rakers (lower scores on PC2) – contrary to the pattern observed in many other fishes (references above).

Correlations between morphology and diet at the individual level support the idea that morphological constraints may impose limits on individual niche breadth in this species, potentially explaining the strong relationship between individual specialization and niche breadth observed across lakes. However, we also found that populations with broader niches (and greater individual specialization) were not more morphologically variable in gill raker morphology, suggesting that trophic morphology is only one of several factors contributing to inter-individual diet variation in *R. argentea*. Other morphological traits (e.g., body size, body shape, fin form, visual acuity), foraging behavior, and/or experience may also play an important role in determining the diet of individual *R. argentea*.

Our stable isotopic values for *R. argentea* from the Napoleon Gulf were similar to those reported from previous studies conducted in Northern Lake Victoria for δ^{15}N; although the δ^{13}C signature of our samples was heavier (-15.75) than reported previously (-16.9 to -20.04; Branstrator et al. 2003; Campbell et al. 2003; Mbabazi 2004). In general, heavier δ^{13}C values indicate a greater importance of littoral/benthic relative to pelagic carbon sources (Hecky and Hesslein 1995; Bootsma et al. 1996; Campbell et al. 2003). In our case, the δ^{13}C values for Napoleon Gulf *R. argentea* in our study closely matched the δ^{13}C values for the prosobranch snails that we sampled from the same area, which graze on littoral epiphyton (Campbell et al. 2003). A similar pattern was observed for Lake Kyoga, where our δ^{15}N values for *R. argentea* matched those reported previously, but δ^{13}C values were heavier (Hecky and Hesslein 1995; Mbabazi 2004). To a certain extent, the enrichment in δ^{13}C in *R. argentea* in our study relative to previous work may represent natural temporal fluctuations and sampling effects. However, it may also suggest that *R. argentea* in Lake Victoria and Kyoga currently derive more of their energy from littoral/benthic carbon sources than they did in the 1990s and early 2000s, consistent with observed changes in gut contents for Lake Victoria.

There was considerable variation in both baseline and *R. argentea* isotopic signatures across lakes; highlighting the importance of quantifying baseline isotope variation in comparative studies (Post 2002). There was a weak (non-significant) trend towards higher trophic position (i.e., baseline-adjusted $\delta^{15}N$) in invaded lakes; however, more replication is needed to confirm this pattern. $\delta^{13}C$ also varied substantially across lakes. *R. argentea* from Kayanja and Omuno had the heaviest $\delta^{13}C$ (-12.50 and -10.00, respectively), indicating strong reliance on benthic/littoral-derived carbon. This finding was consistent with the gut contents analysis, which showed diets dominated by insects and benthic macro-invertebrates in these two lakes. At the other extreme, *R. argentea* from Gigati and Nawampasa had much lighter $\delta^{13}C$ isotopic values (-25.22 and -21.45 respectively), suggesting a primarily pelagic carbon source. This was also consistent with the results of the gut contents analysis, which showed diets dominated by zooplankton and plant matter, most likely waterlilies ($\delta^{13}C$ for *Nymphea spp*. (waterlilies) is -20.90, Hecky and Hesslein 1995).

4.5.3 Conclusions:

Overall, we found mixed evidence for indirect effects of the Nile perch introduction on the trophic ecology and morphology of *R. argentea*. In the most heavily-impacted lake (Victoria), we found good evidence for dietary niche expansion, an increase in inter-individual diet variation, and an increase in morphological variance following the Nile perch introduction. Across lakes; however, strong bottom-up effects (i.e., variation in prey availability) obscured or confounded any potential top-down effects of the Nile perch introduction on the trophic ecology of *R. argentea*. This study thus highlights the challenges of studying the impacts of complex phenomena like biological invasions, and the value of relying on multiple modes of interference (e.g., historical and spatial comparisons) whenever possible.

The indirect effects of introduced species (e.g., competitive release, trophic subdsidies, habitat modification) can have important implications for conservation and management, yet are still poorly understood (Simon and Townsend 2003; Rodriguez 2006). This study makes a particularly interesting contribution to this research area, because *R. argentea* appear to have been influenced both directly and indirectly by the Nile perch introduction. As discussed above, indirect effects potentially include competitive release due to the decimation of other fishes, particularly the zooplanktivorous haplochromines, after the Nile perch introduction. Direct effects include predation from the Nile perch (Hughes 1986; Ogutu-Ohwayo 1990, 1993; Mbabazi 2004), which appears to have contributed to contemporary changes in life history traits (Wanink 1998; Sharpe et al. 2012) and morphology in *R. argentea* (Chapter 3). The fact that *R. argentea* now accounts for almost 60% of the biomass of Lake Victoria suggests either that: (i) the positive demographic impacts of indirect interactions (competitive release) have outweighed the negative impacts of direct interactions (predation); and/or (ii) that rapid contemporary phenotypic change in response to both indirect (positive) and direct (negative) interactions have enabled *R. argentea* to thrive in the highly anthropogenically-altered ecosystem of modern-day Lake Victoria. Understanding these complex direct and indirect interactions, and their evolutionary consequences, is vital to the management of the *R. argentea* fishery, and of the Lake Victoria ecosystem as a whole. As discussed above, the recent recovery of a subset of the haplochromine cichlid fauna in parts of the Lake Victoria basin (Chapman et al. 2003; Witte et al. 2000, 2007) has been dominated by several zooplanktivores whose diets seem to overlap considerably with that of *R. argentea* (Ojwang et al. 2004; but see Campbell et al. 2003). A detailed understanding of the trophic ecology and morphology of *R. argentea* will be critical for managing this important stock in light of the ongoing ecological changes in this very dynamic ecosystem.

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Table 4.1. Summary of the 10 Ugandan lakes included in the present study.
Surface area was estimated from satellite images downloaded from Google Earth. Mean depth was estimated from three replicate depth measurements taken in the pelagic zone of each lake during our 2010 field survey. For Lake Victoria, we specify the surface area and depth for the Napoleon Gulf, where all of our sampling was carried out, and for Lake Victoria as a whole (in parentheses). For Lake Kyoga, we specify the surface area for the main lake where we carried out our sampling, as well as the entire surface area including additional branches (in parentheses). With the exception of lakes Victoria, Kyoga and Nabugabo, detailed published ecological data are not available for many of these lakes, so the current status of native fish communities was estimated by compiling information from unpublished reports, theses, and/or by consultation with NaFIRRI scientists. References for these data are as follows: (1) Numulemo, G. MSc. Thesis; (2) Mbabazi 2004; (3) NaFIRRI 2007; (4) Sharpe and Chapman, *unpl. data*; (5) Ogutu-Ohwayo 1993; (6) Chapman et al. 2003; (7) Schwartz et al. 2006; (8) Kaufman 1992, (9) Witte et al. 1992; (10) Seehausen et al. 1997a; (11) Seehausen et al. 1997b; (12) Witte et al. 2000

Lake	Surface area (km^2)	Mean depth (m)	Nile perch established?	Status of native fish community
Kayanja	1.25	2.61	No	**Intact** (15 species total; community dominated by haplochromine cichlids[1,2])
Omuno	5.56	1.37	No	**Intact?**
Gigati	7.52	2.03	No	**Intact** (Haplochromine cichlids abundant[3,4])
Nawampasa	8.53	1.62	Transient (1998-Present?)	**Intact** (36 species total; community dominated by haplochromine cichlids[2,3,4])
Bisina	349.31	3.86	Transient (1970s – 1990s?)	**Intact** (38 species total; community dominated by haplochromine cichlids[2])
Meito	14.64	2.79	Yes	**Depleted?** (Low abundance of haplochromine cichlids[4])
Nabugabo	33.99	4.53	Yes (1960,63)	**Depleted, some recovery in 1990s:** (Of 30 native fish species caught in 1962, approximately half

				disappeared or were very rare by 1992[5]; evidence of some recovery of native fish fauna from 1995-2000[6])
Nakuwa	95.79	2.22	Yes (1970s)	**Depleted** (13 species total; community dominated by Nile perch[2]; haplochromine cichlids rare[4,7])
Kyoga	1971.35 (2047)	2.46	Yes (1955)	**Depleted, limited recovery in 2000s?** (21 species total; community dominated by Nile perch[2]; some increase in abundance of haplochromine cichlids in 2008-2010[4])
Victoria (Napoleon Gulf)	63.50 (68,800)	10.40 (40)	Yes (1954, 1960s)	**Depleted, limited recovery in 2000s** (Approximately 50% of non-littoral haplochromine cichlids disappeared from the Lake Victoria by the late 1980s[8,9,10,11]; evidence of limited resurgence of some native taxa in the Mwanza Gulf in the 2000s[12])

Table 4.2. Summary of samples used for the gut contents analysis of *R. argentea*. Sample sizes (n) indicate the number of non-empty guts examined. Also shown are the range of body sizes (standard length, SL) of fish included in the analysis, the proportion that were sexually mature, and the proportion that contained macro-parasites in the abdominal cavity.

Population	Collection date	n	SL range (mm)	Proportion mature	Proportion parasitized
Seasonal diet variation (Nabugabo):					
Nabugabo (Dry)	Jan 2009	20	47-55	1.00	0.00
Nabugabo (Dry)	Feb 2009	20	47-60	1.00	0.00
Nabugabo (Wet)	May 2009	20	48-58	1.00	0.00
Nabugabo (Wet)	Oct 2008	19	48-56	1.00	0.00
Nabugabo (Wet)	Nov 2008	14	49-54	1.00	0.00
Nabugabo (Wet)	Dec 2008	19	45-55	1.00	0.00
Across-lake diet variation:					
Kayanja	June 2010	26	31-45	0.54	0.38
Omuno	June 2010	29	46-56	1.00	0.00
Gigati	June 2010	30	43-54	0.97	0.00
Nawampasa	June 2010	29	36-44	0.83	0.00
Bisina	June 2010	30	34-45	0.83	0.00
Nabugabo	May 2009	20	48-58	1.00	0.00
Kyoga	June 2010	28	36-52	0.82	0.00
Victoria	Aug. 2011	28	28-50	0.29	0.61
Historical diet variation:					
Victoria: pre-Nile perch	July 1966	30	44-64	0.93	0.27
Victoria: post-Nile perch	Aug. 2011	28	28-50	0.29	0.61

Table 4.3. Size-standardized gill raker traits (mean ± SE) for *R. argentea* from the Napoleon Gulf of Lake Victoria, from 1966 to 2010.

Raker length, raker width and inter-raker space were size-standardized to a common body length of 44.49mm; the number of rakers was uncorrelated to body size. Letters indicate homogeneous subsets based on post-hoc Tukey tests.

Year	Number of rakers			Raker length (mm)			Raker width (µm)			Inter-raker space (µm)		
1966	15.71^{a}	±	0.22	1.005^{a}	±	0.018	130.607^{a}	±	1.766	245.259^{a}	±	4.223
2000	16.20^{a}	±	0.42	1.010^{a}	±	0.034	140.707^{a}	±	4.949	239.577^{a}	±	5.516
2008	15.79^{a}	±	0.21	0.896^{a}	±	0.016	132.748^{a}	±	2.719	241.039^{a}	±	3.185
2009	16.36^{a}	±	0.25	0.902_{b}	±	0.015	128.073^{a}	±	3.255	228.476^{b}	±	3.417
2010	15.63^{a}	±	0.26	0.909_{b}	±	0.015	135.748^{a}	±	2.606	229.236^{a}	±	4.540

Table 4.4. The prevalence of individual specialization in the diet of *R. argentea* across eight Ugandan lakes.

The overall level of individual specialization (IS) is the mean of individual PS_i values (± 1 SE) in each population. For IS, values close to 1 indicate high similarity between each individual and the population as a whole, while low values indicate the converse (i.e., higher individual specialization).

Lake	IS	Mean pairwise overlap
NP absent:		
Kayanja	0.93 ± 0.02	0.93
Omuno	0.53 ± 0.03	0.42
Gigati	0.87 ± 0.01	0.83
NP transient:		
Nawampasa	0.57 ± 0.03	0.45
Bisina	0.81 ± 0.03	0.79
NP established:		
Nabugabo	0.49 ± 0.03	0.39
Kyoga	0.86 ± 0.01	0.82
Victoria	0.38 ± 0.02	0.30

Table 4.5. Summary of δ^{15}N and δ^{13}C stable isotope composition for *R. argentea*, and two types of primary consumers used to establish the isotopic baselines in each lake.
Snails included species from the genera *Bulinus*, *Melanoides*, *Biomphalaria*, and from the subclass *Prosobranchia*. Data shown are means ±1 SE, with sample sizes in parentheses.

	R. argentea		Snails		Clams	
Lake	**δ^{15}N (‰)**	**δ^{13}C (‰)**	**δ^{15}N (‰)**	**δ^{13}C (‰)**	**δ^{15}N (‰)**	**δ^{13}C (‰)**
NP absent:						
Kayanja	6.94 ± 0.28 (10)	-12.50 ± 0.28 (10)				
Omuno	6.28 ± 0.06 (10)	-10.09 ± 0.12 (10)	1.11 ± 1.26 (4)	-18.74 ± 1.36 (4)		
Gigati	4.82 ± 0.10 (10)	-25.22 ± 0.10 (10)	4.03 ± 1.21 (2)	-22.98 ± 0.33 (2)		
NP transient:						
Nawampasa	6.53 ± 0.21 (10)	-21.45 ± 0.31 (10)	0.1 (1)	-23.58 (1)		
Bisina	6.26 ± 0.07 (10)	-16.60 ± 0.19 (10)	2.70 ± 0.84 (5)	-16.63 ± 2.22 (5)		
NP established:						
Meito	7.17 ± 0.10 (10)	-19.87 ± 0.16 (10)	1.37 ± 0.46 (4)	-17.30 ± 1.20 (4)		
Nabugabo	7.36 ± 0.07 (10)	-18.56 ± 0.11 (10)	-0.61 ± 0.76 (10)	-19.97 ± 0.43 (10)		
Nakuwa	5.60 ± 0.10 (4)	-16.40 ± 0.21 (4)	1.43 ± 0.20 (3)	-21.12 ± 0.36 (3)	1.70 ± 0.32 (3)	-20.33 ± 0.37 (3)
Kyoga	7.16 ± 0.10 (10)	-16.04 ± 0.31 (10)	0.92 ± 0.75 (10)	-15.45 ± 0.69 (10)	3.53 (1)	-17.19 (1)
Victoria	8.18 ± 0.46 (10)	-15.75 ± 0.40 (10)	3.39 ± 0.11 (10)	-15.23 ± 0.85 (10)	4.30 (1)	-18.33 (1)

Table 4.6. Size-standardized gill raker traits (mean ± SE) for *R. argentea* from nine Ugandan lakes.

Raker length, raker width and inter-raker space were size-standardized to a common body length of 44.49 mm; the number of rakers was not significantly correlated with body size.

Lake	Number of rakers	Raker length (mm)	Raker width (μm)	Inter-raker space (μm)
Kayanja	15.00 ± 0.12	0.816 ± 0.011	140.16 ± 1.56	257.16 ± 2.88
Omuno	15.60 ± 0.20	0.858 ± 0.015	131.40 ± 2.61	234.37 ± 5.43
Gigati	15.46 ± 0.21	0.822 ± 0.012	134.63 ± 1.59	240.71 ± 2.94
Nawampasa	15.81 ± 0.14	0.927 ± 0.012	136.80 ± 1.72	247.84 ± 2.38
Bisina	16.04 ± 0.22	0.972 ± 0.015	123.26 ± 1.93	250.81 ± 3.86
Nabugabo	15.63 ± 0.14	0.841 ± 0.011	132.76 ± 1.56	247.17 ± 2.99
Nakuwa	16.05 ± 0.23	0.909 ± 0.017	113.58 ± 3.27	236.88 ± 4.36
Kyoga	15.53 ± 0.15	0.834 ± 0.013	125.90 ± 2.42	246.63 ± 3.26
Victoria	15.89 ± 0.14	0.901 ± 0.009	132.37 ± 1.68	234.31 ± 2.20

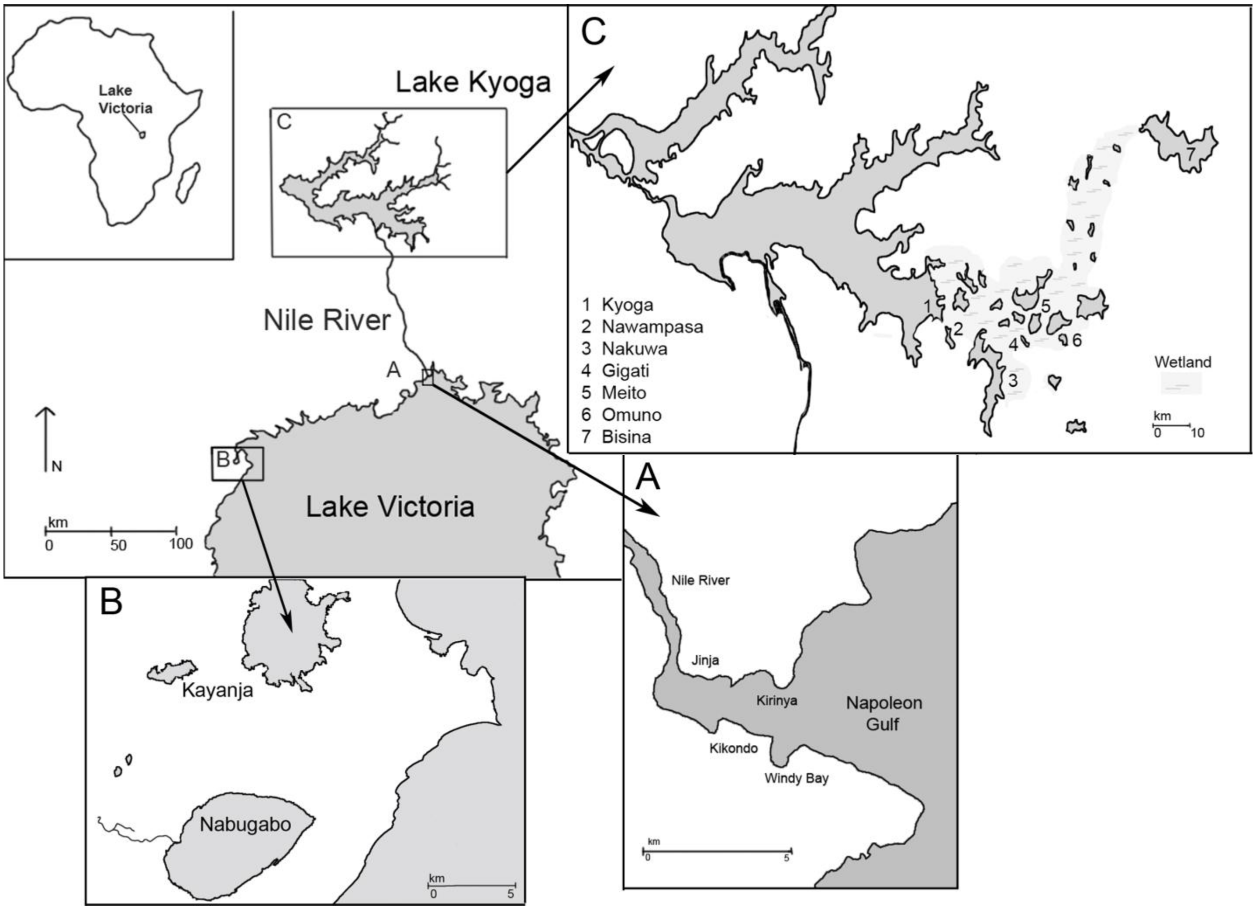

Fig. 4.1. Lakes sampled for *Rastrinebola argentea* in 2010.
Reproduced with permission from Sharpe et al. 2012. For additional details on sampling sites, please see Table 4.1

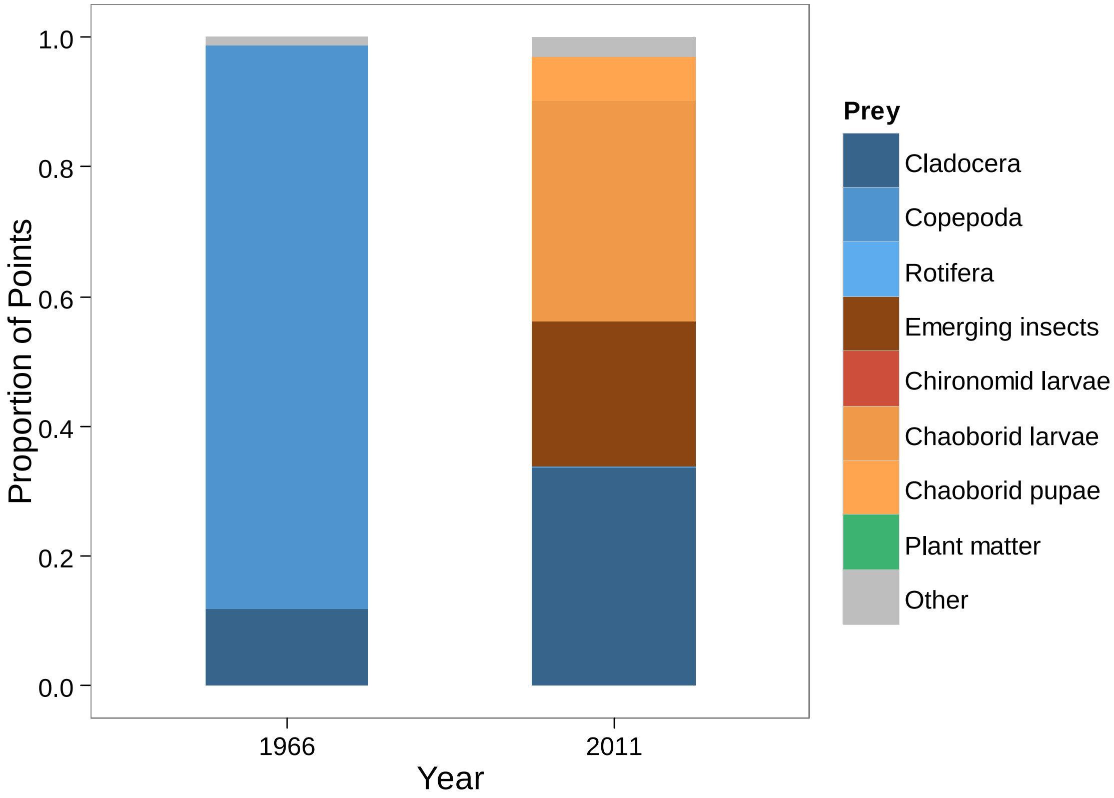

Fig. 4.2. Relative importance of the different prey types in the diet of *R. argentea* from Lake Victoria before (1966) versus after (2011) the establishment of the introduced Nile perch.

Sample sizes ranged from 28-30 individuals per year. See text for further details on the calculation of the proportion of points (p_j).

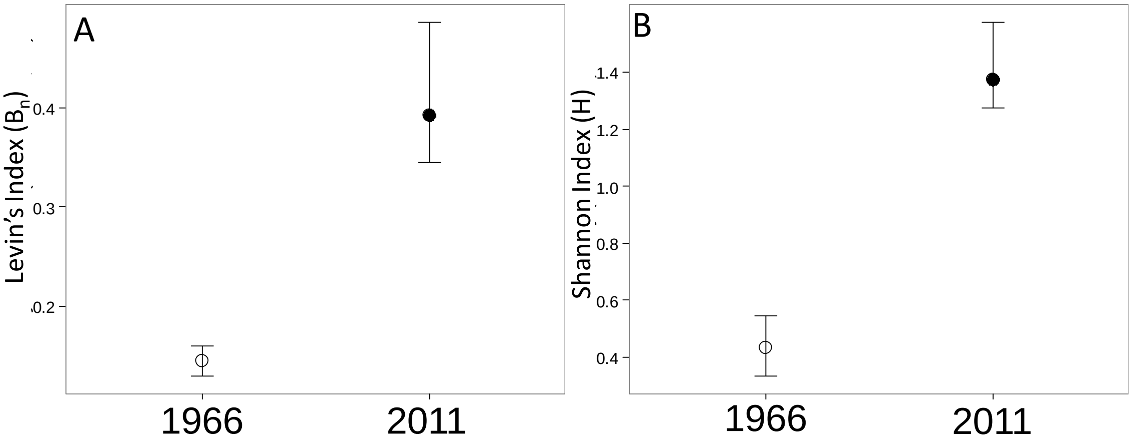

Fig. 4.3 Dietary niche width of *R. argentea* from Lake Victoria before (1966) versus after (2011) the establishment of the introduced Nile perch.

Niche breadth was estimated using Levin's niche breadth index, B_n (panel A), and the Shannon diversity index, H (panel B). Lower values of both indices indicate narrower niches, while higher values indicate broader niches. Error bars represent boot-strapped 95% confidence intervals, estimated using 1000 permutations in R.

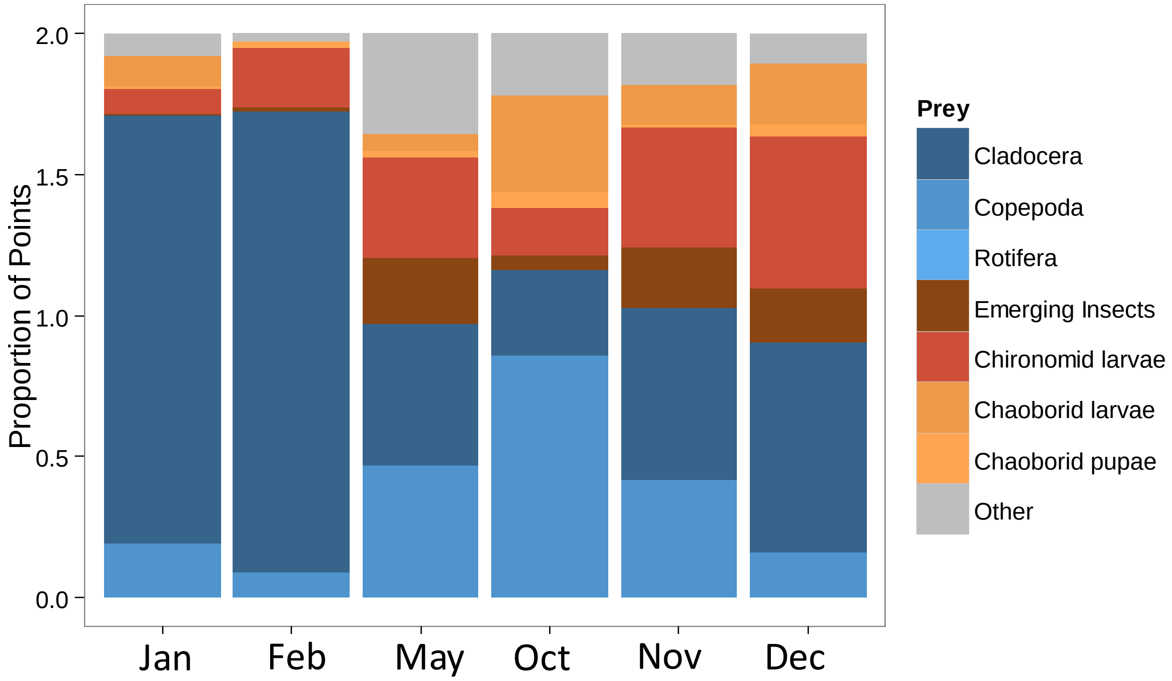

Fig. 4.4 Relative importance of the different prey types in the diet of *R. argentea* across six months in Lake Nabugabo, Uganda.

Sample sizes ranged from 15-20 individuals per month (sites pooled). See text for further details on the calculation of the proportion of points (p_j).

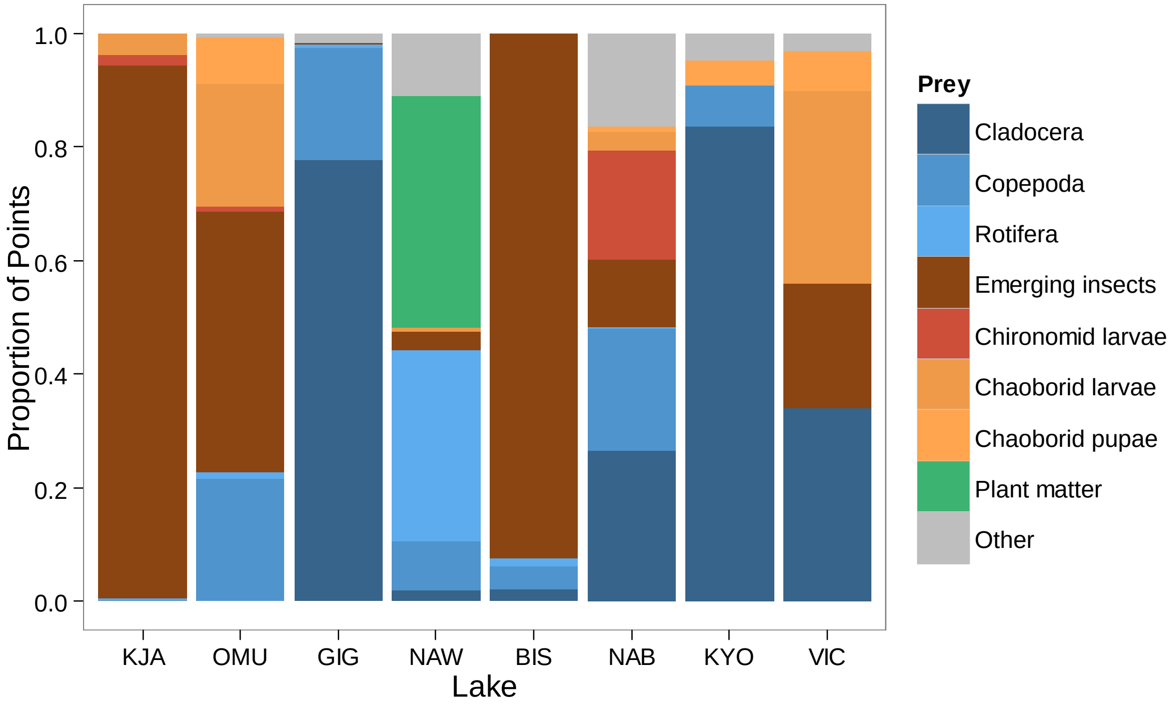

Fig. 4.5 Relative importance of the different prey types in the diet of *R. argentea* across eight lakes in Uganda.

Lakes are ordered based on Nile perch invasion history; going from lakes where Nile perch are absent (Kayanja, Omuno and Gigati), to transient (Nawampasa and Bisina), and fully established (Nabugabo, Kyoga and Victoria). Sample sizes ranged from 20-30 individuals per lake. See text for further details on the calculation of the proportion of points (p_j).

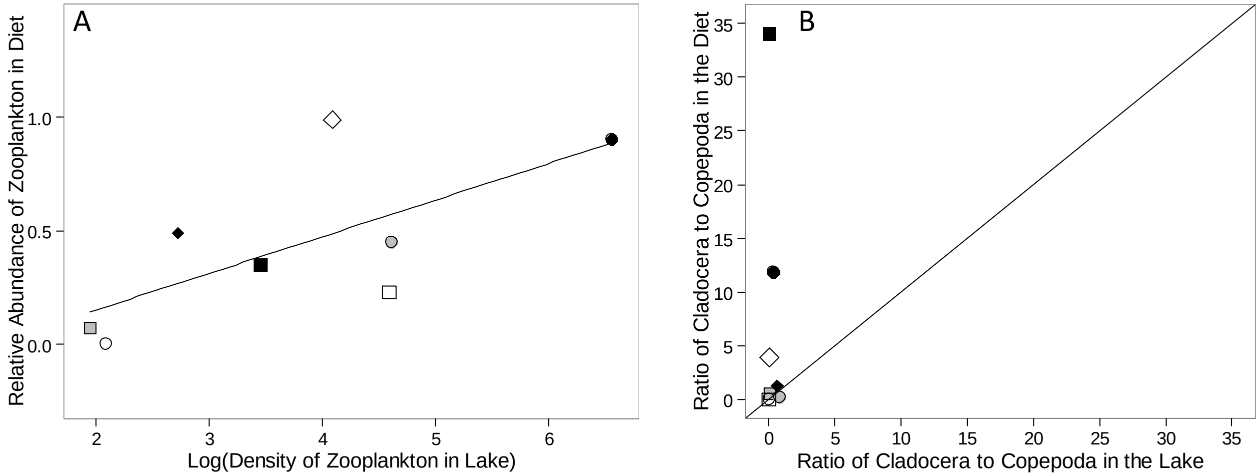

Fig. 4.6 Comparison of zooplankton abundances and ratios in the diet of *R. argentea* versus the water column. Panel A: Correlation between the relative importance of zooplankton in the diet of *R. argentea* and the density of zooplankton in each of eight Ugandan lakes. Zooplankton in the diet included Cladocera, Copepod and Rotifera; and in the water column included the latter taxa as well as copepod nauplii. The relative importance of zooplankton in the diet was calculated as the relative proportion of points attributed to zooplankton (p_j, see text for equation). The density of zooplankton in the lake is the mean numerical density of individuals in four replicate vertical plankton net hauls over the whole water column, standardized by mean lake depth. The importance of zooplankton in the diet was positively correlated to the density of zooplankton in the environment ($r = 0.70$, $p = 0.054$). Panel B: The ratio of Cladocera:Copepoda in the diet of *R. argentea* was consistently higher than would be expected based on unselective sampling of the zooplankton community of each lake (illustrated by the solid 1:1 line). The lakes shown are: Kayanja (white circle), Omuno (white square), Gigati (white diamond), Nawampasa (grey circle), Bisina (grey square), Nabugabo (black diamond), Kyoga (black circle), and Victoria (black square).

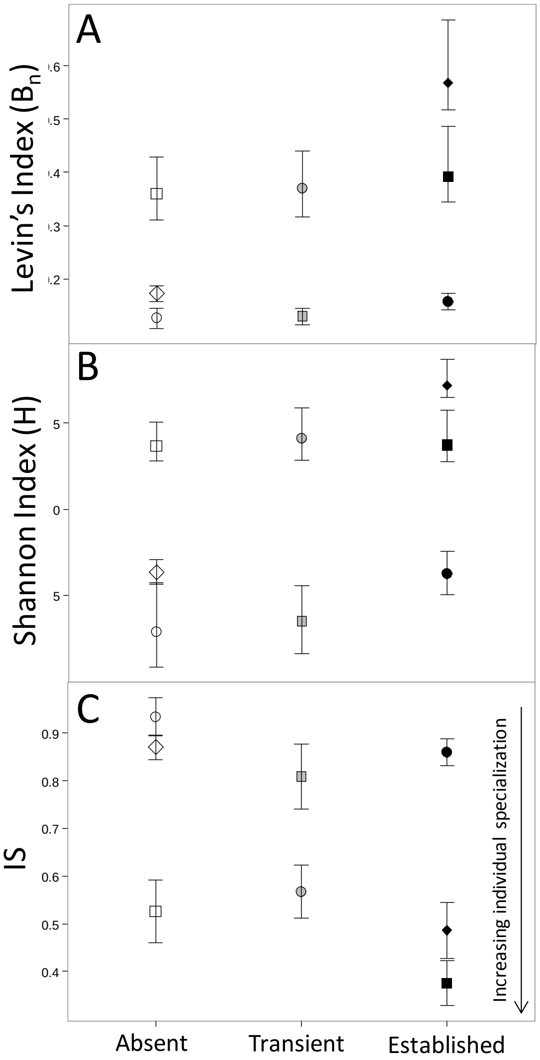

Fig. 4.7 Dietary niche width and individual specialization for *R. argentea* across eight Ugandan lakes.

Niche breadth was estimated using the normalized version of Levin's index, B_n (panel A), and the Shannon Diversity Index, H (panel B). Lower values of both indices indicate narrower niches, while higher values indicate broader niches. Error bars represent boot-strapped 95% confidence intervals, estimated using 1000 permutations in R. Neither index varied significantly across Nile perch invasion categories. Panel C shows the prevalence of individual specialization (Mean PSi ± 2 SE) in the diet of *R. argentea* across eight Ugandan lakes. PSi Values close to 1 indicate that populations are composed primarily of individual generalists; while lower values indicate increasing individual specialization. Overall, the prevalence of individual specialization did not vary across Nile perch invasion categories. For an explanation of symbols, please see caption for Fig. 4.6.

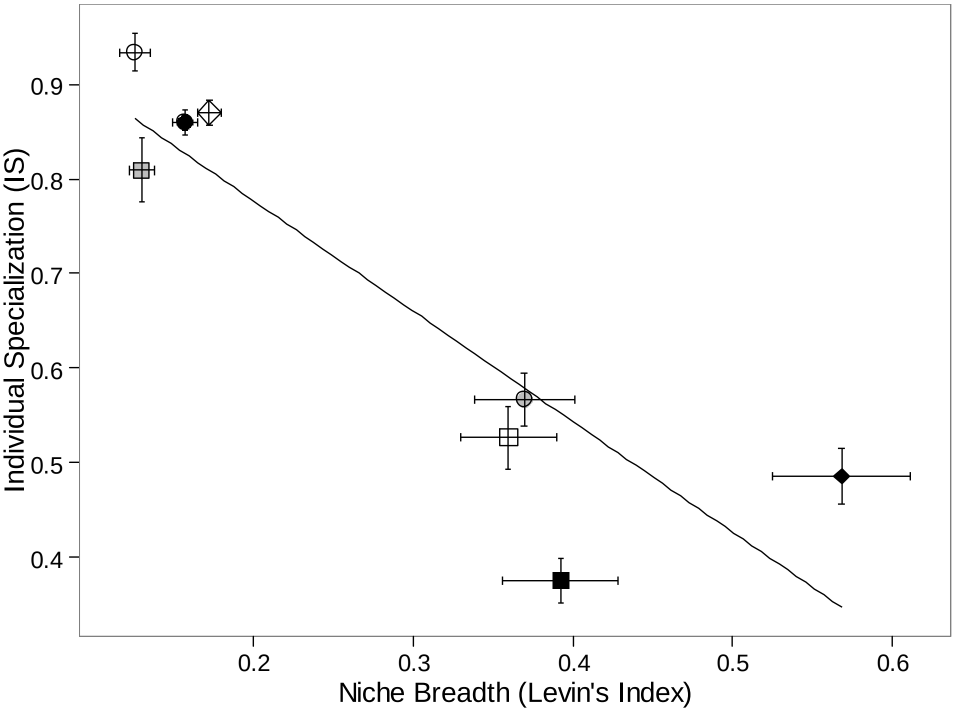

Fig. 4.8 Correlation between the level of individual specialization (IS), and Levin’s index of niche breadth (r = -0.89, p = 0.003).

Data are lake means ± 1 SE. For Levin’s index, higher values indicate broader niches; for IS, lower values indicate greater individual specialization. For an explanation of symbols, please see caption for Fig. 4.6. A similar pattern was observed for the Shannon index (not shown).

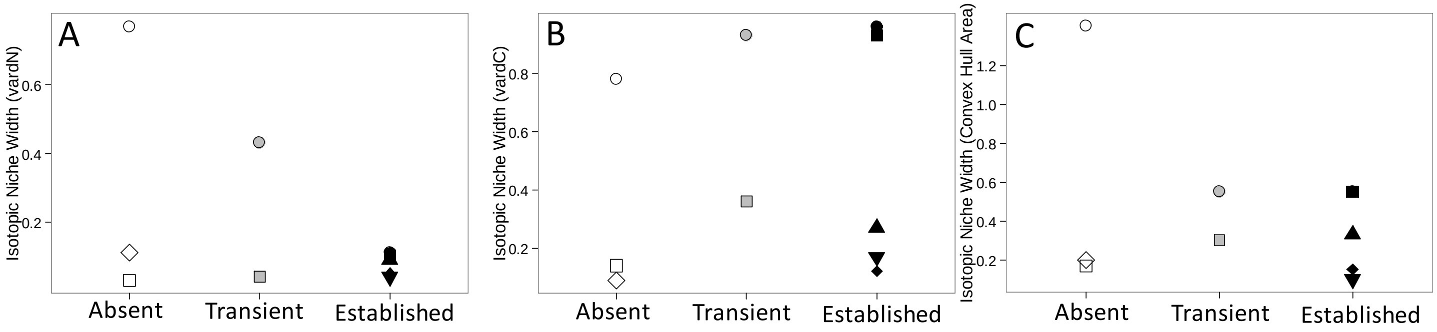

Fig. 4.9 Isotopic niche width of *R. argentea* across 10 Ugandan lakes.
Niche breadth was estimated using the variance in δ^{15}N values (panel A), the variance in δ^{13}C (panel B), and the convex hull area method (panel C). Lower values of all three indices indicate narrower isotopic niches, while higher values indicate broader niches. One outlier (from Lake Victoria) has been excluded from these calculations. Overall, none of the indices were significantly different across Nile perch invasion categories. The lakes shown are: Kayanja (white circle), Omuno (white square), Gigati (white diamond), Nawampasa (grey circle), Bisina (grey square), Meito (black upwards triangle), Nabugabo (black diamond), Nakuwa (black downwards triangle) Kyoga (black circle), and Victoria (black square).

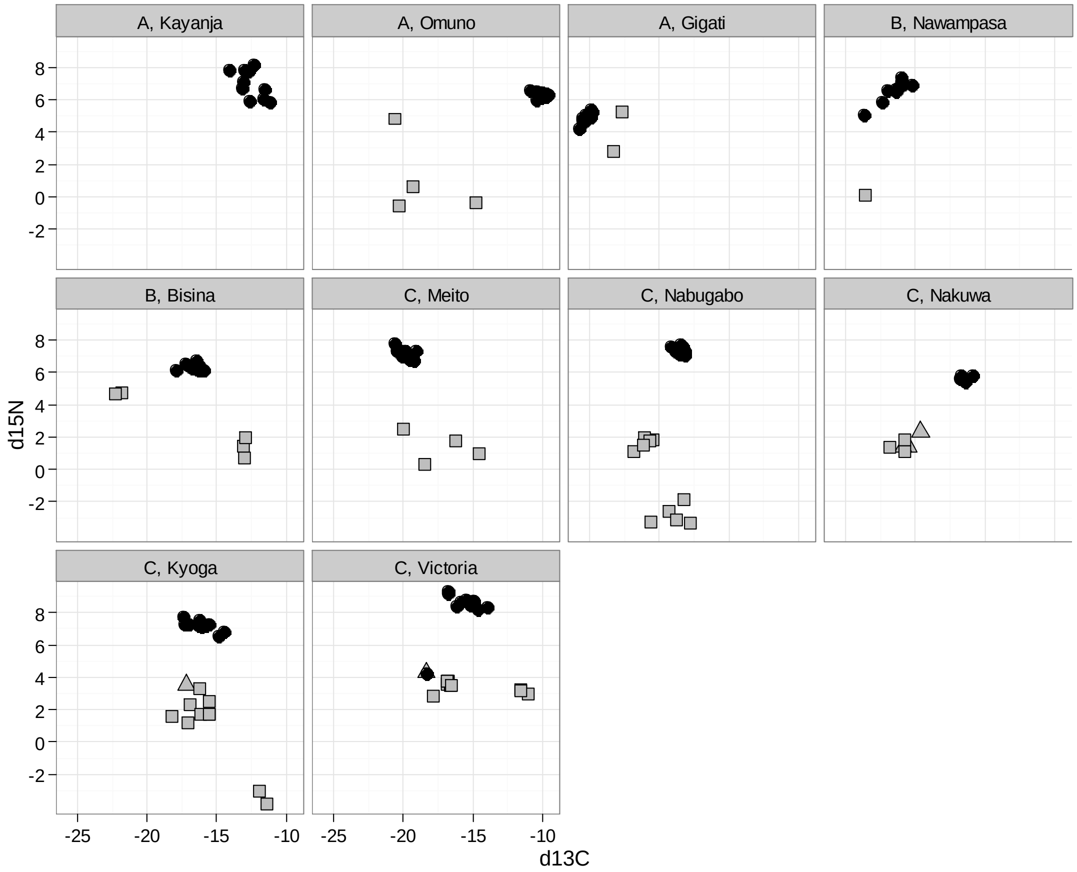

Fig. 4.10 Stable isotope composition of *R. argentea* (black circles), snails (grey squares), and clams (grey triangles) from 10 Ugandan lakes.
Lakes are ordered depending on Nile perch introduction history: from lakes where introduced Nile perch are absent (A), to transient (B), to fully established (C).

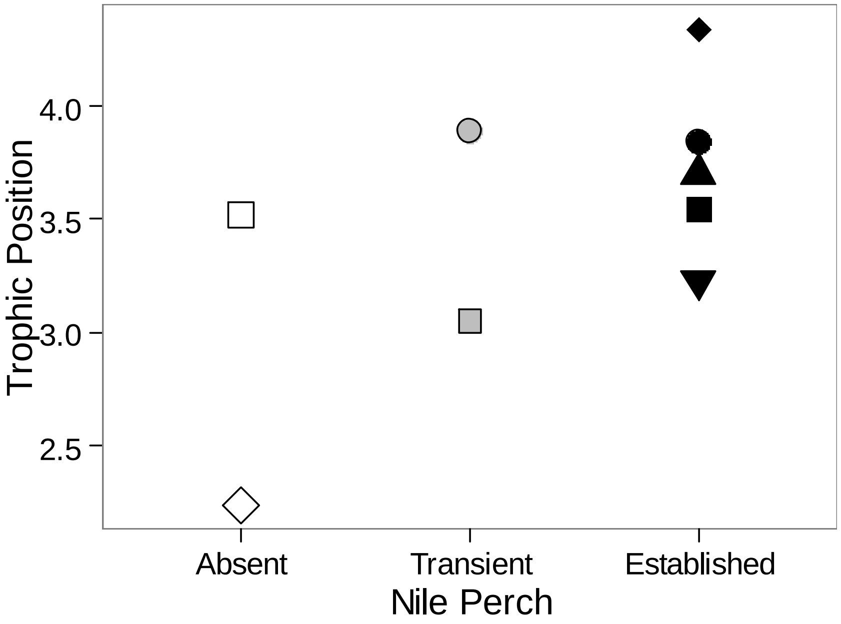

Fig. 4.11 Trophic position of *R. argentea* across nine Ugandan lakes, calculated relative to the isotopic baseline in each lake (Post 2002).

One outlier (from Lake Victoria) was excluded during the calculation of trophic position for this plot. For an explanation of symbols see legend for Fig. 4.9.

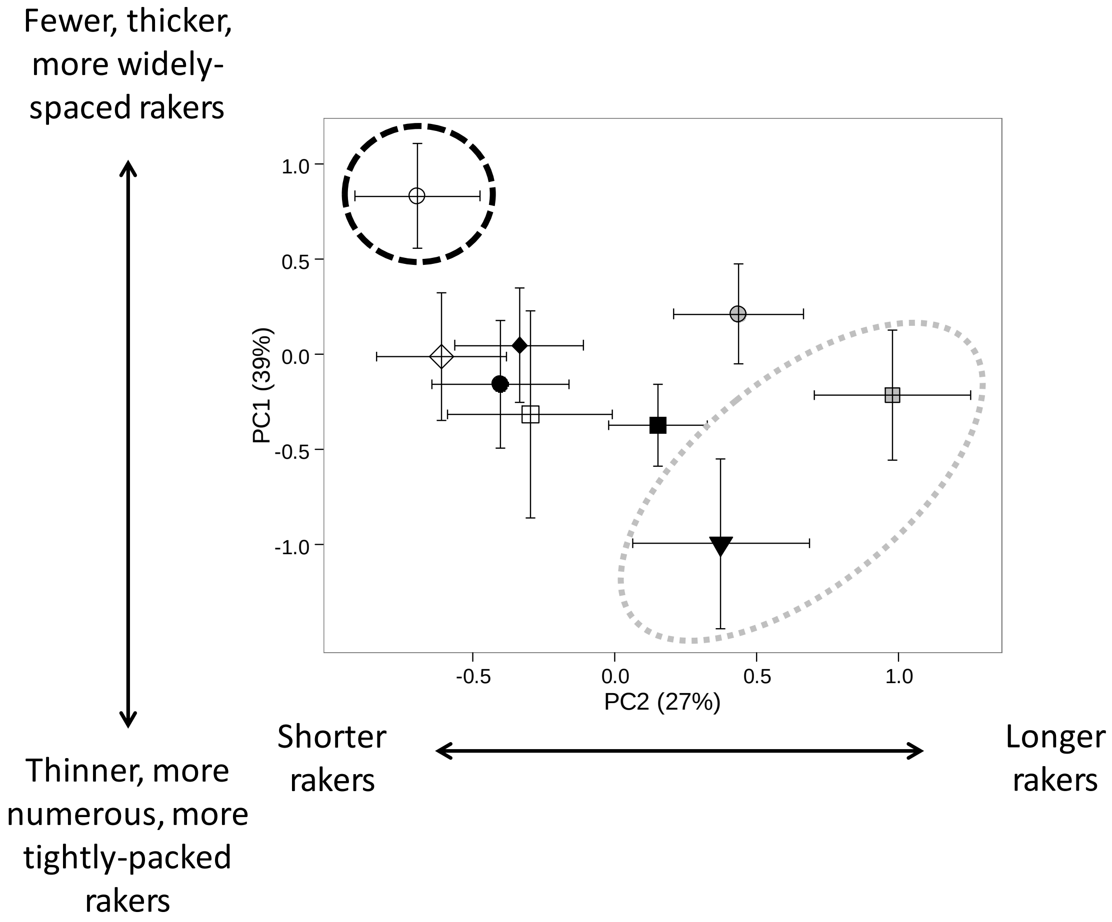

Fig. 4.12 Principal components analysis of four gill raker traits of *R. argentea* across nine Ugandan lakes.

PC1 explained 39% of the variation in the data-set, and was positively associated with fewer, thicker, more widely-spaced gill rakers. PC2 explained 27% of the variation in the data-set, and was associated with longer gill rakers. Data shown are lake means ± 2 SE. The lakes with *R. argentea* showing the most zooplanktivirous morphology (grey dotted circle) and most benthivorous morphology (black dashed circle) are emphasized. The lakes shown are: Kayanja (white circle), Omuno (white square), Gigati (white diamond), Nawampasa (grey circle), Bisina (grey square), Nabugabo (black diamond), Nakuwa (black downwards triangle) Kyoga (black circle), and Victoria (black square).

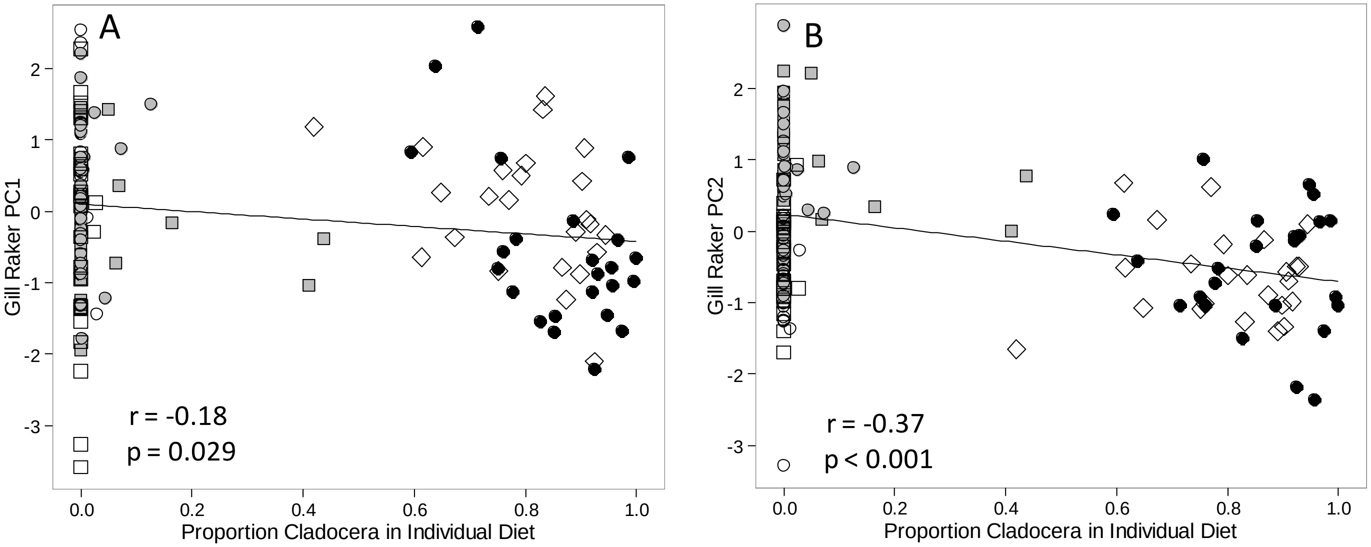

Fig. 4.13 Individual-level correlations between trophic morphology and diet.
Individuals with more Cladocera in their gut tended to have lower scores on PC1 (thinner, more numerous, and more tightly-packed rakers – panel A), as well as lower scores on PC2 (shorter rakers – panel B). For an explanation of symbols, please see caption for Fig. 4.6.

5 General Conclusions

The goal of this dissertation was to explore the phenotypic consequences of two important anthropogenic stressors (commercial fishing and the introduction of non-native predators) both generally in aquatic systems, and specifically, in the case of *R. argentea* in the Lake Victoria basin of East Africa. Below, I summarize the main findings and contributions of each chapter, and then I discuss three important themes that emerge from the dissertation as a whole: (i) understanding the impacts of multiple stressors in natural ecosystems, (ii) predicting the likelihood of evolutionary rescue in natural populations, and (iii) using evolutionary principles to develop applied management strategies. I conclude by outlining some future research directions, both for *R. argentea* in Lake Victoria, and more broadly for the field of contemporary/applied evolution.

5.1 Summary of findings

In a meta-analysis (Chapter 1), I showed that fishing is significantly associated with declining size and age at maturity in the majority of global stocks for which long-term phenotypic data are available. This was the first study to statistically link rates of fishing mortality with rates of phenotypic change across a broad range of stocks, and provides strong evidence for a general causal role of fishing in driving observed patterns of life history change in exploited fish stocks. These trends do not appear to be restricted to the large-bodied, long-lived, temperate, marine species that have been the focus of most scientific study to-date, as I found strikingly similar patterns of declining body size and size at maturity in the small-bodied, short-lived, tropical cyprinid *R. argentea* from Lake Victoria associated with predation from both fishers and a non-indigenous piscivore (Chapter 2). Rates of fishing-associated contemporary life history change in *R. argentea* were extremely rapid, suggesting (a) that dramatic changes may occur in the first few decades of commercial fishing – a period that has been typically “missed” by ecologists studying marine stocks that have been fished since the 18th and 19th centuries (Jackson et al. 2001); and (b) that tropical inland fisheries based on simple technologies may also generate surprisingly strong selection on life history traits. This study is, to my knowledge, the first well-documented example of fisheries-induced life history change in a tropical, freshwater fish stock, and thus extends our understanding of this phenomenon to a previously-overlooked, but important, subset of global fisheries.

I also found evidence to suggest that the introduced Nile perch influenced *R. argentea* in complex, and sometimes indirect ways. I found that Nile perch predation (in tandem with fishing pressure) appears to have driven contemporary changes in life history traits of *R. argentea*, in a direction consistent with an adaptive response to increased mortality (Chapter 2). There was some evidence that the Nile perch may also have driven changes in overall body morphology, in a direction that would be expected to improve burst swimming ability (Chapter 3), although these effects were subtle, and context-dependant. Specifically, we found different outcomes (more streamlined bodies over time) in the offshore waters of Lake Victoria, which may reflect the influence of behavioural responses to predation (e.g., selection for increased schooling rather than fast-start escape ability), and/or the influence of other factors, such an increasing hypoxia over time. This chapter provides an important empirical test of existing eco-morphological predictions (Langerhans and Reznick 2010) in a taxonomically and geographically distinct taxon, and is also one of only a few known examples of contemporary morphological change in a native prey species associated with an introduced predator. Finally, I found some evidence for cascading effects of the Nile perch introduction on the diet and trophic morphology of *R. argentea* (Chapter 4), although these were again context-dependent. In the most heavily-impacted lake (Victoria), I found good evidence for dietary niche expansion, an increase in inter-individual diet variation, and an increase in morphological variance following the Nile perch introduction. Across lakes; however, strong bottom-up effects (i.e., variation in prey availability) obscured or confounded any potential top-down effects of the Nile perch introduction on the trophic ecology of *R. argentea*. This chapter addresses a frequently overlooked aspect of biological invasions: the potential *indirect* ecological and phenotypic impacts of invaders on native species, mediated through changes in community composition. Furthermore, it provides an example of how biological invasions can be used to empirically test long-standing theoretical questions in ecology in a novel way (in this case Van Valen's (1965) Niche Variation hypothesis).

5.2 Interactions between multiple stressors

Anthropogenic stressors rarely occur in isolation in nature. For example, lakes in densely-populated catchments are likely to simultaneously experience nutrient loading, eutrophication, shoreline deforestation, increased turbidity, water withdrawals, stocking of non-native species and increased fishing pressure (Beeton 2002). Understanding the combined and interactive effects of these various stressors is critical to management, particularly because stressors that interact synergistically can sometimes produce unexpectedly large negative impacts, resulting in undesirable "ecological surprises" (Darling and Côté 2008). However, few studies have rigorously disentangled the interactions between multiple stressors in nature, and almost none have explicitly looked at the combined effects of introduced species and fishing. For example, in a recent meta-analysis, Crain et al. (2008) found that only 19 out of 202 (9%) studies looking at interactive effects of human stressors on marine ecosystems were conducted in the field. Furthermore, only 3 of these studies looked at the impacts of fishing when combined with another stressor, and none tested the combined effects of fishing and invasive species. This gap is not surprising, given that it is often difficult to impossible to achieve the replication needed to conduct such a factorial experiment in the field. Furthermore, it would usually be and unethical or impractical to manipulate the spread of introduced species, or control the intensity and spatial extent of fishing for experimental purposes.

Lake Victoria is a classic example of an ecosystem that has been subject to multiple anthropogenic stressors (Chapman et al. 2008), and provides an (albeit imperfect) opportunity to begin to explore interactions between these stressors in a natural setting. For instance in Chapter 2, I considered the combined effects of fishing and introduced species on *R. argentea*. My ability to rigorously examine the interaction between these two stressors was limited by the fact that this natural experiment does not have a true factorial design, i.e., there are no lakes (or time periods) where *R. argentea* have been fished commercially, but Nile perch are absent. Furthermore, replication was low and imperfect (i.e. no two lakes were identical in all aspects). Nevertheless, I can draw some tentative and qualitative conclusions. For several life history traits, I observed little or no effect of the Nile perch alone, but a significant effect of Nile perch combined with fishing (e.g., L_{50} over time, Fig. 2.5), while for others a roughly equal, additive negative effect of the two stressors (e.g., standard length across lakes, Fig. 2.2). Generally, fishing seemed to have a greater effect on life history traits of *R. argentea* than Nile perch predation, perhaps because it imposes higher mortality. Finally, in this chapter, we showed that the effects of fishing and Nile perch predation remained robust even when we considered the effects of other potential abiotic stressors (e.g., temperature and dissolved oxygen) in our models.

In Chapters 3 and 4, I observed patterns of phenotypic variation suggestive of antagonistic interactions between Nile perch and hypoxia (although my study was not formally designed to consider the effects of hypoxia). For example, in Chapter 3, I observed an increase in head size over time in *R. argentea*, contrary to the expected morphological response to predation, but consistent with an observed increase in gill size, potentially in response to increasing hypoxia. Similarly, in Chapter 4, I observed a decrease in gill raker spacing over time in *R. argentea*; contrary to the expected morphological response to observed diet changes following the Nile perch introduction, but consistent with the observed increase in gill size, again hypothesized to be a phenotypic response to increasing hypoxia. Finally, integrating across various chapters, it is interesting to speculate whether there have also been facilitative interactions between stressors. For example, could the apparent competitive release of *R. argentea* following the decline of the haplochromine cichlids due to intense fishing and predation from the Nile perch (Chapter 4) have facilitated *R. argentea*'s ability to adapt to fishing pressure later on (Chapter 2)? Specifically, could the strong increase in population size of *R. argentea* in the 1980s (putatively due to competitive release) have facilitated adaptation by providing greater genetic variation, and greater resilience to the negative demographic impacts of selection (i.e. greater probability of evolutionary rescue, see below)?

5.3 Evolutionary rescue in natural populations

As human impacts on the natural world continue to intensify, evolutionary biologists have become increasingly interested in understanding the extent to which evolution may be able to "rescue" natural populations threatened by anthropogenic stressors. Evolutionary rescue occurs when a population is able to adapt rapidly enough to compensate for demographic declines incurred following a disturbance, allowing for renewed population growth and persistence in the altered environment, rather than extinction. Theory suggests that evolutionary rescue may be possible when initial population sizes are large, genetic variation is high, and the degree of initial maladaptation is low (Gomulkiewicz and Holt 1995; Kinnison and Hairston 2007). An elegant series of laboratory experiments on yeast, *Saccharomyces cerevisiae*, adapting to high salt stress provide some of the only empirical support to-date for this process (Bell and Gonzalez 2009; Bell and Gonzalez 2011). While there are many examples of natural populations undergoing phenotypic and/or evolutionary changes in response to human stressors (reviewed in Hendry et al. 2008), the process of evolutionary rescue itself has not yet been clearly demonstrated in nature. Expanding on the approach of Bell and Gonzalaz (2009), to empirically demonstrate evolutionary rescue in nature, one would need to have replicate populations exposed to a stressor, coupled with replicate control populations that were not exposed to the stressor. One would then have to demonstrate trait changes in the stressed populations (showing a change in phenotype, ideally supported by evidence of genetic change), and in doing so, had managed to survive and grow in their new, stressful environment. Finally, one would then compare the fitness (growth, survival and/or fecundity) of both adapted and unadapted lines in both control and stressful environments.

Could such an approach be undertaken with *R. argentea* to test for evolutionary rescue in the wild? *R. argentea* conforms well to the main theoretical criteria for evolutionary rescue: population sizes are large, and the initial degree of maladaptation to novel stressors (Nile perch and fishing) was likely lower than most of the haplochromine cichlids in Lake Victoria, given that *R. argentea* have high fecundity, no parental care, and a short life cycle (Wanink 1998). We do have replicate populations (lakes) that have been exposed to stressors (fishing, Nile perch predation), along with populations that have not, although replication is of course lower than what could be achieved in a laboratory setting. We have demonstrated that there are significant differences in life history traits (Chapter 2) and body morphology (Chapter 3) between these populations, although we do not know if these differences have a genetic basis. We know that *R. argentea* has increased 5 fold in abundance since the 1980s in Lake Victoria (Wanink 1999), suggesting that they have adapted somehow to this stressful environment. The next step would be test whether these phenotypic differences between lakes have any fitness consequences, and thus could be the cause of *R. argentea'*s success. One way to do this would be to perform a reciprocal transplant involving tagged individuals from both perturbed (i.e., fished and invaded lakes) and unperturbed (i.e., not fished and uninvaded) lakes, and test for fitness differences. If the changes in morphology and life history that I have documented are adaptive, then I would expect that, in perturbed lakes, individuals from perturbed lakes would have higher fitness then individuals from unperturbed lakes. Furthermore, if there is "fitness cost" to adaptation (Bell and Gonzalez 2009), then adapted (high perturbation) populations would have lower fitness than their "unadapted" counter-parts from unperturbed environments. Such an experiment would be logistically challenging to perform, but provides an interesting starting point for thinking about future experimental approaches in this system.

5.4 Management implications

What novel insights can the study of contemporary phenotypic change provide for the development of conservation and management policies? In the context of fisheries, there is good theoretical and empirical evidence that trait changes can reduce yields, fitness, and the potential for recovery, and thus are of management concern (Heino 1998; Walsh et al. 2006; Hutchings 2005; Enberg et al. 2009; Kuparinen and Hutchings 2012). It has also been proposed that rapid life history changes can be used as an indicator of extreme, perhaps unsustaintable, levels of fishing pressure (Trippel 1995). Olsen et al. (2004) calculated that declines in probabilistic maturation reaction norms in Northern Atlantic cod stocks were statistically detectable 3-7 years before the catastrophic population collapse of 1992, and proposed that in the future, such changes in maturation-related traits could be used as a "warning signal" of over-fishing. These ideas are well-accepted among evolutionary ecologists, but are still not widely appreciated by fisheries managers, and are rarely put into practice. The *R. argentea* fishery is a case in point: trait-based analyses such as ours (Chapter 2) point to high levels of fisheries selection and potentially detrimental changes in life history traits; yet some fisheries biologists relying on more traditional demographic indices point to recent increases in the biomass of *R. argentea* and argue that there is no cause for concern (Kolding et al. 2012). However, in Lake Victoria, as in many inland fisheries in the developing world, stock assessments are limited or non-existent, and fisheries statistics therefore are often incomplete and unreliable (Cowx et al. 2003). In the case of *R. argentea* in Uganda in particular, a considerable proportion of catches likely go unreported, for a number of reasons. *Rastrinebola argentea* catches are typically landed at dawn, and only during some times of the month, and so are easily missed during the infrequent catch assessments that are conducted (*pers. obs.*). Furthermore, much of the catch is for local consumption (subsistence), or is sold through informal, unmonitored markets. Current lake-wide biomass estimates are based exclusively on hydro-acoustic surveys, but these data are somewhat problematic, because *R. argentea* cannot always be clearly distinguished from haplochromines (e.g., Getabu et al. 2003). In such a context, phenotypic data can provide a much-needed alternative perspective, and should be used to guide management decisions as well.

In the context of invasive species, the study of phenotypic change (both in the invader, and in native species) is essential to fully understanding the interactions between them. This is because trait changes may be a key factor contributing to the persistence of native species (as has been argued for example for life history changes in *R. argentea*; Wanink 1998, Sharpe et al. 2012), and also because trait changes may potentially have further ecological consequences for interactions between introduced and native species in the altered ecosystem (i.e., eco-evolutionary feedbacks, Palkovacs et al. 2011). My work shows that an invader can sometimes select on multiple aspects of the phenotype of a single native species (e.g., life history traits and morphology), and can act on both through direct and indirect pathways (e.g., predation, and removal of competitors, respectively). Taken together, my findings suggest that the phenotypic outcomes of biological invasions are complex, and extremely difficult to predict beforehand. Given that most introductions are irreversible, this calls for extreme caution, and improved efforts by managers to limit or avoid future introductions of freshwater fishes.

5.5 Future directions

The themes discussed above provide important directions for future research, both in Lake Victoria and more broadly for evolutionary ecologists interested in contemporary evolution and its management and conservation applications. First, understanding how large-scale stressors such as fishing and introduced species interact in nature is a challenging, but important priority. One way forward will be to combine larger-scale spatial and temporal field data linking stressors to ecological/phenotypic change (as I have done in this dissertation) with smaller-scale field or laboratory experiments that directly test causal mechanisms in a more controlled setting, for example using the type of “weight of evidence” approach outlined by Lowell et al. (2000). Future work should also attempt to integrate the effects of additional stressors. For example, in Lake Victoria, future research should try to also incorporate the effects of increasing hypoxia, declining water quality, and climate change. Second, documenting phenotypic changes must be followed up by determining their genetic basis, and functional/fitness consequences. Finally, much more of this research needs to be conducted in the tropics, which harbour most of the planet's biodiversity, but are also experiencing the fastest rates of human population growth. In the Lake Victoria basin, the current human population of approximately 30 million is growing at over 3% per year, the fastest growth rate on the African continent (UNEP 2006), and one of the fastest in the world. The additional demand that this will place on Lake Victoria's already stressed fisheries, including that of *R. argentea*, is troubling. A sound knowledge of the ecological and evolutionary dynamics of this ecosystem is essential so that the governments of the riparian states can develop policies that will meet the nutritional and economic needs of their citizens while also preserving the remaining biodiversity of Lake Victoria for future generations.

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6 Appendices

Appendix A. Rates of change in length at 50% maturity (Chapter 1).
Note: Only those rate estimates retained for the stock-level analysis are shown. Fishing mortality estimates are the mean of annual fishing mortality rates over the time period indicated. The location of each stock is indicated in parentheses. See footnotes for details of how rates of phenotypic change and fishing mortality were calculated for each stock.

Stock	Time period	Sex	Time (yr)	Time (gen)	Fishing Mortality (year^{-1})	Rate Darwins (x10^3)
American plaice						
(*Hippoglossoides platessoides*)						
NAFO Div. 3LNO[1] (Atlantic)	1962-94	F	32	2	0.461	-5.77
NAFO Div. 3Ps[2] (Atlantic)	1961-93	F	32	2	0.257	-3.21
Atlantic cod						
(Gadus morhua)						
NAFO Div. 4Vs[3] (Atlantic)	1992-02	F	10	1	0.000	-13.48
NAFO Div. 4W[3] (Atlantic)	1979-93	F	12	1	0.616	-8.28
ICES Div 25-28 (Baltic Sea)[4]	1984-97	F	13	-	0.860	-24.78
European plaice						
(Pleuronectes platessa)						
North Sea[5]	1955-95	F+M	40	7	0.343	-0.89
Grayling						
(Thymallus thymallus)						
Lake Lesjaskogsvatn[6] (Norway)	1903-98	F+M	95	16	0.350	-2.50
Spring-spawning herring						
(Clupea harengus)						
Norwegian Sea[7]	1930-55	F+M	25	4	0.119	-0.314
Pink salmon						
(Oncorhynchus gorbuscha)[8]						
Area 10 (Pacific)	1952-74	F+M	22	11	1.201	-22.83
Area 3 (Pacific)	1952-74	F+M	22	11	0.469	-23.22
Area 4 (Pacific)	1952-74	F+M	22	11	0.667	-17.55
Area 5 (Pacific)	1952-74	F+M	22	11	0.658	-17.50
Area 7 (Pacific)	1952-74	F+M	22	11	1.068	-19.11
Area 9 (Pacific)	1952-74	F+M	22	11	1.134	-22.66
Chum salmon						
(Oncorhynchus gorbuscha)[9]						
Area 11 (Pacific)	1951-75	F+M	24	6	0.529	5.62

Area 12 (Pacific)	1951-75	F+M	24	6	0.529	-3.73
Area 13 (Pacific)	1951-75	F+M	24	6	0.529	-1.92
Silver hake *(Merluccius bilinerias)*						
NAFO Div. 4VWX[10] (Atlantic)	1970-90	F	20	-	0.579	-6.97

1. 3LNO American plaice: Rates of phenotypic change calculated from Dwyer et al. (2007), Fig. 21. The time series was split in 1994 because a moratorium was imposed in this year. Generation length estimated as 16 years (average for all American plaice stocks; Busby et al. (2007)). F estimates are mean values for ages 9-14, estimated from VPA (Dywer et al. (2007), Fig. 27).
2. 3Ps American plaice: Rates of phenotypic change calculated from Morgan et al. (2002), Fig. 15. The time series was split in 1993 because a moratorium was imposed in this year. Generation length estimated as 16 years (average for all American plaice stocks; Busby et al. (2007)). F estimates are mean values from Myers (2007).
3. 4Vs and 4W cod: Rates of phenotypic change calculated from Hutchings (2005), Fig. 2b, for periods pre- and post-moratorium (1993). Generation length estimated as 9 years (COSEWIC 2003). F values pre-1993 estimated from Myers (2007). F values post-1993 estimated from Trzcinsky et al. (2006).
4. Baltic cod: Rates of phenotypic change calculated from Cardinale and Modin (1999), Table 2. Generation length unknown. F values from Cardinale and Modin (1999), Table 1.
5. North Sea plaice: Rates of phenotypic change calculated from Grift et al. (2003), Fig. 4. Generation length estimated as 5.5 years (Grift et al. 2003). F estimates are mean values for ages 2-10, from Grift et al. (2003), Fig. 1c.
6. Grayling: Rates of phenotypic change taken directly from Haugen and Vollestad (2001), Table 4. Generation length estimated as 5.81 years (Haugen and Vollestad 2001). F estimates are the maximum estimates from Haugen and Vollestad (2001).

7. Spring-spawning herring: Rates of phenotypic change calculated from Engelhard and Heino (2004), Fig. 2b. The time series was split in two at 1955, corresponding to exploitation periods defined by the authors (Engelhard and Heino, 2004, Fig. 1). Generation length estimated as 6 years (G. Engelhard, pers. comm.). F values are mean estimates for ages 5-13 from Engelhard and Heino (2004), Fig. 1b.
8. Pink salmon: Rates of phenotypic change calculated from Ricker (1981), Tables 2-3 (based on data from commercial seines only). Actual values were for mean weight of fish in commercial seines; however, since all fish caught were age 2, and all pink salmon mature at age 2, we considered this to be analogous to size at maturity. Generation length estimated as 2 years (Ricker 1981). F estimates were from Myers (2007). Annual F estimates were only available for a subset of years (1970-75) in most cases.
9. Chum salmon: Rates of phenotypic change calculated from Ricker (1981), Tables 5 (based on data from commercial seines only). Actual values were for mean weight of fish in commercial seines; however, since all harvested fish are mature for this species (Ricker 1981), we considered this to be analogous to size at maturity. Generation length estimated as 3 years (Ricker 1981). F estimates were from Myers (2007).
10. Silver hake: Rates of phenotypic change calculated from Showell et al. (2003), Fig. 21. Generation length unknown. F estimates are mean values from Myers (2007).

Appendix B. Rates of change in age at 50% maturity (Chapter 1).

Note: Only those rate estimates retained for the stock-level analysis are shown. Fishing mortality estimates are the mean of yearly fishing mortality rates over the time period indicated. The location of each stock is indicated in parentheses. See footnotes for details of how rates of phenotypic change and fishing mortality were calculated for each stock.

Stock	Time period	Sex	Time (yr)	Time (gen)	Fishing Mortality (year^{-1})	Rate Darwins (x 10^3)
American plaice						
(Hippoglossoides platessoides)						
NAFO Div. 3LNO[1] (Atlantic)	1950-94	F	44	3	0.422	-7.49
NAFO Div. 3Ps[2] (Atlantic)	1961-93	F	32	2	0.257	-8.28
Atlantic cod						
(Gadus morhua)						
NAFO Div. 2J[3] (Atlantic)	1992-03	F	11	1	0.246	-5.96
NAFO Div. 3K[3] (Atlantic)	1992-03	F	11	1	0.246	-3.95
NAFO Div. 3L[3] (Atlantic)	1982-92	F	10	1	0.818	-3.82
NAFO Div. 3NO[4] (Atlantic)	1971-94	F	23	2	0.511	-9.99
NAFO Div. 3Ps[5] (Atlantic)	1954-93	F	39	4	0.603	-8.78
NAFO Div. 4T[6] (Atlantic)	1959-79	F	20	2	0.533	-26.20
NAFO Div. 4Vn[6] (Atlantic)	1959-79	F	20	2	0.533	-41.22
NAFO Div. 4Vs[7] (Atlantic)	1979-92	F	11	2	0.616	12.62
NAFO Div. 4W[8] (Atlantic)	1959-79	F	20	2	0.541	-27.25
NAFO Div. 4X[9] (Atlantic)	1959-79	F	20	3	0.541	-12.80
NAFO Div. 5Z[10] (Atlantic)	1986-93	F+M	7	1	0.701	-29.57
ICES Div. 25-28 (Baltic Sea)[11]	1988-97	F	7		0.832	-35.32
NE Arctic[12]	1923-76	F+M	53		0.416	-6.42
European plaice						
(Pleuronectes platessa)						
North Sea[13]	1955-95	F	40	7	0.343	-8.63
Grayling						
(Thymallus thymallus)						
Lake Lesjaskogsvatn[14] (Norway)	1903-98	F+M	95	16	0.350	-3.00
Haddock						
(Melanogrammus aeglefinus)						
NAFO Div. 4TVW[15] (Atlantic)	1958-93	F	33	5	0.525	-6.487
NAFO Div. 4Vn[16] (Atlantic)	1959-79	F	20	3	0.634	-10.87
NAFO Div. 4Vs[16] (Atlantic)	1959-79	F	20	3	0.634	-22.65
NAFO Div. 4W[16] (Atlantic)	1959-79	F	20	3	0.634	-17.35
NAFO Div. 4X[17] (Atlantic)	1959-79	F	20	3	0.432	-21.15
Spring-spawning herring						

(Clupea harengus)						
Norwegian Sea[18]	1955-78	F+M	23	4	0.723	-4.65
Striped Bass						
(Morone saxatilis)						
Rhode Island[19] (Altantic)	1941-87	F	46		0.150	3.08
Walleye						
(Stizostedion vitreum)						
Lake Erie[20] (Canada/USA)	1927-66	F	39		1.895	-10.40

1. 3LNO American plaice: Rates of phenotypic change calculated from Dwyer et al. (2007), Fig. 20. The time series was split in 1994 because a moratorium was imposed in this year. Generation length estimated as 16 years (average for all American plaice stocks; Busby et al. (2007)). F estimates are mean values for ages 9-14, estimated from VPA (Dywer et al. (2007), Fig. 27).
2. 3Ps American plaice: Rates of phenotypic change calculated from Morgan et al. (2002), Fig. 14. The time series was split in 1993 because a moratorium was imposed in this year. Generation length estimated as 16 years (average for all American plaice stocks; Busby et al. (2007)). F estimates are mean values from Myers (2007).
3. 2J, 3K, 3L cod: Rates of phenotypic change calculated from Olsen et al. (2005), Fig. 4. Time series were split 1992, because a fishing moratorium was imposed at this time. Generation length estimated as 11 years (COSEWIC 2003). F values pre-moratorium (1992) estimated from Myers (2007). F values post-moratorium estimated from Lilly et al. (2003), Table 44.
4. 3NO cod: Rates of phenotypic change calculated from Olsen (2005), Fig. 4. The time series was split in 1994, because a fishing moratorium was imposed at this time. Generation length estimated as 11 years (COSEWIC 2003). F estimates are mean values for ages 6-9, estimated from ADAPT (Morgan et al. (2007), Table 24).
5. 3Ps cod: Rates of phenotypic change calculated from Brattey et al. (2004), Fig. 23a. The time series was split in 1993, because a fishing moratorium

was imposed at this time. Generation length estimated as 11 years (COSEWIC 2003). F estimates are mean values from Myers (2007).

6. 4T and 4Vn cod: Rates of phenotypic change calculated from Trippel (1995), Table 1. Generation length estimated as 9.5 years (COSEWIC 2003). F estimates are mean values from Myers (2007).
7. 4Vs cod: Rates of phenotypic change calculated from Hutchings (2005), Fig. 2a, for periods pre- and post-moratorium (1993). Generation length estimated as 9 years (COSEWIC 2003). F values pre-1993 estimated from Myers (2007).
8. 4W cod: Rates of phenotypic change calculated from Trippel (1995), Table 1. Generation length estimated as 9 years (COSEWIC 2003). F values estimated from Myers (2007).
9. 4X cod: Rates of phenotypic change calculated from Trippel (1995), Table 1. Generation length estimated as 7.5 years (COSEWIC 2003). F estimates are mean values from Myers (2007).
10. 5Z cod: Rates of phenotypic change calculated from Trippel (1995), Table 1. Generation length estimated as 7.5 years (COSEWIC 2003). F estimates are mean values from Myers (2007).
11. Baltic cod: Rates of phenotypic change calculated from Cardinale and Modin (1999), Fig. 3c. Generation length unknown. F values from Cardinale and Modin (1999), Table 1.
12. NE Arctic cod: Rates of phenotypic change calculated from Trippel (1995), Table 1. Generation length unknown. F estimates are mean values from Myers (2007).
13. North Sea plaice: Rates of phenotypic change calculated from Grift et al. (2003), Fig. 4. Generation length estimated as 5.5 years (Grift et al. 2003). F estimates are mean values for ages 2-10 from Grift et al. (2003), Fig. 1c.
14. Grayling: Rates of phenotypic change calculated from Haugen and Vollestad (2001), Fig. 4. Generation length estimated as 5.81 years (Haugen and Vollestad 2001). F estimates are maximum estimates from Haugen and Vollestad (2001).

15. 4TVW haddock: Rates of phenotypic change calculated from Mohn and Simon (2002), Fig. 7. The fishery collapsed and was closed in 1993, so the time series was cut in this year. Generation length estimated as 6.56 years, calculated from the formula A50 + 1/M, where A50 is the mean age at maturity between 1965 and 1993 (3.7), and M= 0.35 (Mohn and Simon (2002)). F estimates pre-1969 are from Mohn and Simon (2002), Fig. 13. F estimates post-1969 are mean values for ages 5-7, estimated from SPA (Frank et al. (2001), Table 21).
16. 4Vn and 4Vs and 4W haddock: Rates of phenotypic change calculated from Trippel (1995), Table 2. Generation length estimated as 6.56 years, calculated from the formula A50 + 1/M, where A50 is the mean age at maturity between 1965 and 1993 (3.7), and M= 0.35 (Mohn and Simon (2002)). F estimates are from Mohn and Simon (2002), Fig. 13.
17. 4X haddock: Rates of phenotypic change calculated from Trippel (1995), Table 2. Generation length estimated as 6.56 (same as neighbouring haddock stocks). F estimates are mean values for ages 5-7, estimated from SPA (Hurley et al. (1999), Table 25).
18. Spring-spawning herring: Rates of phenotypic change calculated from Engelhard and Heino (2004), Fig. 2a. The time series was split in two at 1955, corresponding to exploitation periods defined by the authors (Engelhard and Heino, 2004, Fig. 1). Generation length estimated as 6 years (G. Engelhard, pers. comm.). F values are mean estimates for ages 5-13 from Engelhard and Heino (2004), Fig. 1b.
19. Striped bass: Rates of phenotypic change calculated from Trippel (1995), Table 3. Generation length unknown. F estimates are mean values from Myers (2007). F estimates were only available for a subset of years in the time series (1982-87).
20. Walleye: Rates of phenotypic change calculated from Trippel (1995), Table 3. Generation length unknown. F estimates are mean values from Myers (2007). F estimates were only available for a subset of years in the time series (1949-66).

Appendix C. Rates of change in mid-points of probabilistic maturation reaction norms (Chapter 1).

Note: Only those rate estimates retained for the stock-level analysis are shown. Fishing mortality estimates are the mean of yearly fishing mortality rates over the time period indicated. The location of each stock is indicated in parentheses. See footnotes for details of how rates of phenotypic change and fishing mortality were calculated for each stock.

Stock	Time period	Sex	Age	Time (yr)	Time (gen)	Fishing Mortality (year^{-1})	Rate Darwins (x10^{3})
American plaice							
(Hippoglossoides platessoides)							
NAFO Div. 3LNO[1] (Atlantic)	1970-93	F	7	23	1	0.572	-10.02
NAFO Div. 3Ps[2] (Atlantic)	1973-92	F	7	19	1	0.257	-8.02
Atlantic cod							
(Gadus morhua)							
NAFO Div. 2J[3] (Atlantic)	1992-02	F	5	10	1	0.246	0.13
NAFO Div. 3K[3] (Atlantic)	1992-02	F	5	10	1	0.246	-5.18
NAFO Div. 3L[3] (Atlantic)	1983-92	F	5	9	1	1.000	-15.71
NAFO Div. 3NO[4] (Atlantic)	1994-01	F	5	7	1	0.099	7.26
NAFO Div. 3Ps[4] (Atlantic)	1976-93	F	5	17	1	0.633	-20.70
NAFO Div. 5Y[6] (Atlantic)	1970-94	F	3	24	2	1.106	-27.48
NAFO Div. 5Zjm[7] (Atlantic)	1970-94	F	3	24	4	0.653	-18.85
European plaice							
(Pleuronectes platessa)							
North Sea[8]	1955-95	F	4	40	7	0.343	-2.60
Spring-spawning herring							
(Clupea harengus)							
Norwegian Sea[10]	1930-55	F+M	5	25	4	0.119	0.34

1. 3LNO American plaice: Rates of phenotypic change calculated from Barot et al. (2005), Fig. 4. The time series was split in 1993, the year a moratorium was imposed for this stock. PMRN midpoints were calculated for ages 4-9; however, we only included one (age 7) in the final analysis to avoid pseudoreplication. The choice of age should not influence our results because temporal trends were similar, and statistically significant for all ages (Barot et al. 2005). Generation length estimated as 16 years (average for all American plaice stocks; Busby et al. (2007)). F estimates

are mean values for ages 9-14, estimated from VPA (Dywer et al. (2007), Fig. 27).

2. 3Ps American plaice: Rates of phenotypic change calculated from Barot et al. (2005), Fig. 4. The time series was split in 1994, because fishing mortality dropped dramatically after this year. As above, PMRN midpoints were calculated for ages 4-9; however, we only included one (age 7) in the final analysis to avoid pseudoreplication. The choice of age should not influence our results because temporal trends were similar, and statistically significant for all ages (Barot et al. 2005). Generation length estimated as 16 years (average for all American plaice stocks; Busby et al. (2007)). F estimates are mean values from Myers (2007).
3. 2J, 3K, 3L cod: Rates of phenotypic change calculated from Olsen et al. (2005), Fig. 6and7. Time series were split in 1992, because a fishing moratorium was imposed at this time. PMRN midpoints were calculated for ages 5 and 6; however we only included one in the final analysis (age 5 because it was the most complete) to avoid pseudoreplication. Generation length estimated as 11 years (COSEWIC 2003). F values pre-moratorium (1992) estimated from Myers (2007). F values post-moratorium estimated from Lilly et al. (2003), Table 44.
4. 3NO cod: Rates of phenotypic change calculated from Olsen (2005), Fig. 6and7. Time series were split in 1994, because a fishing moratorium was imposed at this time. As above, PMRN midpoints were calculated for ages 5 and 6; however we only included one in the final analysis (age 5 because it was the most complete) to avoid pseudoreplication. Generation length estimated as 11 years (COSEWIC 2003). F estimates are mean values for ages 6-9, estimated from ADAPT (Morgan et al. (2007), Table 24).
5. 3Ps cod: Rates of phenotypic change calculated from Olsen et al. (2005), Fig. 6and7. Time series were split in 1993, because a fishing moratorium was imposed at this time. As above, PMRN midpoints were calculated for ages 5 and 6; however we only included one in the final analysis (age 5 because it was the most complete) to avoid pseudoreplication. Generation

length estimated as 11 years (COSEWIC 2003). F estimates are mean values for ages 5-10, estimated from QLSPA, run B (Brattey et al. (2004), Fig. 33f).

6. 5Y cod: Rates of phenotypic change calculated from Barot et al. (2004), Fig. 5. The time series was split in1994, because fishing mortality decreased dramatically after this year. PMRN midpoints were calculated for ages 1-5; however we only included one in the final analysis (age 3 because it was the longest) to avoid pseudoreplication. The choice of age should not influence our results because temporal trends were similar for all ages (Barot et al. 2004). Generation length estimated as 10.8 years (NEFSC 2002). F estimates are mean values for ages 4-5, estimated from Mayo and O’Brien (2006), Fig. 1.6.
7. 5Z cod: Rates of phenotypic change calculated from Barot et al. (2004), Fig. 5. The time series was split in1994, because fishing mortality decreased dramatically after this year. PMRN midpoints were calculated for ages 1-5; however we only included one in the final analysis (age 3 because it was the longest) to avoid pseudoreplication. The choice of age should not influence our results because temporal trends were similar for all ages (Barot et al. 2004). Generation length estimated as 7.5 years (COSEWIC 2003). F estimates are mean values from Myers (2007).
8. North Sea plaice: Rates of phenotypic change calculated from Grift et al. (2003), Fig. 7. PMRN midpoints were calculated for ages 2-6; however we only included one in the final analysis (age 4 because it had the smallest confidence intervals) to avoid pseudoreplication. The choice of age should not influence our results because temporal trends were similar for all ages (Grift et al. 2003). Generation length estimated as 5.5 years (Grift et al. 2003). F estimates are mean values for ages 2-10 from Grift et al. (2003), Fig. 1c.
9. Spring-spawning herring: Rates of phenotypic change calculated from Engelhard and Heino (2004), Fig. 4. The time series was split in two at 1955, corresponding to exploitation periods defined by the authors

(Engelhard and Heino, 2004, Fig. 1). PMRN midpoints were calculated for ages 3-8; however, we only included one in the final analysis (age 5 because it was one of the most complete and in the middle of the range of possible ages) to avoid pseudoreplication. Generation length estimated as 6 years (G. Engelhard, pers. comm.). F values are mean estimates for ages 5-13 from Engelhard and Heino (2004), Fig. 1b.

Appendix D: Study sites (Chapter 2).

Lake	Years Sampled	Location	Surface area (km^2)	Mean Depth (m)	Elevation (m)	Secchi Depth (m)	Temperature (°C)	Dissolved Oxygen (mg/L)	Nile Perch Introduced	*R. argentea* Fishery	Native piscivores (predation on *R. argentea?*)
Victoria	2008-10	N00°24'52.7" E 033°12'26.9"	63.50 (68,800)	10.40 (40)	1136	1.17 ± 0.05	27.20 ± 0.50	7.68 ± 0.50	Yes (1954, 1960s)	Yes (1989)	S.v (no)[1]
Nabugabo	2008-10	S00°21'24.38" E31°52'26.02"	33.99	4.53	1151	0.73 ± 0.04	24.62 ± 0.21	6.51 ± 0.36	Yes (1960,1963)	Minimal (2011)	S.i. (yes)[1,2]
Kayanja	2009-10	S00°16'30.85" E31°52'10.16"	1.25	2.61	1165	0.50 ± 0.02	25.33 ± 0.08	7.68 ± 0.33	No	No	C.g. (no)[1,2], G.v (yes)[1,2]
Kyoga	2008-10	N01°18'40.3" E 033°18'22.4"	1971.35 (2047)	2.46	1033	0.61 ± 0.06	30.56 ± 0.56	10.48 ± 0.27	Yes (1955)	Yes (1995)	C.g (yes)[1], S.v. (yes)[1,3], S.i. (no)[1,3]
Nawampasa	2009-10	N01°16'59.0" E 033°21'35.6"	8.53	1.62	1029	0.48 ± 0.02	29.65 ± 0.26	6.61 ± 0.24	Yes (1998)	No	C.g. (no)[1,4], S.v. (no)[1,3]
Nakuwa	2009-10	N01°13'07.8" E 033°27'18.5"	95.79	2.22	1034	0.38 ± 0.02	31.27 ± 0.44	4.85 ± 0.72	Yes (1970s)	No	C.g. (no)[1,4], S.i.(no)[1,3,4], S.v. (no)[1,3]
Gigati	2009-10	N01°16'12.3" E 033°33'44.4"	7.52	2.03	1035	0.62 ± 0.03	28.83 ± 0.61	7.02 ± 0.48	No	No	None[4]
Meito	2010	N01°17'09.4" E 033°33'56.7"	14.64	2.79	1034	1.35 ± 0.08	26.90 ± 0.31	5.52 ± 0.43	Yes	Minimal (2005)	S.v.(unknown)[4]
Omuno	2010	N01°16'00.3" E 033°38'45.8"	5.56	1.37	1025	0.26 ± 0.00	28.87 ± 0.23	8.09 ± 0.12	No	No	C.g.(unknown)[4]
Bisina	2009-10	N01°37'26.1" E 033°55'21.4"	349.31	3.86	1043	1.96 ± 0.08	27.81 ± 0.17	6.63 ± 0.47	Yes (1970s)	No	C.g. (no)[1,4]

Physical attributes of the 10 lakes sampled for this study. Geographic co-ordinates and elevation refer specifically to the landing site on each lake from which our sampling was based. Surface area was estimated from satellite images downloaded from Google Earth. Mean depth was estimated from three replicate depth measurements taken during our 2010 field survey at sites sampled. For Lake Victoria, we specify the surface area and depth for the Napoleon Gulf, where all of our sampling was carried out, and for Lake Victoria as a whole (in parentheses). For Lake Kyoga, we speficy the surface area for the main lake where we carried out our sampling, as well as the entire surface area including additional branches (in parentheses). The values for Secchi depth, water temperature and dissolved oxygen are the means (± 1 SE) of three replicates taken at the surface in the afternoon at each sampling site. For the Nile perch, the approximate year of introduction is indicated in parentheses. For *the R. argentea* fishery, the approximate year that the fishery started is indicated in parentheses. The *R. argentea* fisheries on lakes Nabugabo and Meito are considered minimal because only 1 or 2 fishers are active, and only sporadically. The final column indicates the presence/absence of 4 native piscivores known to sometimes feed on *R. argentea*: *Clarias gariepinus* (C.g), *Gnathonemus victoriae* (G.v.), *Schilbe intermedius* (S.i.), and *Synodontus victoriae* (S.v.). Where data are available, we have indicated whether these fish species are known to feed on *R. argentea* in the lake in question (yes, no, or unknown). References for the distribution and diet of the native piscivores: (1) Mbabazi (2004); (2) Namulemo, et al. unpl. data; (3) Schwartz et al. (2006); (4) Sharpe and Chapman, unpl. data

Appendix E. Data sources for historical analysis (Chapter 2)
Historical data and specimens of *R. argentea* available from lakes Victoria and Kyoga.

Lake	Year	Site	n (females)	Traits	Source
Victoria	1966	Napoleon Gulf	39	L_{50}, fecundity, egg traits	NaFIRRI Museum
Victoria	1989	Napoleon Gulf	204	L_{50}	S.B. Wandera, unpl. data
Victoria	1991	Napoleon Gulf	174	L_{50}	S.B. Wandera, unpl. data
Victoria	1992	Napoleon Gulf	1075	L_{50}, fecundity	S.B. Wandera, unpl. data
Victoria	1993	Napoleon Gulf	1012	L_{50}	S.B. Wandera, unpl. data
Victoria	2000/2003	Napoleon Gulf	35	L_{50}	NaFIRRI Museum
Kyoga	1991	Bukungu Landing	44	fecundity	S.B. Wandera, unpl. data

Appendix F. Assessing the effect of environment variables (Chapter 2).

Results of a principal components analysis on the 5 environmental variables measured for each lake (lake area, lake depth, Secchi depth, temperature and dissolved oxygen). The variance explained by each principal component is indicated in parentheses. The values shown are the loadings of each environmental variable onto each of the first three principal component axes. The variables that loaded most heavily onto each component (>0.50) are indicated in bold.

	PC1 (35.3%)	PC2 (32.1%)	PC3 (19.3%)
Lake area	-0.02	**0.74**	-0.20
Lake depth	**0.58**	0.24	0.24
Secchi depth	**0.59**	0.26	-0.38
Temperature	**-0.54**	0.36	-0.41
Dissolved oxygen	-0.18	0.44	**0.77**

Appendix G. Assessing the impact of environmental variablesII (Chapter 2). Results of a series of general linear models examining the effects of perturbation level and environmental variables (first 3 PCs, Table C2) on life history traits.

	Effect	df	F	p	R^2
Standard Length	Perturbation	2	216.61	< 0.001	0.60
	Env PC1	1	327.93	< 0.001	
	Env PC2	1	141.01	< 0.001	
	Env PC3	1	190.33	< 0.001	
	Residual	2477			
Log Fecundity	Perturbation	2	5.95	0.003	0.77
	Log Somatic Weight	1	381.13	< 0.001	
	Env PC1	1	5.11	0.025	
	Env PC2	1	3.96	0.048	
	Env PC3	1	1.40	0.239	
	Residual	161			
Egg Volume	Perturbation	2	6.78	0.001	0.23
	Log Somatic Weight	1	1.01	0.317	
	Env PC1	1	0.30	0.584	
	Env PC2	1	0.30	0.582	
	Env PC3	1	37.55	<0.001	
	Residual	155			
Log Clutch Volume	Perturbation	2	5.27	0.006	0.73
	Log Somatic Weight	1	194.77	< 0.001	
	Env PC1	1	4.74	0.031	
	Env PC2	1	3.33	0.070	
	Env PC3	1	14.80	< 0.001	
	Residual	155			
Log Ovary Weight	Perturbation	2	10.10	< 0.001	0.82
	Log Somatic Weight	1	490.56	< 0.001	
	Env PC1	1	5.53	0.020	
	Env PC2	1	8.22	0.005	
	Env PC3	1	28.08	< 0.001	
	Residual	213			

Appendix H. Assessing the impact of environmental variablesII (Chapter 2). Results of a general linear model that examined the effects of perturbation level and environmental variables (first 3 PCS, Table C2) on L_{50}.

	Effect	df	Deviance	p
L_{50}	Perturbation	2	208.32	< 0.001
	Standard Length	1	430.68	< 0.001
	Env PC1	1	48.60	< 0.001
	Env PC2	1	61.56	< 0.001
	Env PC3	1	34.84	< 0.001

Appendix I. Physical attributes of the 9 lakes sampled for this study (Chapter 3)

Lake	Surface area (km^2)	Mean Depth (m)	Secchi Depth (m)	Temperature (°C)	Dissolved Oxygen (mg/L)	Native fish predators
Univaded						
Kayanja***	1.25	2.61	0.50 ± 0.02	25.33 ± 0.08	7.68 ± 0.33	C.g. (no)[1,2]
Omuno*	5.56	1.37	0.26 ± 0.00	28.87 ± 0.23	8.09 ± 0.12	C.g.(unknown)[4]
Gigati**	7.52	2.03	0.62 ± 0.03	28.83 ± 0.61	7.02 ± 0.48	None[4]
Transiently Invaded						
Bisina**	349.31	3.86	1.96 ± 0.08	27.81 ± 0.17	6.63 ± 0.47	C.g. (no)[1,4]
Nawampasa**	8.53	1.62	0.48 ± 0.02	29.65 ± 0.26	6.61 ± 0.24	C.g. (no)[1,4], S.v. (no)[1,3]
Invaded						
Meito*	14.64	2.79	1.35 ± 0.08	26.90 ± 0.31	5.52 ± 0.43	S.v.(unknown)[4]
Nabugabo***	33.99	4.53	0.73 ± 0.04	24.62 ± 0.21	6.51 ± 0.36	S.i. (yes)[1,2]
Kyoga***	1971.35	2.46	0.61 ± 0.06	30.56 ± 0.56	10.48 ± 0.27	C.g (yes)[1], S.v. (yes)[1,3], S.i. (no)[1,3]
Victoria***	63.50 (68,800)	10.40 (40)	1.17 ± 0.05	27.20 ± 0.50	7.68 ± 0.50	S.v (no)[1]

For Lake Victoria, we specify the surface area and depth for the Napoleon Gulf, where all of our sampling was carried out, as well as for the entire lake (in parentheses). The former was used in all statistical analyses Values for mean depth, Secchi depth, water temperature and dissolved oxygen concentration are means (±SE) from afternoon measurements at three replicate sites in the pelagic zone, either from 2010 (*), or averaged over 2009-2010 (**), or averaged over 2008-2010 (***). The final column indicates the presence/absence of 3 native fish known to sometimes feed on *R. argentea*: *Clarias gariepinus* (C.g), *Schilbe intermedius* (S.i.), and *Synodontus victoriae* (S.v.). Where data are available, we have indicated whether these fish species are known to feed on *R. argentea* in the lake in question (yes, no, or unknown). References for the distribution and diet of the native predators: (1) Mbabazi (2004); (2) Namulemo, et al. unpl. data; (3) Schwartz et al. (2006); (4) Sharpe and Chapman, unpl. data

Appendix J. Relative Warp Analysis (Chapter 3)

Methods:

In addition to the MANCOVA, we performed a principal components analysis (PCA) on the 18 partial warps and 2 uniform components, using TpsRelw. Using separate ANCOVAs, we then tested whether the most important principal components (referred to as relative warps (RWs) in the context of geometric morphometrics) differed across Nile perch categories (or years). We included centroid size as a covariate, but it was non-significant in all cases, and so was removed from the final models. There were also no significant interactions between Nile perch categories (or years) and centroid size, so these terms were also removed. For the spatial analysis, lake was nested as a fixed factor within Nile perch category.

Results:

Across lakes:

The first 3 RWs cumulatively explained 58.1% of the variation in body shape across lakes, so we focused our analysis on these. RW1 explained 29.1% of the variation, but seemed largely related to lateral bending of the specimens, likely due to variation in preservation and/or placement for photographs (Fig. J.1), and so was not considered further. RW2 explained 17.7% of the variation, and was related to changes in overall body depth, depth of the caudal peduncle, and anal fin length (Fig. J.2a). RW3 explained 11.3% of the variation, and was also related to changes in overall body depth, and the shape of the caudal peduncle (Fig. B.Jb). Both RW2 and RW3 varied significantly across lakes and Nile perch categories (Table BJ). *R. argentea* from invaded lakes tended to be deeper-bodied and had longer anal fins (more negative scores along RW2, Fig. B.Ja), as well as shorter but deeper caudal regions (more positive scores along RW3, Fig. B.Jb).

Through time:

The first 2 RWs cumulatively explained 52.0% of the variation in body shape across years in Lake Victoria, so we focused our analysis on these. RW1 explained 37.9% of the variation, but seemed largely related to lateral bending of the specimens, likely due to variation in preservation and/or placement for photographs (Fig. J.3), and so was not considered further. RW2 explained 14.2% of the variation, and was related to changes in dorsal and fin lengths, and the size and shape of the caudal region (Fig. J.4). *R. argentea* from contemporary (post-Nile perch) years tended to have longer dorsal fins, shorter anal fins, and smaller caudal regions (more positive scores along RW2, Fig. J.4), but this trend was not statistically significant (Year: $F_{5,173} = 0.81$, $p = 0.547$).

Table J1. Results of nested ANOVAs examining variation in RW2 and RW3 across lakes and Nile perch invasion categories. Centroid size and the interaction between centroid size and Nile perch categories were non-significant, and so were removed from the final model.

Effect	df	F	p
RW2			
Nile perch	2,261	6.425	0.002
Lake(Nile perch)	6,261	2.922	0.009
RW3			
Nile perch	2,261	4.301	0.015
Lake(Nile perch)	6,261	3.259	0.004

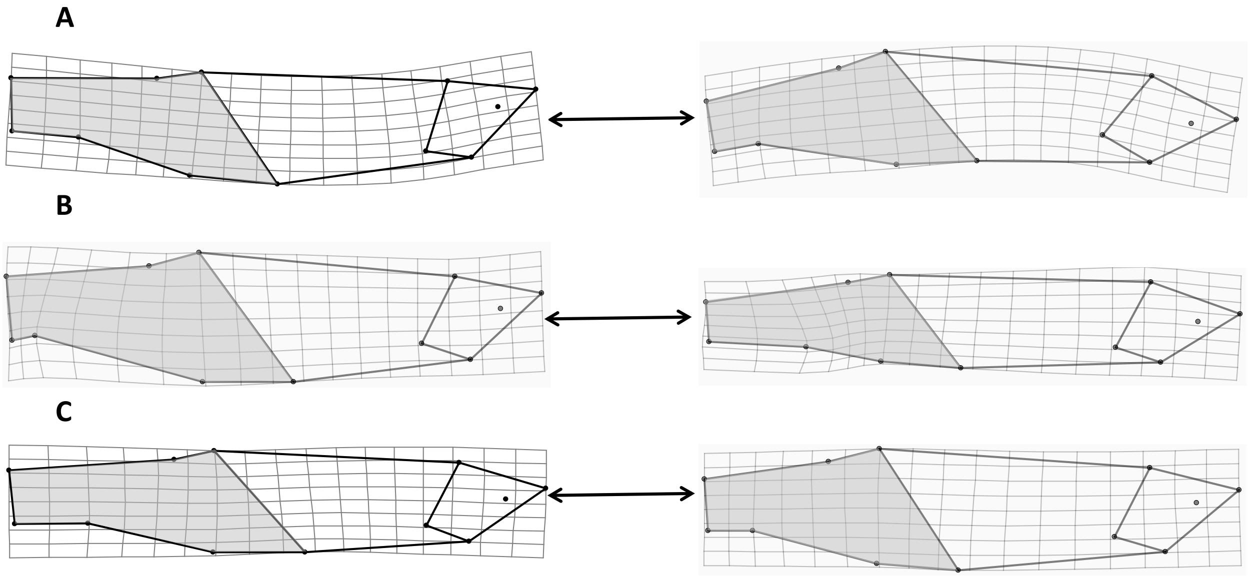


Fig. J.1

Thin-plate spline deformations illustrating the negative (left) and positive (right) extremes of relative warps 1 (A), 2 (B), 3 (C), which cumulatively explained 58.1% of total variation in body shape in *R. argentea* across lakes.

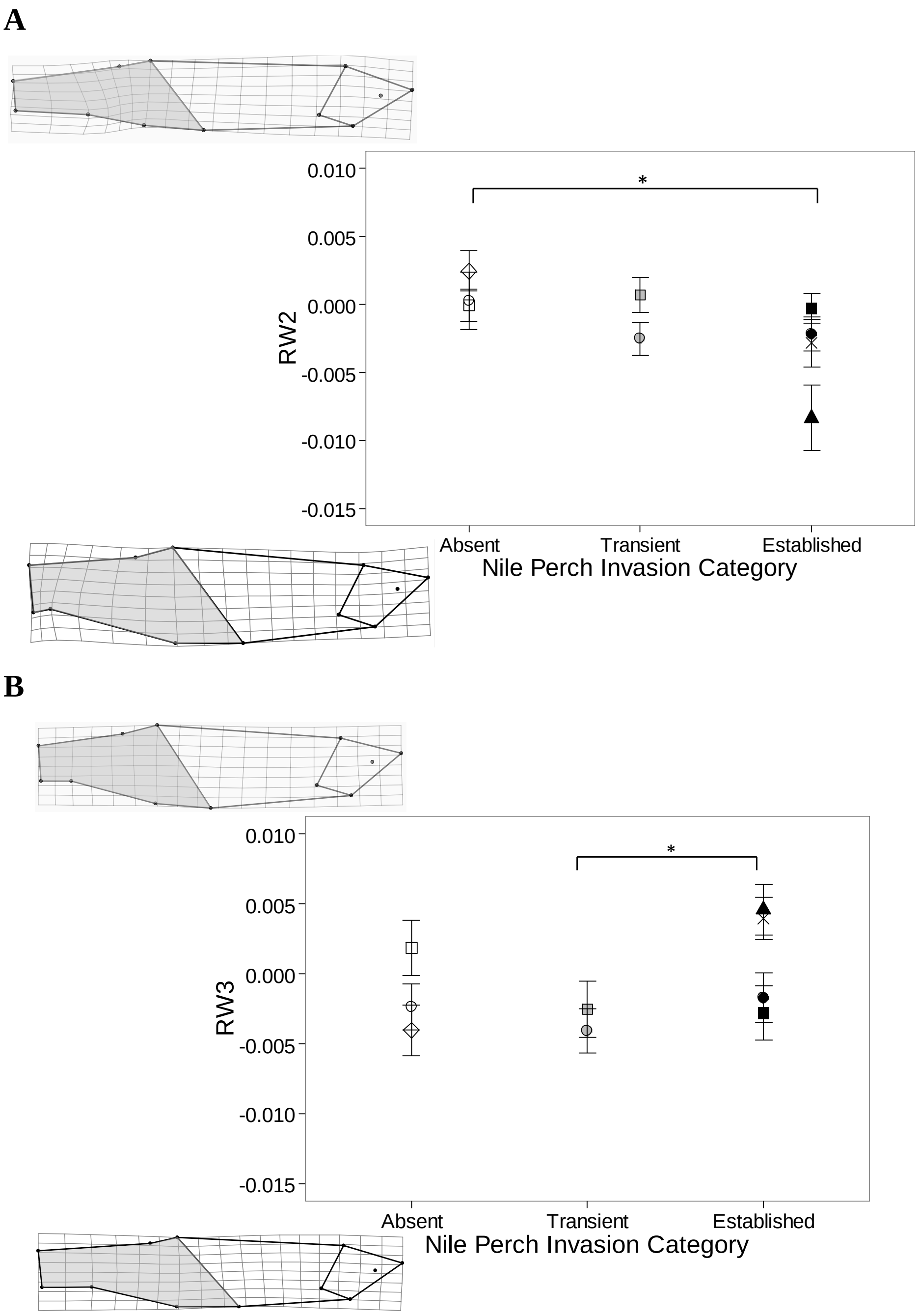


Fig. J.2

Mean scores (±1 SE) for each lake along RW2 (A) and RW3 (B), which accounted for 17.7% and 11.3% of the total variation in the data respectively. The thin-plate spline deformations show the extremes of the observed range for each RW. The lakes shown are: Kayanja (white circle), Omuno (white square), Gigati (white diamond), Nawampasa (grey circle), Bisina (grey square), Meito (black triangle), Nabugabo (black cross), Kyoga (black circle), and Victoria (black square). Significant differences among invasion categories, based on post-hoc Tukey tests, are indicated by *.

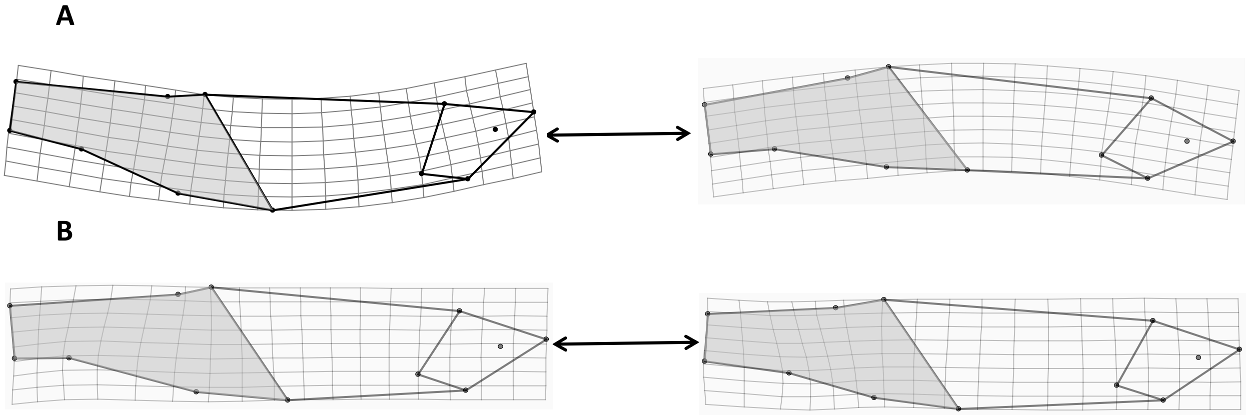


Fig. J.3 Thin-plate spline deformations illustrating the negative (left) and positive (right) extremes of relative warps 1 (A), and 2 (B), which cumulatively explain 52.0% of total variation in body shape in *R. argentea* in Lake Victoria through time.

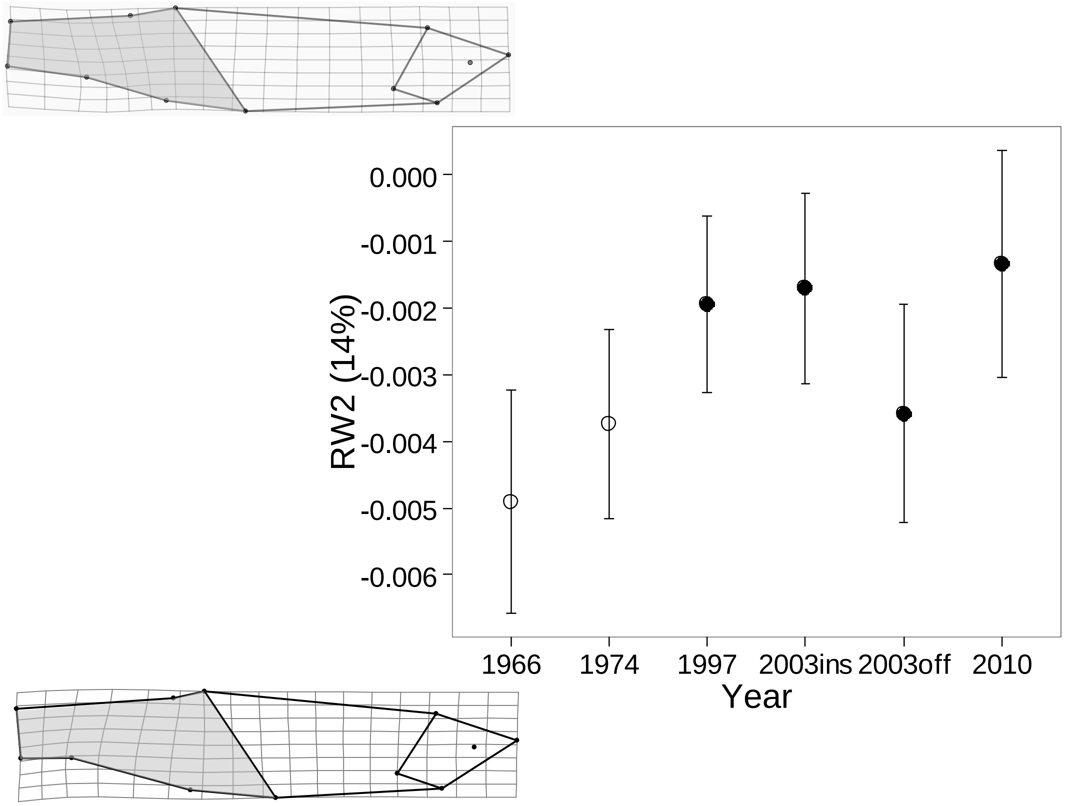


Fig. J.4 Mean scores (+- 1 SE) for each year along RW2. The thin-plate spline deformations illustrate the extremes of this axis. The colours indicate years before (white) versus after (black) the Nile perch boom in Lake Victoria.

Appendix K: Measurement of univariate traits (Chapter 3)

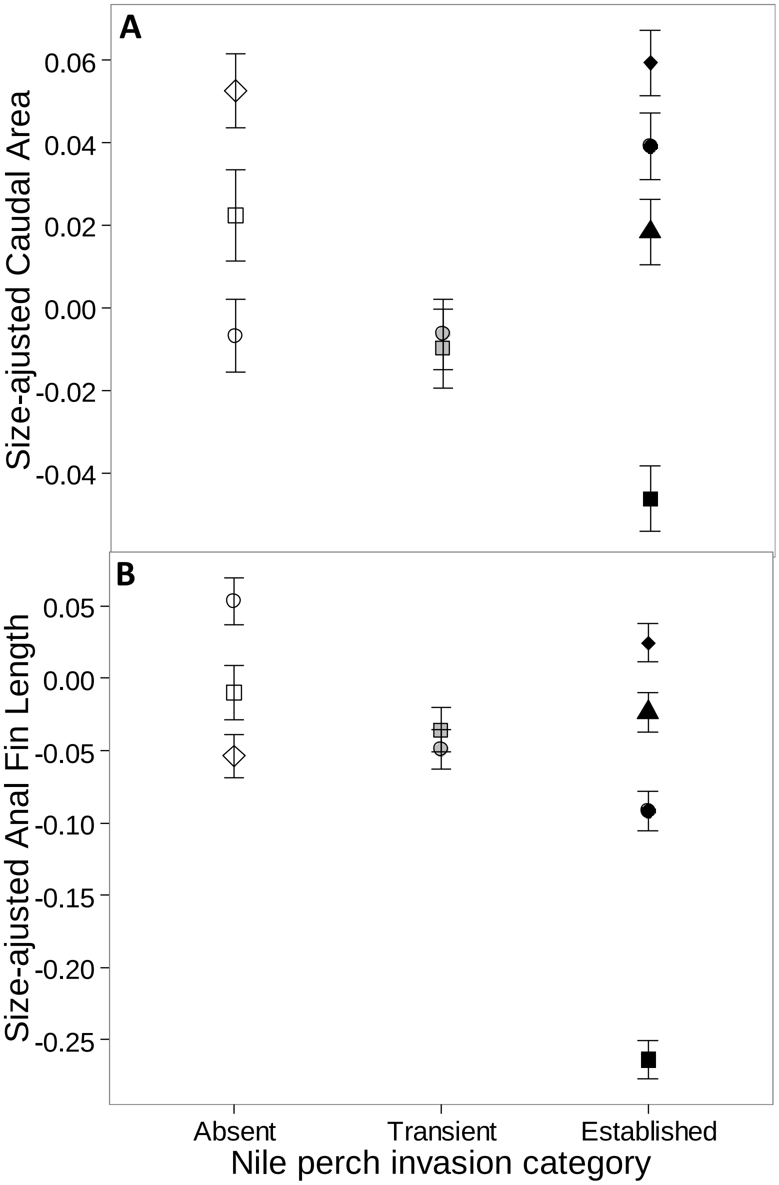


Fig. K1 Variation in size-standardized mid-body/caudal area (A) and anal fin length (B) of *R. argentea* across lakes (Chapter 3). Data are size-standardized population means (±1 SE), i.e., adjusted means from ANCOVAs with either log(total lateral body area) or log(standard length) as covariates. For an explanation of the symbols, please see the caption for Fig. 3.3.

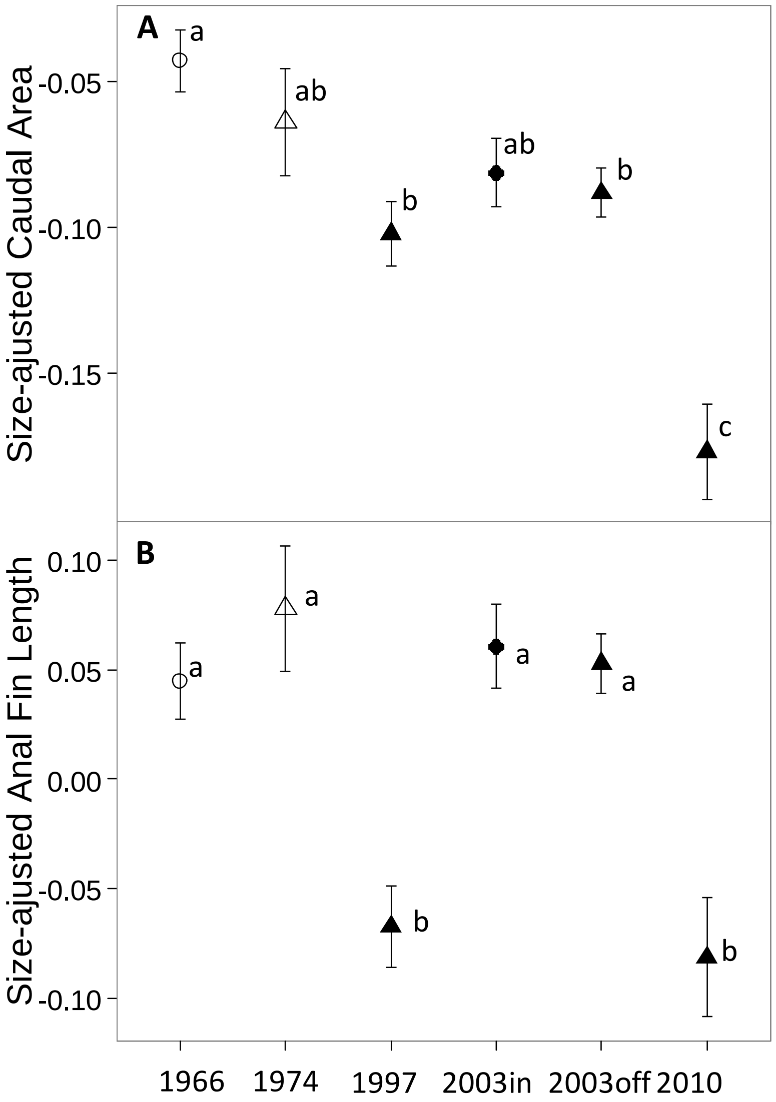
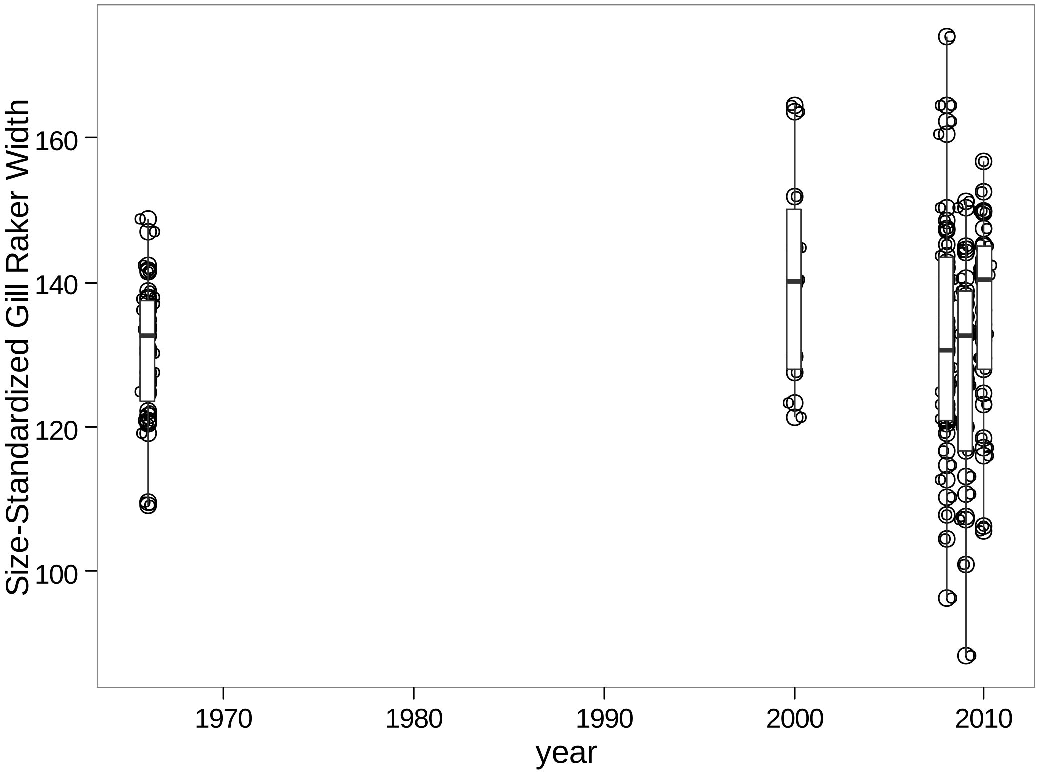


Fig. K2 Variation in size-standardized mid-body/caudal area (A) and anal fin length (B) of *R. argentea* across time in Lake Victoria. Data are size-standardized population means (±1 SE), i.e., adjusted means from ANCOVAs with either log(total lateral body area) or log(standard length) as covariates. The colours indicate years before (white) versus after (black) the Nile perch boom in Lake Victoria. Letters indicate homogenous subsets, based on post-hoc Tukey's tests.

Appendix L Relative importance of the different prey types in the diet of *R. argentea* in Lake Victoria in 1966 and 2011 (Chapter 4).

Data shown are the proportion of points (p_j) and frequency of occurrence (FO) for each prey type. For each time period, the most important prey type is emphasized in bold. See text for further details on the calculation of p_j and FO.

	Copepoda	Cladocera	Rotifera	Emerging insects	Chironomid larvae	*Chaoborus* pupae	*Chaoborus* larvae	Plant matter	Other
Proportion of points									
Victoria 1966	**0.87**	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Victoria 2011	0.00	**0.34**	0.00	0.22	0.00	0.07	**0.34**	0.00	0.03
Frequency of occurrence									
Victoria 1966	**1.00**	0.70	0.00	0.00	0.00	0.00	0.00	0.00	0.43
Victoria 2011	0.11	**0.57**	0.00	0.36	0.00	0.21	0.50	0.00	0.29



Appendix M Box and whiskers plot of size-standardized gill raker width of *R.argentea* from Lake Victoria, through time (Chapter 4).

Raw data are plotted (open circles), along with boxplots showing the median (black line), the interquartile range (box), and full range (whiskers) of the data. Variance in gill raker width was significantly different across years (Barlett's K^2= 11.31, p = 0.02).

Appendix N Relative importance of the different prey types in the diet of *R. argentea* across six months in Lake Nabugabo, Uganda (Chapter 4).

Data shown are the proportion of points (p_j) and frequency of occurrence for each prey type. For each sample, the most important prey type is emphasized in bold

Month	Copepoda	Cladocera	Rotifera	Emerging insects	Chironomid larvae	*Chaoborus* pupae	*Chaoborus* larvae	Other
Proportion of points								
January	0.09	**0.77**	0.00	0.00	0.04	0.00	0.05	0.03
February	0.05	**0.81**	0.00	0.01	0.11	0.01	0.00	0.01
May	0.22	**0.27**	0.00	0.12	0.19	0.01	0.03	0.16
October	0.16	**0.43**	0.00	0.03	0.08	0.03	0.16	0.11
November	0.16	0.31	0.00	0.05	**0.31**	0.01	0.06	0.11
December	0.07	**0.39**	0.00	0.09	0.28	0.02	0.10	0.05
Frequency of occurrence								
January	0.95	**1.00**	0.00	0.45	0.25	0.05	0.40	0.85
February	0.95	**1.00**	0.00	0.25	0.40	0.10	0.00	0.85
May	**1.00**	**1.00**	0.35	0.85	0.55	0.15	0.45	0.95
October	0.85	0.81	0.00	0.31	0.23	0.15	0.23	**0.88**
November	0.86	**0.93**	0.00	0.29	0.64	0.21	0.57	**0.93**
December	0.89	**1.00**	0.00	0.32	0.79	0.16	0.32	0.95

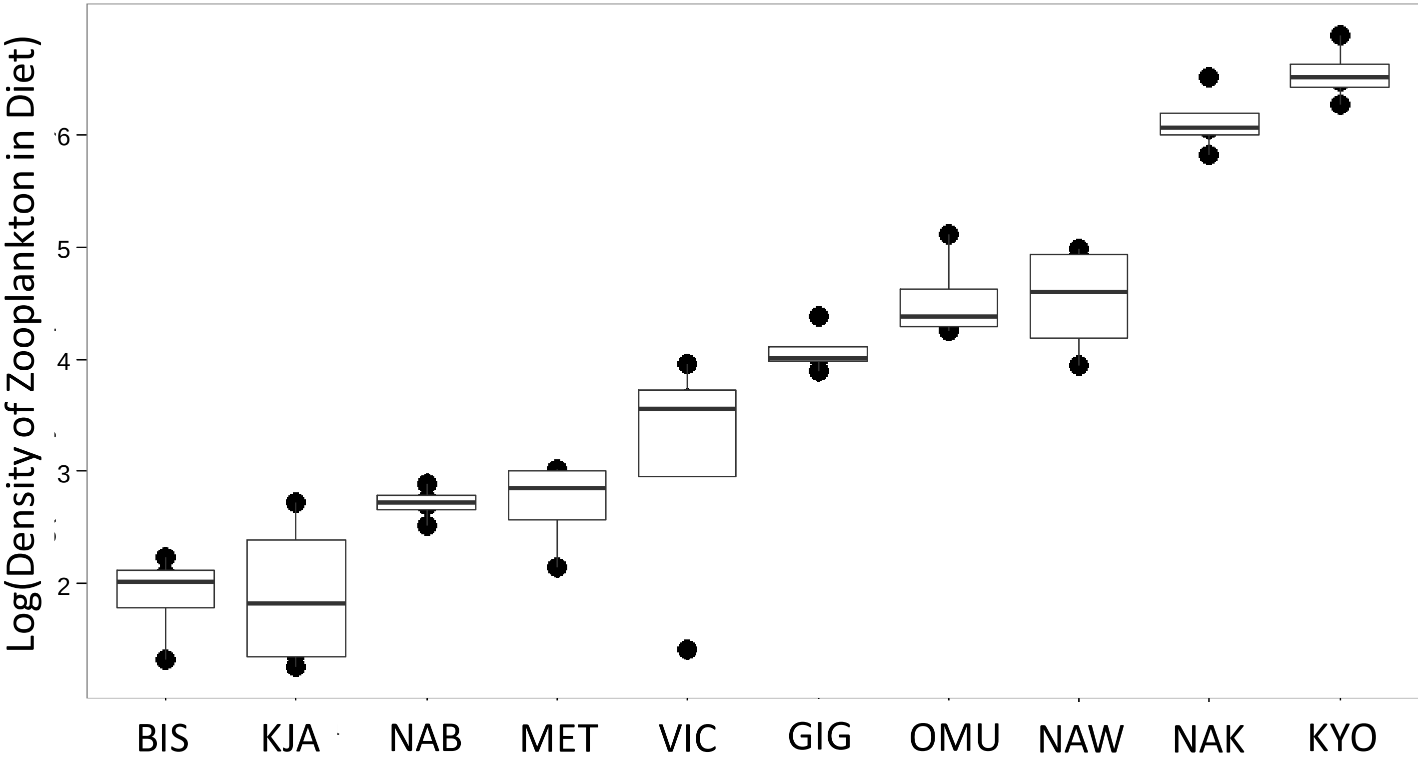
Appendix O Percent similarity (Schoener's index) between pairs of months for the diet of *R. argentea* in Lake Nabugabo (Chapter 4).

	January	February	May	October	November	December
January	1.00					
February	0.89	1.00				
May	0.47	0.46	1.00			
October	0.66	0.59	0.69	1.00		
November	0.54	0.50	0.82	0.75	1.00	
December	0.60	0.58	0.71	0.74	0.83	1.00

Appendix P Relative importance of the different prey types in the diet of *R. argentea* across eight Ugandan lakes (Chapter 4).

Data shown are the proportion of points (p_j) and frequency of occurrence for each prey type. For each lake, the most important prey type is emphasized in bold. See text for further details on the calculation of p_j.

		Copepoda	Cladocera	Rotifera	Emerging insects	Chironomid larvae	*Chaoborus* pupae	*Chaoborus* larvae	Plant matter	Other
Nile Perch	**Proportion of points**									
Absent	Kayanja	0.00	0.00	0.00	**0.94**	0.02	0.00	0.04	0.00	0.00
Absent	Omuno	**0.22**	0.00	0.01	0.46	0.01	0.08	**0.22**	0.00	0.01
Absent	Gigati	0.20	**0.78**	0.01	0.00	0.00	0.00	0.00	0.00	0.02
Transient	Nawampasa	0.09	0.02	0.34	0.03	0.00	0.00	0.01	**0.41**	0.11
Transient	Bisina	0.04	0.02	0.01	**0.92**	0.00	0.00	0.00	0.00	0.00
Established	Nabugabo	0.22	**0.27**	0.00	0.12	0.19	0.01	0.03	0.00	0.16
Established	Kyoga	0.07	**0.83**	0.00	0.00	0.00	0.05	0.00	0.00	0.05
Established	Victoria	0.00	**0.37**	0.00	0.23	0.00	0.06	0.33	0.00	0.01
	Frequency of occurrence									
Absent	Kayanja	0.12	0.12	0.15	**1.00**	0.04	0.00	0.04	0.00	0.00
Absent	Omuno	0.79	0.07	0.31	**0.86**	0.10	0.48	0.55	0.00	0.24
Absent	Gigati	**1.00**	**1.00**	0.37	0.10	0.00	0.00	0.00	0.00	0.70
Transient	Nawampasa	0.90	0.31	0.93	0.07	0.00	0.00	0.03	0.79	**1.00**
Transient	Bisina	0.20	0.20	0.30	**0.97**	0.00	0.03	0.00	0.00	0.00
Established	Nabugabo	**1.00**	**1.00**	0.35	0.85	0.55	0.15	0.45	0.00	0.95
Established	Kyoga	0.86	**1.00**	0.00	0.00	0.00	0.21	0.00	0.00	0.75
Established	Victoria	0.11	**0.57**	0.00	0.36	0.00	0.18	0.54	0.00	0.32



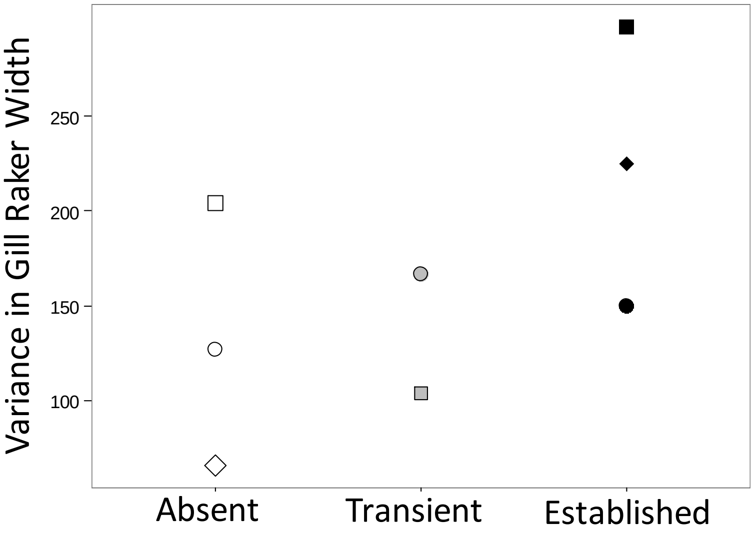
Appendix Q Total density of zooplankton (Cladocera, Copepoda, Rotifera, and copepod nauplii) across 10 Ugandan lakes (Chapter 4).

Densities were calculated as the number of individual zooplankton in subsamples from vertical hauls with a 80 μm plankton net, standardized by the volume of the sub-sample, and the mean depth of the lake. Data shown are medians (dark line), inter-quartile ranges (box), and total ranges (whiskers).

Appendix R Trophic position and indices of isotopic niche breadth for *R. argentea* from 10 Ugandan lakes (Chapter 4).

Trophic position was calculated relative to separate isotopic baselines derived for each lake (Post 2002, see text for equation and details). Note that we could not calculate the trophic position of *R. argentea* in Lake Kayanja because we could not find any snails in this lake. The width of isotopic niche was estimating using the variance in δ^{15}N and δ^{13}C (Bearhop et al. 2004), and the convex hull area – the minimum convex polygon drawn between individuals in isotopic space (Layman et al. 2007). Units for the convex hull area are arbitrary and should only be used to compare among populations in this data-set. For Lake Victoria, all statistics were calculated with and without the one major outlier (the latter is given in parentheses).

Lake	Var(δ^{15}N)	Var(δ^{13}C)	Convex hull area	Trophic position
NP absent:				
Kayanja	0.77	0.78	1.40	
Omuno	0.03	0.14	0.17	3.52
Gigati	0.11	0.09	0.20	2.24
NP transient:				
Nawampasa	0.43	0.93	0.55	3.89
Bisina	0.04	0.36	0.30	3.05
NP established:				
Meito	0.09	0.27	0.33	3.70
Nabugabo	0.05	0.12	0.15	4.34
Nakuwa	0.04	0.17	0.10	3.23
Kyoga	0.11	0.96	0.55	3.84
Victoria	2.08 (0.10)	1.59 (0.93)	3.05 (0.55)	3.41 (3.54)



Appendix S Variance in size-standardized gill raker width of *R. argentea* across eight Ugandan lakes (Chapter 4).

Variances were significantly different across invasion categories (Barlett's K^2 = 15.40, p = 0.0004). For an explanation of symbols see caption of

.