

**INVASION STATUS AND POTENTIAL IMPACTS OF BLUEGILL
Lepomis macrochirus Rafinesque, 1819 IN THE KARIEGA RIVER,
EASTERN CAPE, SOUTH AFRICA**

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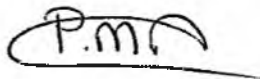
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A handwritten signature in black ink, consisting of the letters 'P.M.' followed by a stylized flourish.

ABSTRACT

The impact of alien invasive species is one of the greatest threats to biodiversity globally. All of the major drainages of South Africa are invaded by non-native fishes, yet little information is available on their impact. This thesis focusses on providing a better understanding of the potential impacts of bluegill *Lepomis macrochirus* Rafinesque, 1819, a species introduced into South Africa from the USA in 1938. The study assesses the distribution, establishment success and feeding ecology of *L. macrochirus* in an invaded South African River system in order to better understand and document its potential impacts. Specifically; this thesis (1) assesses the distribution and relative abundance of *L. macrochirus* in the Kariega System of the Eastern Cape, (2) determines the diet of the species in one of the major impoundments of the system, and (3) uses an experimental comparative functional response approach to assess whether this species has heightened predatory capabilities when compared with fishes with which it co-occurs.

Ninety-six sites in the Kariega River system were sampled from the headwaters down to the estuary. Small native fish species (*Enteromius anoplus* and *Enteromius pallidus*) occurred mostly in the upper reaches, while in the middle and lower reaches, the centrarchid alien largemouth bass *Micropterus salmoides* and bluegill *L. macrochirus* dominated. There was overlap between the centrarchids and introduced banded tilapia *Tilapia sparrmanii* and southern mouthbrooder *Pseudocrenilabrus philander*, but never with small-bodied native species. The stomach contents of *L. macrochirus* were examined during winter and summer and prey were identified to family level. Crustaceans and insects were an important component in their diet, but in summer fish eggs were common. Comparisons of bluegill diet with published literature indicated that there was potential for competition with largemouth bass, banded tilapia and southern mouthbrooder. Feeding experiments were conducted to compare the functional responses of these four species using a common prey item. Banded tilapia had significantly lower attack rates than the other species with no significant difference observed in other species. Bluegill has a similar impact to that of banded tilapia and southern mouthbrooder, but lower than that of largemouth bass. Results of the present study highlight that *L. macrochirus* introduced into dams will likely result in both upstream and downstream invasion of river systems. It is likely that this species does not, however, have as much of a predatory impact as *M. salmoides* in that its predatory capacity is relatively reduced and more comparable to South African native cichlids. These results are discussed within the context of invasion success/failure in other regions of southern Africa

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CHAPTER 1: General introduction

Introduction

Freshwater ecosystems are important to humans who use them for drinking, domestic purposes, industrial processes, irrigation, power generation and waste disposal (Frederick et al. 1996). They are also home to a host of aquatic organisms (Curtis et al. 1998; Dudgeon et al. 2006), many of which provide ecosystem services. Freshwater aquatic biodiversity is important for economic productivity (fisheries), production of medicines, tourism (Dudgeon et al. 2006), animal farming, irrigation, aquaculture, wastewater dilution and municipal supply (Bordalo et al. 2001). However, increasing demand for resources due to the increase in human population may result in the destruction of ecosystems and the extinction of aquatic species (Gleick 1998). The major threats to freshwater biodiversity include; habitat destruction, water pollution, over-exploitation, flow modification and non-native species invasion (Dudgeon et al. 2006).

South Africa is a semi-arid country (Department of Water and Sanitation 2000). As a result, large natural bodies of standing freshwater do not naturally occur as prominent features of the South African landscape (Department of Water and Sanitation 2000). The growth of the human population over the last 100 years has resulted in an increased demand for access to potable water (van Zyl et al. 2007), and standing water is considered more readily available for human needs (Frederick et al. 1996). As a result, flowing water has been impounded to create standing bodies of water that act as more reliable sources of water for human needs (Johnson et al. 2008). In South Africa, for example, there are more than 3000 dams that cover an area of more than 3000 km² (Department of Water and Sanitation 2000) with 452 major dams (Wang et al. 2015). The construction of dams impacts freshwater ecosystems by changing the water quality, water flow and habitat (Baxter 1977), and by becoming sites for the introduction of non-native species (Johnson et al. 2008). On the other hand impoundments can also alter the water quality as still waters allow for the increased settlement of sediments (Baxter 1977).

Freshwater invasion is frequently facilitated by the construction of impoundments as they alter the ecosystem, and invasions are often expedited by disturbances (Johnson et al. 2008). For example, in the Laurentian Great Lakes region, impoundments had more non-native fishes than the natural lakes (Johnson et al. 2008). While such comparisons are largely lacking in the South African context, a comparable example is that of *Micropterus salmoides* introductions. In the Swartkops system in the Eastern Cape Province of South Africa, for example, *M. salmoides*

was introduced into a dam and this species is now wide spread throughout much of the system (Ellender et al. 2011). The role of impoundments in facilitating invasion is, therefore, a worthwhile consideration in freshwater invasion ecology.

Biological invasion is the movement of species beyond the limits of their geographic range and is determined by the species' ability to survive, reproduce and spread to new areas away from the point of introduction (Blackburn et al. 2011). In freshwater environments, invasions have been identified as being particularly problematic and the rate of non-native fish introduction has increased worldwide over the last decade (Ellender and Weyl 2014; Gozlan et al. 2010). Unfortunately, South Africa is considered an invasion hotspot (Leprieur et al. 2008).

According to the literature reviewed by Ellender and Weyl (2014), a total of 55 freshwater fishes have been introduced into South Africa. Forty-four (79 %) managed to establish while 11 (21 %) failed to do so (Ellender and Weyl 2014). Twenty-eight of these non-native fishes were introduced extra-liminally while 27 fishes were alien species (Ellender and Weyl 2014). The reasons for these introductions included angling, conservation purposes, aquaculture, transfer through river connections and the pet trade (Ellender and Weyl 2014). While impacts associated with these introductions are not well researched in South Africa, negative impacts associated with non-native fishes are considered to have contributed to biodiversity loss through loss of genetic integrity by hybridisation with native fishes, alteration of communities through direct predation and competition, and the loss of fitness resulting from the introduction of diseases and parasites (Ellender and Weyl 2014).

Impacts linked to predation appear particularly severe and have been shown to affect habitat selection, abundance and distribution of native fresh-water fish species (e.g., Ellender et al. 2011; Mayekiso and Hecht 1988; Shelton et al. 2008; Van der Walt et al. 2016; Woodford et al. 2005) and composition of invertebrate communities (Weyl et al. 2010). In the Swartkops River in the Eastern Cape, for example, the presence of *M. salmoides* resulted in the exclusion of native fishes from the sites that they occupied (Ellender et al. 2011), while in the Rondegat River in the Western Cape, there was an absence of native fishes in sites where *M. dolomieu* were present (Woodford et al. 2005). Van der Walt et al. (2016) demonstrated that in the Olifants Dooring catchment, only large-sized cyprinids co-occur with *M. punctulatus*, *M. dolomieu* and *M. salmoides* while small-sized fish were absent from the sites invaded by these predators. Competition between native fishes and non-native fishes for food was documented by Mayekiso and Hecht (1988) who showed that *M. salmoides* had a dietary overlap with the

native *Sandelia bainsii*. Similarly, Zengeya and Marshal (2007), who worked on the competition between *Oreochromis niloticus* and *O. macrochir*, demonstrated that these non-native fishes may have a diet overlap with the native fishes. Non-native fishes also change the abundance of aquatic invertebrates in the river systems. This was demonstrated for *M. salmoides* in the Wit River, Sundays River catchment, Eastern Cape, South Africa (Weyl et al. 2010) and for *Clarias gariepinus* in the Great Fish River by Kadye and Booth (2012). *Micropterus* spp. have been identified as a particularly problematic group as they have invaded 81 % of the Cape Floristic Region river basin (Van Der Walt et al. 2016). As a result of the problems associated with invasive species, South Africa has developed a legislation (National Environmental Management: Biodiversity Act Invasive Species Regulations) intended to manage alien fishes in order to mitigate and limit their impacts (Weyl et al. 2015).

Control and monitoring plans for removal of non-native fishes must be developed (Ellender and Weyl 2014). Ellender and Weyl (2014) demonstrated that, for many of the alien and extralimital fishes that have been introduced into South Africa, insufficient information is available for their effective management. Information requirements include data on the distribution, invasion status and impacts as South Africa does not have enough information on non-native fish invasions (Ellender and Weyl 2014). Furthermore, according to the literature, many freshwater systems of the region have not been recently surveyed and some have yet to be surveyed in their entirety. As such, there are gaps in knowledge on the distribution and spread of invasive fish species. The present study aims to address the knowledge gap in both of these areas whereby a previously unassessed system is surveyed, placing particular emphasis on an invasive species that is, to date, largely unstudied in South Africa. Therefore, the current study focuses on providing a better understanding of the distribution and impacts of bluegill, *Lepomis macrochirus* Rafinesque, 1819 in the Kariega River, South Africa.

Review of *L. macrochirus* biology, ecology and impacts

This review section focuses directly on the information required for the application of a formal risk assessment tool such as the FISK (fish invasiveness scoring kit) (Copp et al. 2009). It is therefore not exhaustive, but is intended to provide information on the taxonomy, distribution and biology of the species that can be used for assessing the probability of establishment and impact in South Africa.

Taxonomy, originating environment and climate constraints

Lepomis macrochirus belongs to the family Centrarchidae, which is comprised of 34 species (Cooke and Philipp 2009). In the family Centrarchidae, the genus *Lepomis* is the most species diverse, comprising 13 taxa (Cooke and Philipp 2009). *Lepomis macrochirus* is native to the St. Lawrence-Great Lakes system, and the Mississippi River basin, from New York, Quebec, and Minnesota south to the Gulf of Mexico (Cooke and Philipp 2009). The species prefers lentic water habitats (Yamamoto et al. 2013), such as swamps, lakes, ponds, canals, reservoirs, pools and slow-flowing sections of the river (De Moor and Bruton 1988). In the presence of predators, juveniles inhabit vegetated areas along the margin, while adult fish occur in the open water (Werner et al. 1983). This species has a temperature tolerance from just above freezing to 36 °C (Beitinger 1974; Beitinger and Bennet 2000), but have a preference for water temperatures between 21 – 31 °C (Beitinger 1974).

Morphology

Lepomis macrochirus have a small oblique mouth and compressed body with a long and pointed pectoral fin (Skelton 2001). They have steep heads and a large black projection on the upper corner of the gill (Skelton 2001); the posterior of the dorsal fin has a black spot and the opercula flap is black at the margins (Cooke and Philipp 2009). It has a single complete lateral line with 40 – 44 scales (Figure 1.1) (Skelton 2001).



Figure 1.1: Juvenile *Lepomis macrochirus* from the Kariega River, Eastern Cape, South Africa.

Reproductive strategy

In their native range, reproduction begins from late spring and ends in late summer (Cargnelli and Gross 1996; Santucci Jr and Wahl 2003) as relatively high temperatures ($> 20^{\circ}\text{C}$) are needed for spawning to occur (Yamamoto et al. 2013). Normal reproduction starts at the age of two to four years (Belk and Hales 1993). During mating season, males have a bluish sheen over the body, intense cheek, a bright orange to rust-red breast and the mouth has a blue line which extends posteriorly (Avila 1976). The body size of the reproductive females is bigger than that of the non-reproductive females (Belk 1998). Reproductive behaviour includes the creation of a nest by a male (Gross and Charnov 1980; Gross and MacMillan 1981). Nests are usually constructed in colonies in order to avoid predation and parental males provide care to the developing fry (Avila 1976; Cogliati et al. 2010; Gross and MacMillan 1981). Females prefer to mate with males situated in the centre of the colony (Cogliati et al. 2010). When a female that is swollen with eggs appears, the male fish encircles it and chases it to the nests for mating (Avila 1976). During spawning, females release their eggs into the nests and males deposit

their sperm on the eggs (Avila 1976). The reproductive success of *L. macrochirus* is determined by the individual sizes of the parental males. Fish with stunted growth typically have a shorter reproductive season due to the delay of spawning to later in the season than larger, non-stunted fishes that reproduce earlier and therefore have a longer reproductive season and produce more fry (Aday et al. 2002). Ripe males have the ability to mate more than once during the mating period (Bartlett et al. 2010). Fry produced at the beginning of the mating season have a higher chance of successful survival during the winter period than the fry produced towards the end of the mating season (Cargnelli and Gross 1996).

There is evidence of the existence of satellite and sneaking behaviours. Satellite and sneaker males start to reproduce at younger ages and smaller sizes than the competitive males (Drake et al. 1997; Gross and Charnov 1980). Satellite and sneaker males mimic females and enter the parental male nest with the aim of releasing the sperm cells during spawning (Leach and Montgomerie 2000). They consequently do not provide parental care to the developing fry (Gross and Charnov 1980).

Invasive tendencies

Lepomis macrochirus has been introduced into at least 22 countries: USA, Madagascar, Malawi, Morocco, Iran, South Africa, Congo, Zimbabwe, Japan, South Korea, Canada, Cuba, Mauritius, El Salvador, Mexico, Panama, Puerto Rico, Virgin Islands, Philippines, Swaziland, Hawaii and Venezuela (Picker and Griffiths 2011). Its current distribution range includes Africa, Asia, North and South America (Figure 1.2).

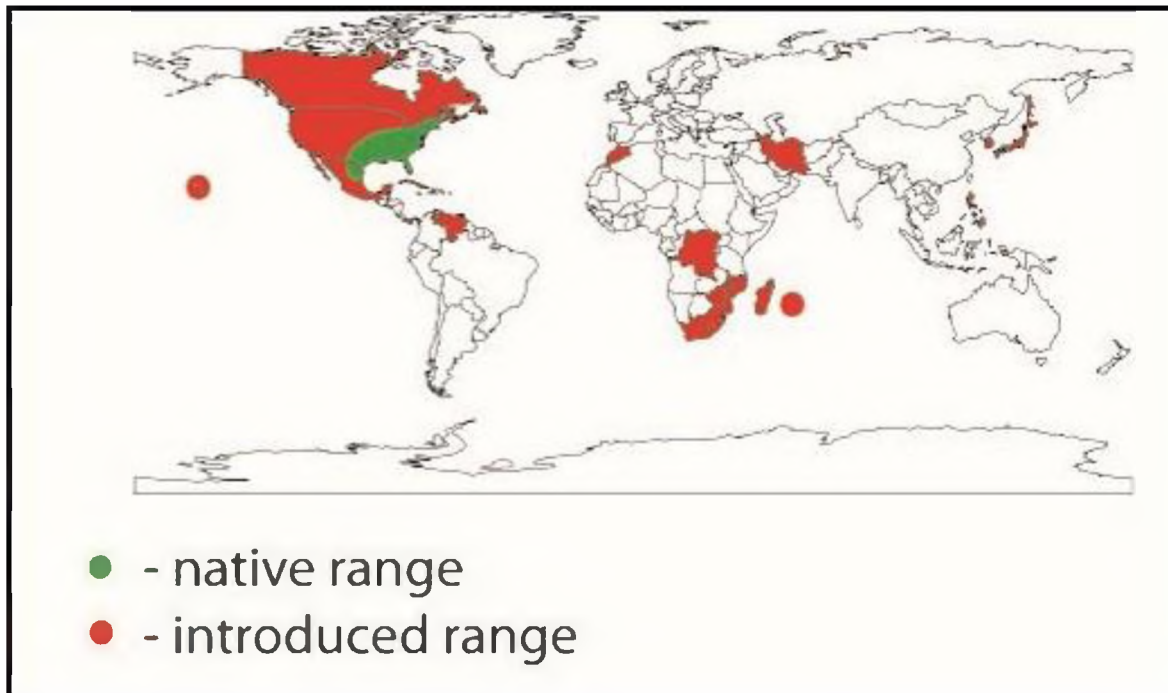


Figure 1.2: World distribution of *Lepomis macrochirus* (Picker and Griffiths 2011).

History of propagation and introductions into South Africa

Lepomis macrochirus (native to North America) was introduced into South Africa in 1938 from Maryland (USA) for angling purposes and as a forage fish for bass (De Moor and Bruton 1988). It was initially introduced into KwaZulu-Natal and to Jonkershoek Hatchery in Stellenbosch in the Western Cape (De Moor and Bruton 1988). Subsequent spread was facilitated by intentional stocking (Ellender and Weyl 2014), and current occurrence records in the South African Institute for Aquatic Biodiversity National Fish Collection (SAIAB 2016) show it to be widespread in the Western Cape, Eastern Cape, KwaZulu-Natal, and some have also been recorded in Mpumalanga and Limpopo Province (Figure 1.3).

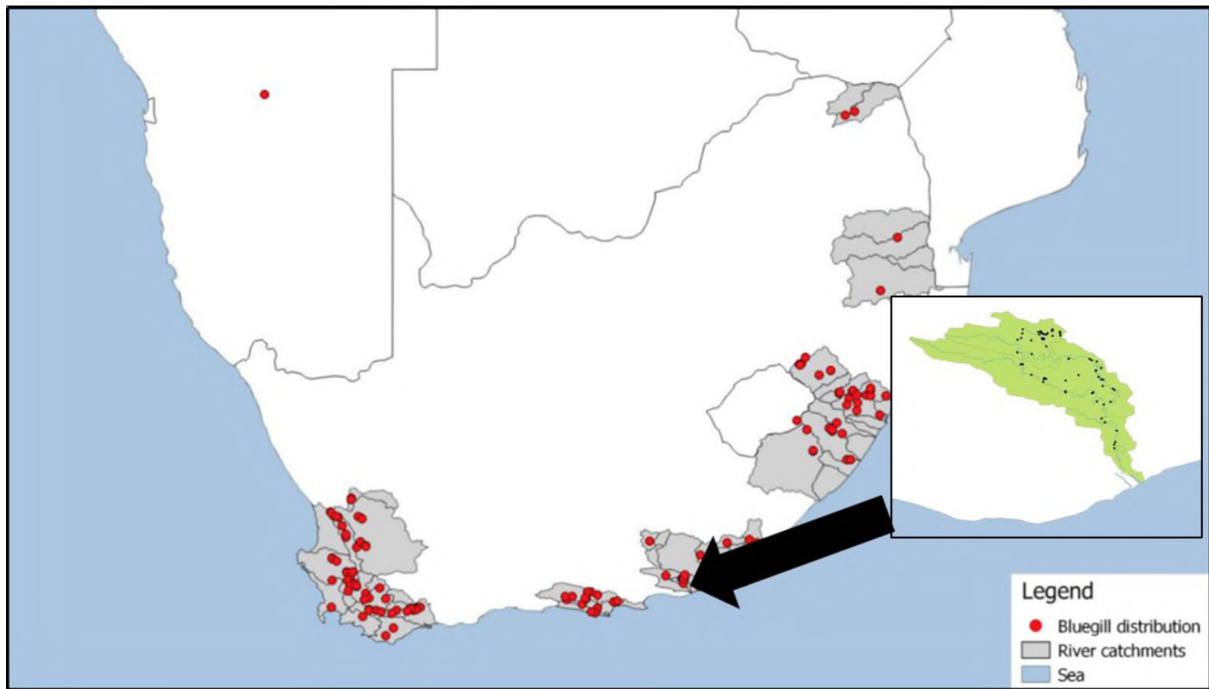


Figure 1.3: The distribution range of *Lepomis macrochirus* in South Africa (Source: SAIAB fish collection records).

Diet

Lepomis macrochirus is omnivorous (Hossain et al. 2013) and therefore does not rely on specific prey species as their diet changes (Kaemingk and Willis 2012), depending on prey availability (Olson et al. 2003; Werner and Hall 1974) and fish size (Mittelbach 1981; Olson et al. 2003). As adult fish, *L. macrochirus* feed in open water while juvenile fish feed in vegetated areas to avoid predation (Dewey 1997; Mittelbach 1981, 1983). Because juveniles inhabit vegetated areas, they have a more limited foraging habitat than the larger fish which inhabit the open water (Mittelbach 1981). Larger-sized *L. macrochirus* (> 100 mm) prefer to consume larger prey as compared with the smaller (< 100 mm) *L. macrochirus* (Dewey et al. 1997). The reported diet of adult *L. macrochirus* includes chironomids, chydorids, gastropods and amphipods, while that of juveniles consists of chironomids, Daphnia, cladocerans and chydorids (Dewey et al. 1997). They may also incorporate plant material (Moffett and Hunt 1945), algae (Kitchell and Windell 1970), isopods (Keast 1978), molluscs (Olson et al. 2003), fish eggs (Gross and MacMillan 1981; Neff 2003) and fish in their diet (Hossain et al. 2013). A study by Werschkul and Christensen (1977) showed that this fish can also feed on the eggs and tadpoles of *Rana sphenoccephala* and *Rana areolate* in the United States. Cannibalism has been observed during the spawning season (Neff 2003).

Age and growth

Belk and Hales (1993) study in South Carolina showed that bluegill can live up to nine years and grows rapidly between ages zero to four years, but the rate decreases from ages four to nine years (Belk and Hales 1993). The growth rate may be affected by the presence of predatory species; for example, Belk and Hales (1993) have shown that the presence of *M. salmoides* affects habitat selection and slow down the growth rate of *L. macrochirus*. Growth rate is, however, also affected by resource availability (Aday et al. 2006).

Reported ecosystem impacts

Due to their ability to reproduce at a younger age (Gross and Charnov 1980) and wide temperature tolerance (Beitinger 1974; Beitinger and Bennet 2000), *L. macrochirus* may overpopulate the waters which they inhabit and outcompete native fishes for food causing reduced growth and weight gain in native fishes (Marchetti 1999). The aggressive behaviour of *L. macrochirus* drive native fishes from open water to shallow vegetated areas (Marchetti 1999). Furthermore, the non-native *L. macrochirus* can change the community structure of freshwater ecosystems (Maezono et al. 2005) by changing the abundance and distribution of fish, crustaceans and other aquatic invertebrates (Maezono and Miyashita 2003), thereby disturbing the food web (Gilinsky 1984). Their predatory impacts have been shown to vary with the season as the fish feed more in summer than in winter (Gilinsky 1984).

Potential as a vector for other introduced organisms

Lepomis macrochirus may also spread disease among our native fishes (Huchzermeyer and Van de Waal 2012). *Lepomis macrochirus* are host to different diseases and parasites, such as *Uvulifer ambloplitis* (trematodes) (Lemly and Esch 1984), *Neascus* sp. (diplostomatidae) (Wilson et al. 1996) and *Posthodiplostomum minimum* (strigeoid trematode) (Wilson et al. 1996). They also spread bacteria e.g. *Aeromonas hydrophila* (Reynolds 1977).

Aims and objectives of this thesis

Lepomis macrochirus is categorised as alien and invasive in South Africa (Weyl et al. 2015), and was categorised as fully invasive by Ellender and Weyl (2014). According to the amended Alien Invasive Species Regulations, *L. macrochirus* is categorised as 1b (species that cannot be owned, moved or stocked) because of its wide distribution in South Africa. As a result, there is a need to better understand the impacts and establishment success of this species. While the impacts and establishment of this fish are well understood in its native range, there is no published information on the impacts of this species in South Africa. For this reason, the aim of this MSc research is to contribute towards the knowledge of the impacts and the establishment success of this species in an invaded South African river system in order to better understand and document its potential impacts.

Specifically this thesis will: (1) assess the distribution and relative abundance of fish species in the Kariega System, Eastern Cape (Chapter 2); (2) determine the diet of this species in an impoundment on the study system (Chapter 3) and (3) use functional response experiments (e.g. Alexander et al. 2014; Dick et al. 2014) to assess whether this species has heightened predatory capabilities when compared with fishes with which it co-occurs (Chapter 4).

CHAPTER 2: Freshwater fish species distribution in the Kariega River, Eastern Cape with special reference to bluegill *Lepomis macrochirus*

Introduction

Fifty-five species of freshwater fishes have been introduced outside their native ranges into South African aquatic ecosystems for the purpose of aquaculture, biological control, angling, ornamental fish trade, and for conservation (Ellender and Weyl 2014). Some of these non-native fishes have become invasive, and documented impacts on native fishes include competition, predation, disease transmission and hybridisation (Ellender and Weyl 2014). As a result, invasive fishes contribute to biodiversity change (Cambray 2003). For example *Micropterus salmoides* disrupts the continuity of fish diversity across the landscape of the river systems by eliminating native fishes from the sites that they have invaded (Ellender et al. 2011; van der Walt et al. 2016). Assessing the invasion status is therefore important (Britton et al. 2011), particularly because South Africa, through its NEM:BA (National Environmental Management: Biodiversity Act) Aquatic Invasive Species (AIS) regulations (Government of South Africa 2014) is attempting to halt the spread of non-native species into new areas. As the scale of such areas ranges from un-invaded tributaries to entire catchments, understanding the distribution and establishment success of fishes within specific river systems is important.

The establishment success of individual species also depends on environment and propagule pressure (Woodford et al. 2013). The construction of impoundments results in altered water flow and transforms lotic ecosystems into lentic ecosystems (Johnsons et al. 2008). This disturbance and alteration of the ecosystem often facilitates invasions by freshwater fishes (Johnson et al. 2008) because it provides a suitable habitat for colonisation by fishes with suitable biological traits (Woodford et al. 2013). Dam construction alters fish diversity along the landscape of freshwater ecosystems (Vitule et al. 2012). For example, in Wisconsin, United States (Johnsons et al. 2008) and in the Guadiana Basin in the southern Iberian Peninsula (Clavero and Hermoso 2011) impoundments contain more non-native fish than the natural river. As a result, assessments of invasion status should include both riverine and impounded habitats. In addition, alien fishes may use impoundments as stepping stones, presenting the risk of spreading alien fishes across a landscape (Johnsons et al. 2008) with concomitant impacts on the composition and abundances of native fishes in river systems (Taylor et al. 2001).

The ability of organisms to establish depends on abiotic and biotic factors of the environment (Moyle and Light 1996), so it is important that objective criteria are applied in determining invasion status. Unified frameworks such as the Blackburn et al. (2011) framework, are becoming increasingly popular as tools for categorising invasive species on the basis of establishment. In the Blackburn et al. (2011) framework, a fully invasive species is defined as species dispersing, occurring and reproducing in many sites across a greater range of habitats and extent. Typical criteria include the occurrence of individuals at multiple sites along a river, and the presence of both juveniles and of adults capable of spawning in the population. For example, Jones et al. (2013) used the population structure (presence of juveniles and adults) to evaluate the establishment of *Pterygioplichthys disjunctivus* in the Nseleni River, South Africa. Similarly, Muller et al. (2015) undertook surveys to determine the establishment of *Pseudocrenilabrus philander* in the Baakens River in the Eastern Cape and classified it as invasive, based on its demography and numerical dominance in all the sampled sites in the river. However, not all introduced fishes establish, an example is the introduction of *Pangasius sanitwongsei* in Breede River, South Africa, where the presence of only a single specimen was considered as evidence that, while able to survive in the wild, there was a failure to establish (Mäkinen et al. 2013).

Despite the availability of distribution data (see Chapter one) there are no South African data on the establishment of bluegill *Lepomis macrochirus* Rafinesque, 1819. *Lepomis macrochirus* were introduced to the Nqutshini hatchery in KwaZulu-Natal and to Jonkershoek in Stellenbosch, Western Cape in 1938 for angling and as a forage fish for *Micropterus salmoides* (De Moor and Bruton 1988). Subsequent spread is badly documented, but current occurrence records indicate that the species is widespread along the coastal drainages of the Western Cape, Eastern Cape and KwaZulu-Natal (see Chapter one). As a result of this wide distribution, *L. macrochirus* was categorised as fully invasive by Ellender and Weyl (2014). Little is known about its distribution patterns and establishment success in different habitats on a river basin scale.

The Kariega River is situated in the south west of Grahamstown, Eastern Cape, South Africa. It has one major tributary, the Assegai River, which joins the Kariega River at 33°30'39.65"S; 26°36'40.47"E (Figure 2.1). There are historical occurrence records for 20 fish species from the system (Table 2.3). As is the case with many Eastern Cape Rivers, the native fish fauna is depauperate and consists of only three primary freshwater fishes: chubbyhead barb *Enteromius anoplus* (Weber, 1897), Goldie barb *Enteromius pallidus* (Smith, 1841), Mozambique tilapia

Oreochromis mossambicus (Peters, 1852), and moggel *Labeo umbratus* (A. Smith, 1841). Other native species are the river goby *Glossogobius callidus* (Smith, 1937) which has a distribution ranging from freshwater to marine environments and the catadromous longfin eel *Anguilla mossambica* Peters, 1852. Species of estuarine origin that are occasionally sampled from the lower reaches of the river are the freshwater mullet *Myxus capensis* (Valenciennes, 1836), dusky sleeper *Eleotris fusca* (Schneider, 1801), groovy mullet *Liza dumerili* (Steindachner, 1870), cape moony *Monodactylus falciformis* Lacepède, 1801, flathead mullet *Mugil cephalus* Linnaeus, 1758 and estuarine round-herring *Gilchristella aestuaria* (Gilchrist, 1913). There are also six non-native species listed in the system. These are banded tilapia *Tilapia sparrmanii* A. Smith, 1840, largemouth bass *Micropterus salmoides* (Lacepède, 1802), bluegill *Lepomis machochirus* Rafinesque, 1819, common carp *Cyprinus carpio* Linnaeus, 1758, smallmouth yellowfish *Labeobarbus aeneus* (Burchell, 1822) and cape kurper *Sandelia capensis* (Cuvier, 1831).

Prior to the current study, there was however, no published information on the distribution and establishment of any of the species across the river scape. The aim of this chapter was, therefore, to undertake a comprehensive survey of the Kariega River system to assess fish species composition and distributions of native and non-native fishes across the river system with a particular emphasis on *L. macrochirus*. It was predicted that non-native fishes are widely distributed and will constitute more species composition in the kariega River system than the native fishes.

Materials and methods

The Kariega River is situated to the south west of Grahamstown in the Eastern Cape of South Africa. The Kariega River has a catchment area of 688 km² (Grange 1992) and flows from its headwaters approximately 24 km west of Grahamstown. Its estuary is approximately 18 km long with an upper channel of about 40 – 60 m and lower reaches that widen up to 100 m (Grange 1992). The river mouth is permanently open to the sea (Grange 1992) and enters the sea at Kenton on sea at 33° 40' 46.6" S and 26° 40' 57.9" E. The upper reaches of the estuary are within the boundaries of the Kariega Park Private Nature Reserve. It has one major tributary, the Assegai River, and has four major dams (height >15 m): Settlers, Howisons Poort, two dams on Mosslands Farm and five smaller, off channel dams (Figure 2.1). Settlers and

Howison's Poort Dams supply water to Grahamstown. The two Mosslands Farm dams are used for irrigation. There are eight dams on the Assegai River which are used mainly for agriculture (irrigation and drinking water for livestock) (Pers. obs).

During the current study, a total of 96 sites from the headwaters down to the estuary were sampled from 15 January to 15 December 2015. Habitats sampled included 13 dams, 80 riverine pools and 3 riffles. Sampling sites were selected based on site accessibility, which was determined by road access and landowner permission (Figure 2.1). At each site, geographic coordinates were taken using a Garmin eTrex Vista C Waterproof Hiking Global Positioning System (Garmin). Temperature, pH and conductivity were recorded using a Hanna HI98129 Combo pH (HANNA Instruments Inc). At riverine sites, stream width and site length measurements were taken to determine the area sampled and mean depth at each site was determined using a graduated pole along multiple transects.

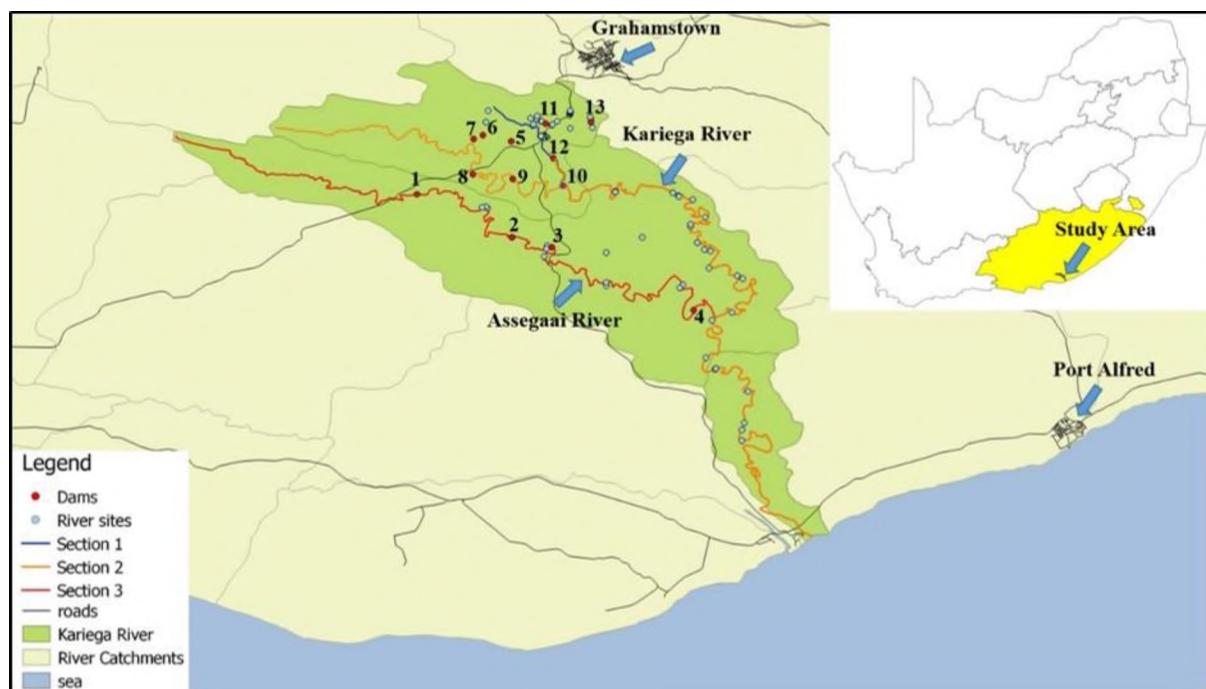


Figure 2.1: South African map showing sampled sites in the Kariega River, 1 = Yarrow Dam, 2 = Lindale Farm Dam, 3 = small farm dam, 4 = small farm dam, 5 = small farm dam, 6 = small farm dam, 7 = small farm dam, 8 = Mosslands Farm Dam, 9 = Mosslands Farm Dam, 10 = Settlers Dam, 11 = Craig Doone Farm Dam, 12 = Howison's Poort Dam, 13 = Rivendell Farm Dam.

Gear used for sampling included electrofishing, seine nets, multi-meshed gill nets and fyke nets. Sampling was supplemented by hook and line fishing. The selection of the sampling technique was determined by the depth and size of the stream/impoundment. Electrofishing was conducted at 56 sites in the upper section of the river (Appendix 1). It was done in shallow, clear sections of the river, which included pools and riffles, using a Samus© 725G backpack electrofisher (SAMUS special electronics). The settings were of 0.3 ms duration and 90 Hz frequency. Two passes were conducted at each site; one in a downstream direction and the other in an upstream direction. Seine net pulls were conducted in all the sampled pools and dams (40 sites), with the number of seine pulls varying from one to three, depending on the size of the dam or pool. Seine nets (5 m long and 1.5 m deep with a 5 mm mesh size) were pulled on clear edges of the pool or dam, away from debris such as fallen trees. Gill netting was conducted in the seven larger dams. Gill nets (45 m long and 3 m deep) of differing mesh sizes (30, 45, 50, 60, 65, 75, 85, 95, 100, 144 and 150 mm) were set in deep pools or dams parallel to the shore. Nets were set overnight (between 16h00 to 18h00) and retrieved the following day (between 07h00 to 10h00). A total of 46 gill nets were set in seven dams. Double-ended fyke nets of 8 m guiding net with first ring diameter of 55 cm and mesh size 10 mm were set on the shallow surface parallel to the shore. A total of 256 fyke nets were set in dams (n = 13) and pools (n = 40). All fyke nets had otter guards to prevent unwanted by-catch. Fyke nets were set overnight between 16h00 to 18h00 and retrieved the following day between 07h00 to 10h00. All fish caught during the surveys were kept in separate buckets containing water until they could be identified to species level (Skelton 2001), measured to the nearest millimetre for Fork Length (FL) or total length (TL) for eels, and released.

Analysis

For analysis, species occurrence during the current survey was compared with SAIAB database records and the river was divided into three sections based on a-priori species occurrences. The three regions were: (1) upper Kariega River upstream of Howison's Poort Dam; (2) the region from Howison's Poort Dam downstream to the estuary and (3) the Assegai River (Figure 2.1). Multidimensional scaling plots MDS (Clarke and Gorley 2001) were used to compare fish composition for dams and rivers in each region using untransformed species presence/absence data. Graphs were plotted in two dimensions using the Bray-Curtis similarity index. For non-native species, establishment was determined using the criterion that the population has to

contain both juvenile and individuals capable of spawning. To do this, length structure was compared with published length-at-maturity values for each species (Table 2.1). In addition, the Blackburn et al. (2011) framework was used to categorise each non-native species in the context of the Kariega River system (e.g., F = failed; C1 = Individuals surviving in the wild in location where introduced but no evidence of reproduction; E = Fully invasive species, with individuals dispersing, surviving and reproducing at multiple sites across a greater or lesser spectrum of habitats).

Table 2.1: Length at 50 % maturity for non-native fish sampled from the Kariega River, Eastern Cape.

Species	Sex	Length at maturity (mm)	Reference
<i>Lepomis macrochirus</i>	Male	146 mm FL	Dredge 2016
	Female	147 mm FL	
<i>Micropterus salmoides</i>	Both male and female	259 mm FL	Taylor 2012
<i>Pseudocrenilabrus philander</i>	Male	55 mm TL	Muller et al. 2015
	Female	62 mm TL	
<i>Tilapia sparrmanii</i>	Male and Female	149 mm	Silva 2005

Results

Physico-chemical properties

The chemical characteristics of dams and river sites for the Kariega River are shown in Table 2.2. There were no significant differences between dams and riverine sites with respect to pH ($p = 0.26$), temperature ($p = 0.39$) nor conductivity ($p = 0.23$).

Table 2.2: Chemical characteristics of 13 Dams and 80 river sites sampled in the Kariega River from January to December 2015.

Parameter	Mean	Min	Max	SD	N
Dams					
pH	7.6	7.1	7.9	0.2	13
Temperature (°C)	21.5	12.5	26.2	4.0	13
Conductivity (µs)	664	156	2143	565	13
River					
pH	7.8	5.9	8.7	0.61	38
Temperature (°C)	21.1	20.4	28.6	2.99	80
Conductivity (µs)	940	110	2628	741	80

Fish species composition

An assessment of historical and current survey data resulted in a list of 20 fish species that had been previously recorded from the Kariega River system (Table 2.3). Thirteen species were identified during the current survey (Table 2.3). Four of the five previously recorded native freshwater fish species were sampled in the current survey. Of notable absence was *Oreochromis mossambicus*, *Cyprinus carpio*, *Labeobarbus aeneus*, *Sandelia capensis*, *Eleotris fusca*, *Liza dumerili* and *Mugil cephalus*, which had previously been sampled from the Kariega River system. Estuarine species *Myxus capensis*, *Monodactylus falciformis* and *Gilchristella aestuaria* were also sampled during the survey in the Kariega River system.

Table 2.3: Fish recorded in SAIAB data base with the dates of first record, and the fish recorded during the 2015 survey of the Kariega River using different gears. Presence of fish in dams and riverine sites is also shown. n = number of fish sampled, Ns = not sampled, E = electrofisher, FN = fyke net, SN = seine net and GN = gill net. Invasion status defined according to Blackburn et al. (2011).

Taxa	Date of first record	Gear	% Composition		TL (mm)		n	Status
			Dam	River	Min	Max		
Native Freshwater species								
Chubbyhead barb <i>Enteromius anoplus</i>	1988	E	0	22.9	97	15	92	N
Goldie barb <i>Enteromius pallidus</i>	1925	FN	0	1.2	1	52	52	N
River goby <i>Glossogobius callidus</i>	1980	FN, SN	0	4.8	45	16	80	N
Moggel <i>Labeo umbratus</i>	1978	GN, FN	7.7	4.8	645	25	476	N
Mozambique tilapia <i>Oreochromis mossambicus</i>	1983	NS	0	0				N
Catadromous species								
Longfin eel <i>Anguilla mossambica</i>	1957	FN	7.7	3.6	5	55	840	N
Non-native freshwater species								
Banded tilapia <i>Tilapia sparrmanii</i>	1962	GN, FN, SN	38.5	33.7	653	10	249	E
Largemouth bass <i>Micropterus salmoides</i>	1962	GN, FN, SN	61.5	4.8	122	10	540	E
Bluegill <i>Lepomis machochirus</i>	1960	GN, FN, SN	69.2	8.4	332	8	413	E
Southern mouthbrooder <i>Pseudocrenilabrus philander</i>	This study	E, SN, FN	23.1	9.6	100	6	100	E
Common carp <i>Cyprinus carpio</i>	1988	NS	0	0				F
Smallmouth yellowfish <i>Labeobarbus aeneus</i>	1972	NS	0	0				F
Largescale yellowfish <i>Labeobarbus marequensis</i>	This study	GN	7.7	0	1	413	413	C1
Cape kurper <i>Sandelia capensis</i>	1980	NS	0	0				F
Estuarine species								
Freshwater mullet <i>Myxus capensis</i>	1975	FN, SN	0	1.2	2	110	118	N
Dusky sleeper <i>Eleotris fusca</i>	1963	NS	0	0				N
Grooved mullet <i>Liza dumerili</i>	1999	NS	0	0				N
Cape moony <i>Monodactylus falciformis</i>	1982	FN, SN	0	2.4	3	81	91	N
Flathead mullet <i>Mugil cephalus</i>	1983	NS	0	0				N
Estuarine round-herring <i>Gilchristella aestuaria</i>	1978	FN, SN	0	1.2	3	41	55	N

Species composition and distribution

The distribution of fishes down the Kariega River system is illustrated in Figure 2.2 and the results of the MDS are presented in Figure 2.3. Multi-dimensional scaling (MDS) showed that fish communities in dams and rivers in the three catchment areas were more similar to each other than they were among catchment areas. All the fish present in dams were also present in riverine sites below the dams, except for *Labeobarbus marequensis* which was only sampled from one dam. Section Two dams and river sites were also similar to each other in fish composition. All the fish in Section Two were present in both river sites and dams, but the estuarine fishes were only sampled in river pools closer to the estuary resulting in the larger difference in fish species composition between dams and riverine sites for Section Three (Figure 2.3). Three small freshwater species were only sampled from riverine sites closer to the estuary; these were *G. callidus*, *E. pallidus* and *E. anoplus*. The stress value is 0.08, showing that these results are reliable.

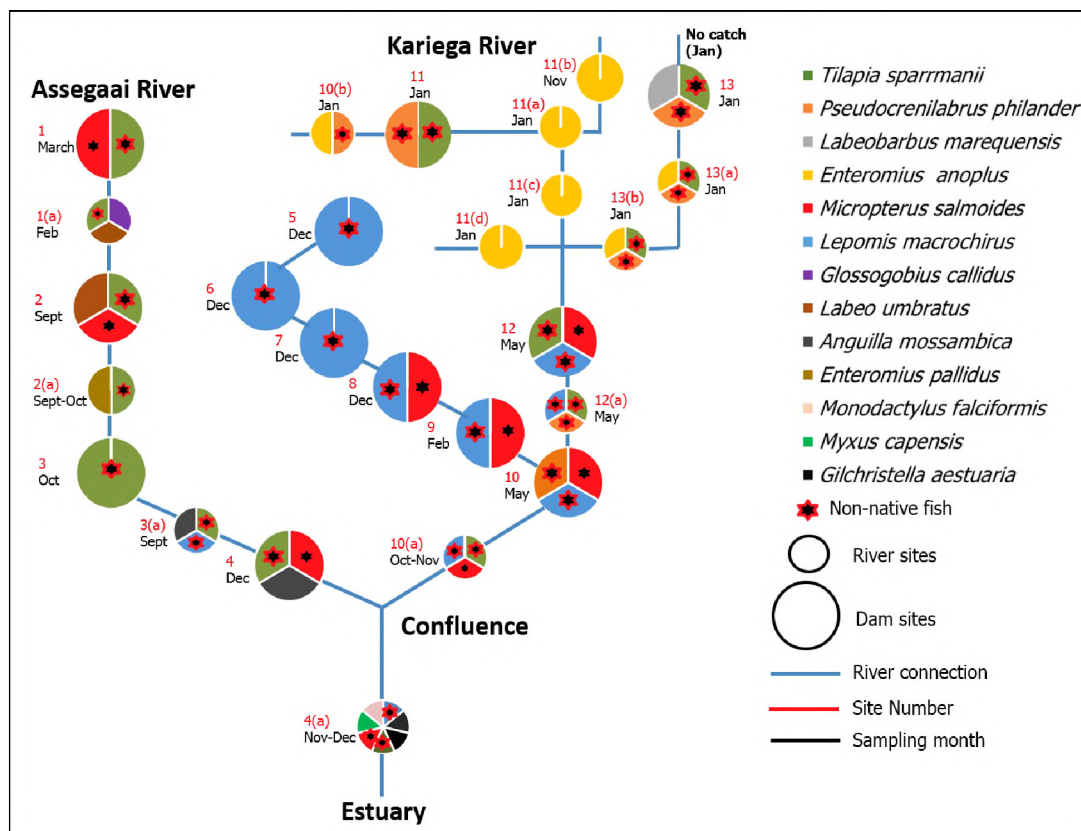


Figure 2.2: Distribution of fish species sampled in the Kariega River system from January to December 2015. Section One includes all river sites between Dam 11 and above Dam 12; Section Two is represented by the river sites and dams between Dam Five, Twelve and the river pools above Dams Four; and Section Three is represented by the dams and river pools between Dam One and Three.

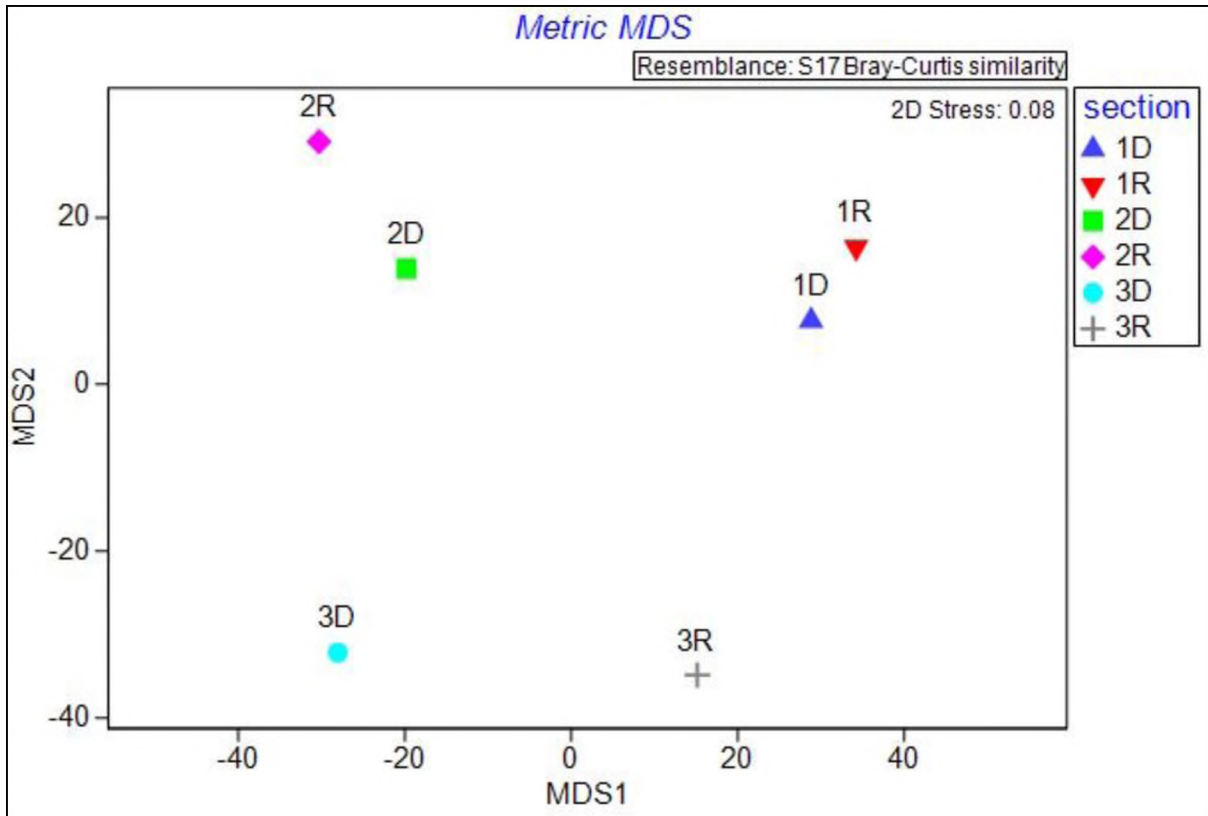


Figure 2.3: MDS plot for similarity in fish distribution for dams and rivers in the three sections of the Kariega River system. Numbers represent different sections, R and D represent riverine and dams sites respectively.

Invasion Status

With regard to the invasion status of the five non-native species, one species, *L. marequensis* was represented by a single 413 mm FL specimen while the other four were sampled from multiple sites in large numbers. Although the *L. marequensis* specimen was spawning capable (Fouché 2009), there was no evidence of reproduction, nor that both sexes were present in the population, and therefore it was evaluated as stage C1: “Individuals surviving in the wild (i.e. outside of captivity or cultivation) in location where introduced, no reproduction” (Blackburn et al. 2011). *Lepomis macrochirus*, *M. salmoides*, *T. sparmanii* and *P. philander* were present at multiple sites (Figure 2.2). On assessment of length against known maturity, *P. philander* juveniles and adults (10 -100 mm FL) were sampled in dam sites; but juveniles were absent from river sites (50 – 100 mm FL) (Figure 2.4). Both juvenile and adult *T. sparrmanii* were present in dams (10 - 150 mm FL) and river (20 – 130 mm FL) sites (Figure 2.4). The population structure of *L. macrochirus* had juveniles and adults for both dams and the river sites with fork length of 10 – 250 and 20 – 190 mm for dams and river sites, respectively

(Figure 2.4). The size of *M. salmoides* ranged from 50 – 550 mm for dam sites, and 50 – 450 mm for riverine sites (Figure 2.4). The presence of both juvenile and adult fish in the population (Figure 2.4) was considered evidence for their establishment in the system. When viewed in conjunction with their presence at multiple sites in the system, they were categorised as Stage E: “Fully invasive species, with individuals dispersing, surviving and reproducing at multiple sites across a greater or lesser spectrum of habitats and extent of occurrence” (Blackburn et al. 2011) (Table 2.3). There was however, no evidence of occurrence of *Labeobarbus aeneus*, *Cyprinus carpio* and *Sandelia capensis*. These are now considered failed introductions.

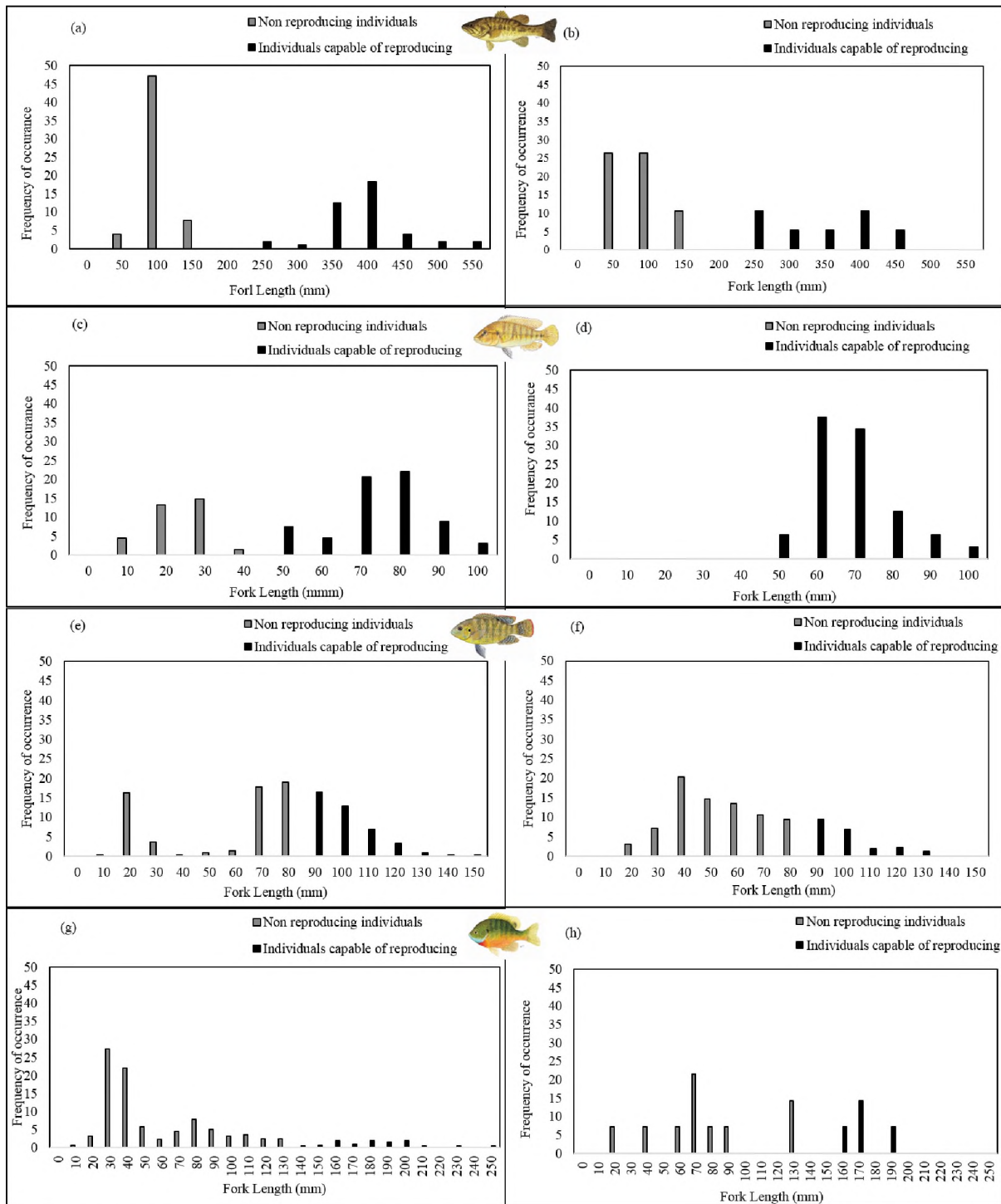


Figure 2.4: Fork length (mm) frequency histogram of *Micropterus salmoides* (a) dams, (b) river sites; *Pseudocrenilabrus philander* (c) dams, (d) river sites; *Tilapia sparrmanii* (e) dams, (f) river sites and *Lepomis macrochirus* (g) dams, (h) river sites sampled from the Kariega River system, Eastern Cape in 2015. *Tilapia zillii* is used as an example for *T. sparrmanii* as there is no published information on reproduction for this species. Black bars represent individuals capable of reproducing; grey bars represent non-reproducing individuals.

Discussion

The results of this survey demonstrated that native fishes in the Kariega River occur mostly in the upper reaches of the river system, above the invasion front of non-native fishes (Figure 2.2). The upper reaches of the Kariega River are invaded by *P. philander* and *T. sparrmanii* which co-occur with native fish and are dominated by *E. anoplus* in both river sites and dams (Figure 2.2). As a result, fish diversity in dams and river sites was similar in the headwaters of the Kariega system (Figure 2.3). In the middle and lower reaches (Section Two) *M. salmoides* mostly co-occurred with *L. macrochirus*, and sometimes with *T. sparrmanii*, *P. philander* and *A. mossambica* both in the river and in dams. In this section, however, *E. anoplus* and *E. pallidus* were absent. In Section Three, river and dam sites contained *T. sparrmanii* while *M. salmoides* was sampled only from dams. The results of this study, therefore imply that non-native *P. philander* and *T. sparrmanii* seem not to impact the small native fishes such as *E. anoplus*, *E. pallidus* and *G. callidus*. This might be because the two species are omnivorous (Muller et al. 2015; Polling et al. 1995) and might not exert significant predation impact on native fishes.

As *L. macrochirus* and *M. salmoides* generally co-occur, it is difficult to separate the potential impact of each. In addition, while the predatory impact of *M. salmoides* is well established in South Africa, that of *L. macrochirus* is not. *Micropterus salmoides* prey on native fish (Wasserman et al. 2011; Weyl and Lewis 2006) resulting in impacts such as habitat shifts of native fishes (Shelton et al. 2008) or complete extirpations from invaded sites (Ellender et al. 2011; Kimberg et al. 2014). Although *L. macrochirus* impacts have not been evaluated in South Africa, this species has been shown to impact on native fish communities elsewhere (see Chapter one) (Marchetti 1999).

The results of this study also support the hypothesis that invasion is a downstream process. An indication that dams prevent upstream migration is provided by the absence of catadromous *A. mossambica*, *M. capensis*, *M. cephalus* and *M. falciformis* upstream of the first major instream barrier, a weir between sites 3 (a) and 4 (a) (Figure 2.2). This is similar to observations by Wassermann et al. (2011) and Woodford et al. (2013) who demonstrated that dams were major barriers to upstream fish migration in the Sundays River system. Similarly, Agostinho et al. (2008) found that dam construction inhibited upstream fish migrations but promoted fish introduction and establishment downstream in the Paraná River basins in Brazil. The findings of this study support the data from South Africa and Brazil as it is evident that non-native fishes

display a distribution which includes river sites below the dams in which they were first introduced but are absent above them. Non-native fishes were present in all 13 dams sampled. Native fishes were present in only five dams. This is similar to the observations of Johnson et al. (2008) in Laurentian Great Lakes where impoundments had more non-native fishes than the natural lakes. Both native and non-native fishes were present in river sites below the dams, further supporting the downstream-invasion hypothesis.

Not all introduced species managed to establish populations in the Kariega River and its dams. *Cyprinus carpio*, *L. aeneus* and *S. capensis* failed to establish after their introduction into the system. This is surprising as all three species have invasive tendencies. *Cyprinus carpio*, for example, present in Lake Gariep, South Africa have a rapid population growth because of their early maturity (2 – 3 years), high natality and rapid growth rate (Winker et al. 2011). *Labeobarbus aeneus* is known to be established in one of the nearby rivers (Great Fish River) due to the presence of reproductive individuals and its occurrence in multiple sites (Weyl et al. 2009). *Sandelia capensis* has established in Twee River catchment of the Cape Floristic Region (Marr et al. 2012). The reasons for establishment failure are unclear, but may be due to low propagule pressure as high propagule pressure promotes the establishment of species in river systems (Woodford et al. 2013).

Microperus salmoides, *L. macrochirus*, *P. philander* and *T. sparrmani* are, however, fully established. In southern Africa, *Microperus salmoides* is not only established in South Africa, it is also established in Zimbabwe and is known to occur in Namibia, Botswana and Mozambique (Hargrove et al. 2015). *Microperus salmoides* and *L. macrochirus* prefer high temperature environments (Beitinger 1974; Díaz et al. 2007), which is why they prefer to inhabit dams. *Tilapia sparrmanii* and *P. philander* were also well established within the system. *Tilapia sparrmanii* was present in all the river sections and *P. philander* was present in Section One and Two, most likely as a result of spread from direct introductions into farm dams in Section One (Figure 2.2). Their further distribution into Section Two was potentially prevented by predation or competition with *L. macrochirus* and *M. salmoides* and their inability to penetrate upstream over dam walls into Section Two (Figure 2.2).

In conclusion, the Kariega River is heavily invaded by non-native fishes which appear to restrict native fishes to relatively few uninvaded habitats. The introduced Centrarchids, *M. salmoides* and *L. macrochirus* appear to exert a higher impact on the native fishes than the extra-limittally introduced *P. philander* and *T. sparrmanii*.

Assessing the potential drivers of these observed trends requires information on the potential for competition between introduced species and an assessment of their relative impacts. This thesis will address this by discussing the potential for competition by comparing the diet of the four species and then using a comparative functional response experiment to compare their potential impacts (Dick et al. 2014). While the diet of *M. salmoides*, *P. philander* and *T. sparrmanii* is fairly well established (Le Roux 1956; Muller et al. 2015; Polling et al. 1995; Wasserman et al. 2011; Weyl and Lewis 2006; Winemiller and Kelso-Winemiller 2003) there is no published information on the diet of *L. macrochirus* in South Africa. In the next chapter (Chapter Three), I therefore undertake a detailed assessment of the diet of this species.

CHAPTER 3: Diet of *Lepomis macrochirus* in Howison's Poort Dam.

Introduction

The bluegill, *Lepomis macrochirus* Rafinesque 1819 (Centrarchidae), is native to the St. Lawrence-Great lakes system, and the Mississippi River system from New York and Quebec to Minnesota to the Gulf of Mexico (Cooke and Philipp 2009). Globally, the species has been widely introduced and now exists in 22 countries across Africa, Asia, South America, North America and Oceania (ASAP, Aquarium Science Association of the Philippines 1996; Bell-Cross and Minshull 1988; Burgess and Franz 1989; Coad 1995; Kim et al. 2005; Martin and Patus 1984; Masuda et al. 1984; Welcomme 1988; Yamamoto 1992). Bluegill were first introduced into South Africa in 1938 from Maryland (USA) into the Jonkershoek Hatchery in Stellenbosch, Jonkershoek Valley, southeast of Stellenbosch, on land occupied by Cape Nature and Natal Hatcheries (De Moor and Bruton 1988). The purpose of this introduction was for angling and as a fodder fish for bass. Bluegill established in the range into which they were introduced in South Africa. They were also successful in certain environments, and are now considered invasive in Eastern Cape, Western Cape and KwaZulu-Natal rivers (Skelton 2001; Source: SAIAB fish collection records). A few samples have been collected in Mpumalanga and Limpopo (Source: SAIAB fish collection records) and they are also known to occur in the Free State (Skelton 2001). Bluegill is listed as widespread and established in South Africa (Ellender and Weyl 2014) and in the National Environmental Management: Biodiversity Act (10/2004): Alien and Invasive Species List, 2014 it is categorised as 1b. In Africa it is established in Swaziland, Zimbabwe (Welcomme 1988) and Mauritius (FAO 1997). In California, bluegill outcompetes *Archoplites interruptus* for food resulting in slow growth on this native fish (Marchetti 1999). Predation of native fishes by *L. macrochirus* resulted in their decline in Japan (Maezono et al. 2005). *Lepomis macrochirus* feeds on aquatic invertebrates (Olson et al. 2003) and this may change the community structure of the ponds and rivers (Gilinsky 1984). Understanding *L. macrochirus* diet will help us to estimate the potential impacts it has on native fauna.

In their native range, *L. macrochirus* are known to be opportunist feeders (Flemer and Woolcott 1966). In Mississippi, adult bluegill are known to feed on chironomids, chydorids and gastropods while juvenile bluegill mostly feed on chironomids and chydorids, but their diet shifts with seasons (Dewey et al. 1997). In Virginia, adult bluegill feed more on dipteran larvae,

coleoptera, hemiptera and hymenoptera, while juveniles feed more on dipteran larvae, hemipteran and copepoda (Flemer and Woolcott 1966).

Lepomis macrochirus are omnivorous (Diggins et al. 1979; Olson et al. 2003), with prey selection influenced by both fish size (Mittelbach 1981; Olson et al. 2003) and prey availability (Kaemingk et al. 2012; Olson et al. 2003). Early life-history stage bluegills have been shown to feed predominantly on cladocerans, shifting towards copepods and ostracods before making the transition to macro-invertebrates such as chironomids, trichopterans and gastropods as juveniles (Dewey et al. 1997; Flemer and Woolcott 1966; Mittelbach 1984; Savino et al. 1992). Adults commonly feed on larger macro-invertebrates such as Odonates (Kaemingk et al. 2012; Olson et al. 2003), large beetles (Flemer and Woolcott 1966) and shrimps (De Moore and Bruton 1988) as well as the eggs and tadpoles of amphibians (Werschkul and Christensen 1977), fish eggs and even small fish (Neff 2003). *Lepomis macrochirus* have even been shown to feed on non-native species thereby reducing the numbers of these non-native fishes (Tetzlaff et al. 2011). While there is a general shift to larger prey with fish size, *L. macrochirus* still incorporate smaller zooplanktonic and macroinvertebrate prey throughout their life-history (Sadzikowski and Wallance 1976). Plant material is also occasionally incorporated into their diets (Flemer and Woolcott 1966; Olson et al. 2003; Sadzikowski and Wallance 1976).

There are relatively few studies that have assessed the feeding biology of these fish outside of North America (Diggins et al 1979; Harris et al. 1999; Olson et al 2003) and there is only one study in Africa (van Someren 1946). In California, *L. macrochirus* outcompetes native fishes for food (Marchetti 1999). The presence of *L. macrochirus* in Willamette Valley (USA) decreases the abundance of aeshnid dragonfly nymphs and this increases the invasion by bullfrogs, as aeshnid dragonfly nymphs feed on bullfrog larvae (Adams et al. 2003). In Nebraska, *L. macrochirus* feeds on insects (Olson et al. 2003) and native fishes (Neff 2003).

A knowledge of the diet of *L. macrochirus* in a South African impoundment will therefore help in developing the understanding of the potential impacts on aquatic macro-invertebrates, competition with native fishes for food, and the predation on native fishes. The present study aims to contribute to the knowledge of the ecology of *L. macrochirus* in South Africa by describing its diet in the Howison's Poort impoundment of the Kariega River. It was predicted that *L. macrochirus* diet would shift within the two seasons (summer and winter) and fish size (FL).

Materials and methods

Field sampling

Lepomis macrochirus were collected from Howison's Poort Dam (S33°23'12.61"; E26°29'4.22") during austral winter (June) and summer (December) of 2015. Howison's Poort Dam named after Alexander Howison is situated in the west of Grahamstown, Eastern Cape Province, South Africa. The dam was constructed in 1832 and supplies water to Grahamstown. Fish present in the dam include *Micropterus salmoides* and *L. macrochirus*.

Multiple methods of sampling were employed to catch *L. macrochirus*: gillnets (stretched mesh sizes: 30, 45, 50, 60, 65, 75, 85, 95, 100, 144, 150 mm), fyke nets (double ended with 8 m guiding net and the first ring diameter of 55 cm and mesh size 10 mm) and a 30 m long, 1.5 m high (stretched mesh size of 5 mm) seine net hauls were set/ conducted. After capture fish were immediately placed in clove oil for humane euthanasia. Once dead, the fish were placed on ice until they reached the laboratory on the same day.

In the laboratory, each fish was measured for fork length (FL) to the nearest mm, and the stomach of the fish then removed via dissection of the peritoneal cavity. Fish stomachs were stored separately in 10 % formalin solution for a period of 1 week for fixation before being transferred to 70 % ethanol.

Each stomach was dissected and the stomach fullness estimated. The contents were then emptied into a customised 5 mm deep dissecting tray with grid markings at increments of 1mm x 1mm to allow for volume determination. The stomach contents were identified to various taxonomic levels, depending on the group and/ or level of digestion. This was done under a dissecting microscope following the identification guides of Day et al. (2003), de Moore et al. (2003), and Gerber and Gabriel (2002) following recommendations of Hyslop (1980). Prey counts were based on heads as the other body parts were often digested. The volume of each prey taxa were determined using an indirect volumetric method where prey were squashed to a uniform depth within the dissection tray and the volume calculated as the grid-area covered.

Data analysis

Data were quantified following the methods outlined by Pinkas et al. (1971). The frequency of occurrence (%F), defined as the number of stomachs containing a particular prey as a percentage of all stomachs, was determined for each prey item. Similarly, abundance of prey (%N), defined as the number of individuals as the proportion of all prey items, was also determined. Prey volume was expressed as percentage volume (%V) by determining the relative contribution of each prey type in relation to the total volume of all stomach contents. Prey index of relative importance (IRI) was calculated using the formulae

$$IRI = (%N + \%V) \times \%F$$

These values were then expressed as the proportion of the sum of IRI values calculated for all prey items (%IRI). IRI was only calculated for the identifiable prey taxa and not unidentified material such as detritus and vegetation, given that it was not possible to numerate such material. As such, all comparative analyses were based only on identified prey taxa, as is common practice in gut content studies (Kramer et al. 2015; Wasserman et al. 2011; Weyl et al. 2010). The %IRI data was used to construct a dietary niche breadth for each size class per season using the equation:

$$B = \frac{1}{\sum Pi^2}$$

Where Pi is the relative frequency for prey item i , in the diet of predator P (Levins 1968). The results were then standardized to the scale of 0 – 1 using the equation:

$$B_a = (B - 1)(n - 1)$$

Where B_a is the Levins standardized niche breadth and n represents the number of prey items.

Niche overlap between each size class for both seasons was calculated using the formula:

$$O_{jk} = \frac{\sum P_{ij}P_{ik}}{\sqrt{\sum P_{ij}^2 \sum P_{ik}^2}}$$
, where O_{jk} is the measure of overlap between size class j and size class k

for both seasons. P_{ij} is the proportion that resource i is of the total resources used by size class j , and P_{ik} is the proportion that resource i is of the total resources used by size class k (Pianka 1986). A community analysis approach was then employed to assess similarities and differences among bluegill size classes across seasons. This was done using the Primer v6 community analysis software package (Clarke and Warwick 2001) to analyse prey communities, based on %IRI values. Classification trees (Euclidean distance) for %IRI were constructed in Primer v6 (Clarke and Warwick 2001) to show the dietary similarities between

size classes for winter and summer seasons and to independently identify groups based on overall dietary similarity. The SIMPER test was used to determine which key taxa were responsible for similarities between groups highlighted by the cluster dendrogram.

Results

A total of 266 bluegill were dissected, comprising 116 winter and 150 summer stomach samples. The proportion of empty stomachs in the winter (19 %) sample was statistically different to that of summer (21 %) ($p < 0.05$) (Table 3.1). To investigate the effect of size on diet, sampled fish were grouped into three size classes: young-of-year (YOY, 26-70 mm FL), juvenile (71-140 mm FL) and adult (>140 mm FL) (Table 3.1). A total of 11 and 16 taxa were identified in the stomach contents of the bluegill in winter and summer, respectively (Table 3.2 and 3.3), with seven groups (Calanidae, Daphniidae, Libellulidae, Araneidae, Pyralidae, Chironomidae and Dytiscidae) encountered in both seasons (Table 3.2 and 3.3).

In winter, although relatively few prey taxa contributed to the overall prey presented in bluegill, there was a clear shift in diet with size class. Diet of YOY bluegills was dominated by the zooplanktonic crustacean, Chydoridae (%IRI = 74.9) and Daphniidae (%IRI = 20.3); juvenile diet was dominated by the closely related Sididae (%IRI = 92.9) and Ostracoda (%IRI = 7.0), and adult fish consumed mostly hexapods, namely libellulids (%IRI = 80.4) and chironimids (%IRI = 16.4) with the only crustacean contribution being the ostracods (%IRI = 3.3). Diets shifts were also clearly evident in summer when YOY fed mainly on Daphniidae (%IRI = 93.9) while juvenile fish fed on Daphniidae (%IRI = 34.3) and fish eggs (%IRI = 64.4), the latter dominating (%IRI = 98.8 %) in adult diets (Table 3.2). Algae and plants were occasionally present in stomachs of all size classes. This was consistent with the four feeding groups identified using cluster analysis (Figure 3.1): (1) YOY (both seasons); (2) juveniles in winter; (3) adults in winter and (4) juveniles and adults in summer.

Table 3.1: Number of empty stomachs for sampled bluegill for each season per size class (FL = fork length).

Size class (mm FL)	Winter		Summer	
	Sampled	Empty	Sampled	Empty
0-70	38	2	59	12
71-140	42	9	66	15
>140	36	11	25	4

Table 3.2: Gut contents of *Lepomis macrochirus* sampled from Howison's Poort impoundment in winter. All prey items were identified to lowest possible taxon (%F is the percentage of all stomachs containing prey, %V is the volume of each prey item consumed, as a percentage of the total volume of stomach contents; %IRI index of relative importance, as a proportion of the total IRI of all species sampled).

Prey		Winter									
		YOY (26-70 mm)			Juveniles (71-140 mm)			Adults (>140 mm)			
		%F	%V	% IRI	%F	%V	% IRI	%F	%V	% IRI	
Crustacea											
	Calanoida	Calanidae	7.9	1.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0
	Anomopoda	Chydoridae	21.1	16.1	74.9	0.0	0.0	0.0	0.0	0.0	0.0
	Diplostraca	Sididae	5.3	1.3	0.8	4.8	6.1	92.9	0.0	0.0	0.0
	Cladocera	Daphniidae	13.2	0.2	20.3	0.0	0.0	0.0	0.0	0.0	0.0
	Podocopida	Cyprididae	2.6	0.1	0.1	7.1	0.1	7.0	2.8	<0.1	3.3
	Araneae	Araneidae	2.6	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Insecta											
	Lepidoptera	Pyralidae	5.3	2.3	0.9	0.0	0.0	0.0	0.0	0.0	0.0
	Odonata	Libellulidae	0.0	0.0	0.0	2.4	<0.1	<0.1	16.7	8.6	80.4
	Diptera	Chironomidae	7.9	4.1	1.9	2.4	<0.1	<0.1	5.6	0.1	16.4
	Coleoptera	Dytiscidae	0.0	0.0	0.0	2.4	<0.1	<0.1	0.0	0.0	0.0
Gastropod											
		Pulmonata	2.6	1.6	NA	2.4	3.9	N/A	2.8	2.2	N/A
Algae											
			2.6	1.3	NA	4.8	1.7	N/A	13.9	8.4	N/A
Invertebrate remains											
			65.8	60.3	NA	66.7	79.1	N/A	47.2	54.3	N/A
Plant remains											
			5.3	5.5	NA	4.8	6.1	N/A	27.8	24.7	N/A

Table 3.3: Gut contents of *Lepomis macrochirus* sampled from Howison’s Poort impoundment in summer. All prey items were identified to lowest possible taxon. %F is the percentage of all stomachs containing prey, %V volume of each prey item consumed, as a percentage of the total volume of stomach contents; %IRI index of relative importance, as a proportion of the total IRI of all species sampled.

Prey		Summer								
		YOY (26-70 mm)			Juveniles (71-140 mm)			Adults (> 140 mm FL)		
		%F	%V	%IRI	%F	%V	%IRI	%F	%V	%IRI
Crustacea										
Calanoida	Calanidae	18.6	3.0	2.2	3.0	0.2	0.1	0.0	0.0	0.0
Cladocera	Daphniidae	37.3	23.3	93.9	10.6	9.1	34.3	0.0	0.0	0.0
Araneae	Araneidae	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.2	<0.1
Insecta										
Lepidoptera	Pyrilidae	1.7	0.4	<0.1	0.0	0.0	0.0	0.0	0.0	0.0
Hemiptera	Naucoridae	0.0	0.0	0.0	1.5	0.1	<0.1	0.0	0.0	0.0
Trichoptera	Hydroptilidae	18.6	5.4	3.1	4.6	2.2	0.6	0.0	0.0	0.0
	Economidae	1.7	0.1	<0.1	1.5	0.2	<0.1	8.0	0.5	0.2
Coleoptera	Gyrinidae	1.7	<0.1	<0.1	0.0	0.0	0.0	0.0	0.0	0.0
Odonata	Libellulidae	10.2	1.2	0.4	4.6	0.2	0.1	0.0	0.0	0.0
Diptera	Chironomidae	5.1	0.1	<0.1	6.1	0.7	0.3	0.0	0.0	0.0
	Ceratopogonidae	1.7	<0.1	<0.1	3.0	0.1	<0.1	0.0	0.0	0.0
Coleoptera	Dytiscidae	0.0	0.0	0.0	1.5	2.0	0.2	0.0	0.0	0.0
Ephemeroptera	Heptageniidae	1.7	1.4	0.1	0.0	0.0	0.0	0.0	0.0	0.0
	Oligoneuridae	1.7	0.5	<0.1	0.0	0.0	0.0	0.0	0.0	0.0
	Teloganodidae	0.0	0.0	0.0	3.0	0.3	0.1	8.0	<0.1	0.6
Gastropoda										
	Pulmonata	1.7	0.5	N/A	0.0	0.0	N/A	0.0	0.0	N/A
Fish										
	<i>L. macrochirus</i>	0.0	0.0	0.0	0.0	0.0	0.0	8.0	1.7	0.3
	Eggs	5.1	0.6	0.3	24.2	10.6	64.4	36.0	16.3	98.8
	Scales	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.7	0.12
Algae		0.0	0.0	N/A	1.5	0.8	N/A	0.0	0.0	N/A
Invertebrate remains		59.3	60.6	N/A	60.6	68.0	N/A	60.0	55.2	N/A
Plant remains		3.4	2.9	N/A	9.1	5.5	N/A	36.0	25.4	N/A
Sand		0.0	0.0	N/A	1.5	0.3	N/A	0.0	0.0	N/A

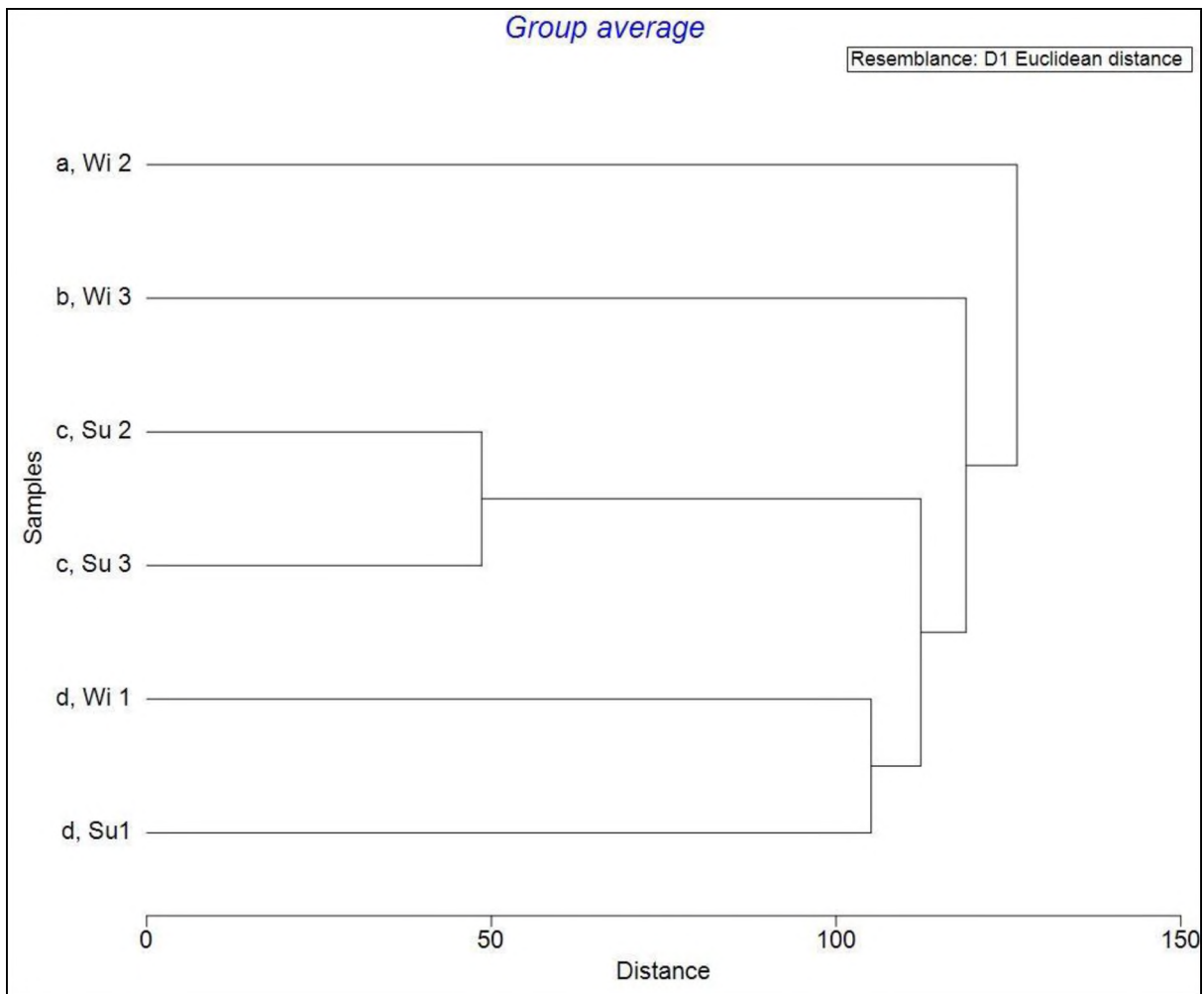
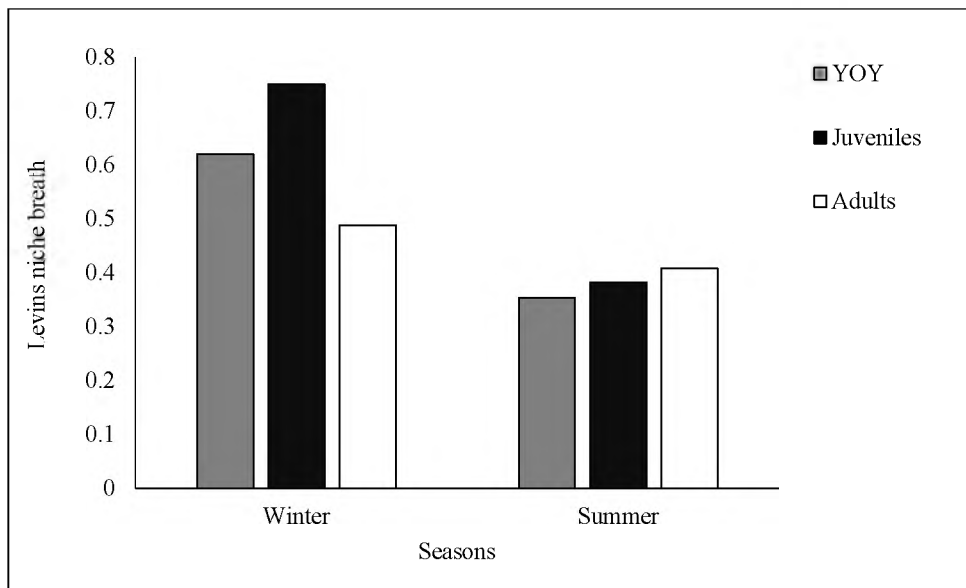


Figure 3.1: Dietary similarities (%IRI) between three size classes of bluegill sampled from Howison’s Poort Dam, South Africa during winter and summer seasons 2015. Each sample is represented by a 4 digit code: a, b, c and d denote groups identified for simpler analyses, Wi = Winter, Su = Summer, 1 = YOY (26 - 70 mm TL), 2 = Juveniles (71 - 140 mm TL), 3 = Adults (>140 mm TL).

Niche breadth varied with seasons and size classes (Figure 3.2a) in bluegill, with all winter size classes exhibiting greater niche breadth than in summer. Juveniles sampled in winter had the largest niche breadth as a result of the incorporation of the smaller cladocerans and the larger insects, unlike YOY fish that specialised in cladocerans or adults which preyed on insects (Figure 3.2a). During summer, niche breadths were more similar, although there was a slight increase in niche breadth with size class (Figure 3.2b). Overlap between seasons within each size class was generally low, with a maximum overlap of 0.5 observed for YOY (Figure 3.2b). Overlap decreased with an increase in size class with no dietary overlap observed between seasons for adult fish.

(a)



(b)

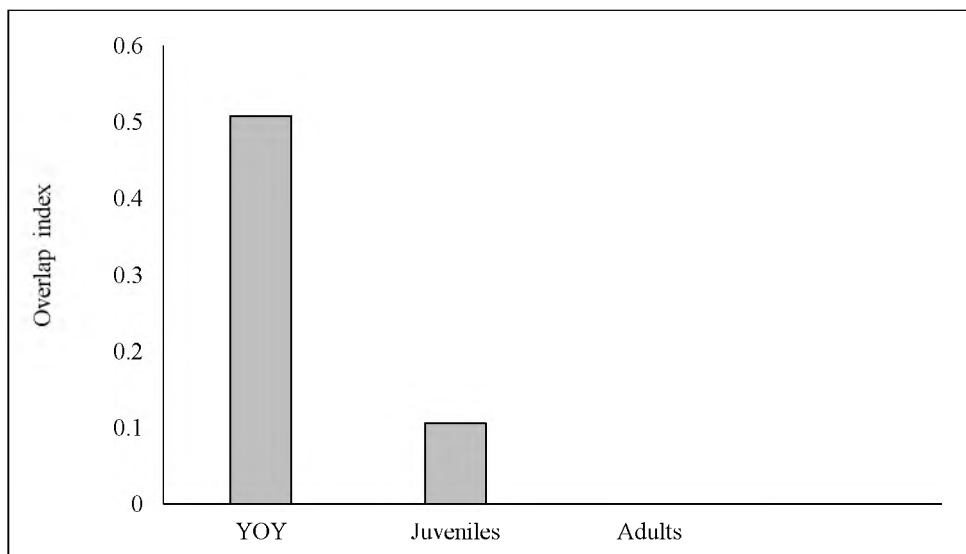


Figure 3.2: (a) Levins niche breadth and (b) dietary overlap for *Lepomis macrochirus* sampled from Howison's Poort Dam, Kariega River, South Africa. (a) Niche breadth is shown for each size class per season. Where YOY is 26 - 70 mm, juveniles is 71 - 140 mm and adults is >140 mm TL. (b) Dietary overlap between the two seasons comparing the size classes.

Discussion

Results from the present study were consistent with observations from Harris et al. (1999), Mittelbach (1984) and Olson et al. (2003). The present study demonstrated a diet shift from

small to large prey organisms with an increase in size and showed that there are large seasonal differences in the diets of *L. macrochirus* in the river system examined.

In contrast with the current study, small *L. macrochirus* in Kenya fed more on cladocera with few hemipteran and Chironomid in their diet (van Someren 1946). Zooplankton contributed more to the diet of bluegill in contrast with other studies, such as Mittelbach (1981) and Werner and Hall (1979).

Comparing the two seasons, small bluegill consumed almost the same species, but as the fish become older the opposite occurred; they fed on different prey items (Figure 3.2 b). While crustacean branchiopods dominated the diet of YOY fish in both seasons, there were subtle differences in these taxa, with chydorids dominating in winter and daphniids dominating in summer. The presence of chydorids suggests that YOY feed on the littoral vegetation (Tremel et al. 2000), and although daphniids inhabit the littoral zone, they sometimes shift their habitats to avoid predation (Burks et al. 2001). There were also clear shifts in prey taxa consumed across size classes and these shifts varied dependant on season. In winter fish shifted predominantly to sididae (benthic feeding) as juveniles before shifting to the larger libellulids (benthic feeding) and chironomids (benthic feeding). In contrast, summer fish shifted from a crustacean dominated diet in YOY while fish egg dominated diet in adults, with juvenile fish incorporating both invertebrates and fish eggs.

There is a strong possibility that the consumed fish and fish eggs belong to bluegill as this fish dominates the ichthyofaunal community in the Howison's Poort Dam surveys (unpublished data) and eggs were present in many of these fish during dissections. It is also possible, however, that the eggs could belong to other fish species, such as the banded tilapia *Tilapia sparrmanii* or largemouth bass *Micropterus salmoides* which are also present in the dam and known to spawn during the month of December in the region (De Moore and Bruton 1988; Polling et al. 1995). It is unlikely the eggs would have belonged to largemouth bass, as this species is known to reproduce in the months of July and October (Beamish et al. 2005; Weyl and Hecht 1999).

Algae and plant material were found in bluegill diet in both seasons. Plant material may have been ingested in association with other prey such as insects. Plant material was more dominant than algae for both seasons with higher %V increasing with the increase in size class during these seasons. In summer, algae were found only in juvenile fish. Plant remains were found in all the size classes, and in both seasons, there was an increase in %V of plant material with the

increase in size class. Smaller-sized fish often have relatively higher protein demands for growth than do larger fish of the same species (Gerking 1952; Page and Andrews 1973). The presence of sand in the diet of this fish could be the result of benthic feeding. It is difficult to determine where the fish were foraging given that most of the dominant prey items utilise multiple zones in the water column. However, the presence of chironomid (Diggs et al. 1979; Lowe et al. 2008) and libellulids suggests that the larger fish feed in benthic marginal vegetation (Lowe et al. 2008). They feed in the littoral zone because of the presence of molluscs in their diet (Vadeboncoeur et al. 2011). Smaller fish seem to be feeding more on the surface water as this is where daphniids are commonly found (Mergeay et al. 2006). However, the presence of Hydroptilidae suggests that these fish are also feeding in epibenthic and littoral zones (Daniels and Moyles 1978).

Overall, the present study highlights that *L. macrochirus* in this impoundment in South Africa have a similar feeding ecology to those in their native range. As is the case in its native range, bluegill are generalist feeders, with crustacea and insects comprising most of the diet. It is likely that the fish in this system are utilising prey relative to their availability, although we have no information on invertebrate community dynamics for Howison's Poort Dam. In addition, the presence of *M. salmoides*, a natural predator of the bluegill (Savino and Stein 1982, Werner and Hall 1988), may also have implications for habitat selection by the *L. macrochirus*. *Micropterus salmoides* were also sampled during the survey in the system and it has been shown that in the native range, *L. macrochirus* avoids open water and inhabits vegetated areas to escape from predation by *M. salmoides* (Dewey et al. 1997; Savino and Stein 1982; Werner et al. 1983).

In the context of invasive impact potential of *L. macrochirus* was the large contribution of fish eggs to the diet of large summer fish. While it is highly likely that this was a form of cannibalism, the incorporation of fish eggs by *L. macrochirus* into their diet has relevance for their potential impact on native African fish species. Many of the indigenous fish species in South Africa have similar spawning habitats to bluegill. Cichlid species construct nests in sand (Morris 1954; Ochi and Yanagisawa 1999) and gravel habitats (Aronson 1945), in which eggs are laid and guarded, similar to that of *L. macrochirus* (Gross and MacMillan 1981; Stevenson et al. 1969). Should *L. macrochirus* readily lay nests and forage on fish eggs throughout their established range in South Africa, there is much potential for impact on native fish species. These fish can reduce the numbers of native fishes (Maezono et al. 2005) and benthic

invertebrates (Mittelbach 1988) because of their ability to feed on invertebrates, fish and fish eggs. Therefore, more studies are needed to monitor the impacts of this invasive fish.

CHAPTER 4: A comparative assessment of the functional responses of the four dominant non-native fish species from the Kariega River system

Introduction

Human activities facilitate species introduction into new areas outside their native range (Leprieur et al. 2008). In certain cases, such introductions can lead to the establishment and further spread of these organisms to other areas, a process referred to as a biological invasion (Williamson 1996). Freshwater ecosystems have been identified as being particularly vulnerable to invasion given that the construction of impoundments promotes the establishment of non-native fishes as they have different physiochemical properties than the natural lakes (Johnson et al. 2008).

In South Africa, many freshwater systems are regarded as heavily invaded (Pimentel 2011). All of the major river systems in South Africa are now home to non-native fish species, with at least 27 freshwater fishes having been introduced into South Africa since 1726 (Ellender and Weyl 2014). Of these introduced fish species, 21 % are regarded as having failed to establish, with the remaining 79 % considered as established (Ellender and Weyl 2014). The subsequent spread of many of the established species has been facilitated by additional intentional stocking, and inter-catchment connections and which have resulted in a variety of impacts on native biota (Ellender and Weyl 2014). These impacts include predation on native fish and competition with native fishes for resources, resulting in the decline of the native fishes and the further spread of alien fish species (Ellender and Weyl 2014).

It is now well established that invasive species need to be monitored, and their effects and potential impacts quantified for the optimal management of invaded aquatic systems (Puth and Post 2005). Management interventions or recommendations may vary, depending on the state of the invasion (Blackburn et al. 2011), with control methods needed for the improvement of the conservation status of native species (McGeoch et al. 2010). If the non-native species have negative impacts, their movement should be stopped (Puth and Post 2005). Puth and Post (2005) have suggested that it is better to study the non-native fish during the dispersal stage so that the species can be controlled before it can cause more damage to the environment. However, in the South African context, many of the invasive fishes are well established and spread throughout entire systems (Ellender and Weyl 2014).

Since it is well recognised that not all non-native species will become invasive (Ellender and Weyl 2014) and not all invasive species will have the same levels of impact (Ellender and Weyl 2014; Leunda 2010; Simon and Townsend 2003), identification of particularly problematic species is important for managers trying to initiate mitigation measures in invaded systems. One of the major limitations in invasion biology, however, is the quantification of impact or potential impact in order to prioritise and manage such species adequately (Weyl et al. 2013). With regard to invasive species that are more or less predatory at certain life-history stages, their predatory impact has been identified as a potentially useful measure of field impact (Dick et al. 2002; Mittelbach 1981). As such, the present study investigates aspects of predation for some invasive species that are now common in river systems of South Africa, using a functional response experimental approach.

Aspects of the foraging ability of predators can be characterised by determining the functional response of the predator (Ohlberger et al. 2008). A predator's functional response is essentially the relationship between its consumption rate and the availability of prey (Solomon 1949). Functional responses have recently been identified as a useful tool for determining the potential ecological impacts of invasive organisms (Dick et al. 2013a; b). By contrasting the functional responses of multiple species, the predatory impact potential of the species can be characterised, highlighting potentially problematic species (Alexander et al. 2014; Dick et al. 2013a, b). For example, a study by Alexander et al. (2014) found that non-native *Micropeterus salmoides* and *Clarias gariepinus* consumed more prey than did the native *Sandelia capensis* and *Glossogobius callidus*, suggesting that the invasive fishes may have a greater predation effect on native prey in invaded areas than do the native predators. Similarly, Dick et al. 2002 showed that invasive amphipods had a higher functional response than did native amphipods, consuming more invertebrates than the native amphipods and this explained why there was a rapid decline of invertebrates after invasion by this amphipod. As such, functional response information may be used to predict the impacts an invasive organism could have on prey (Alexander et al. 2014; Dick et al. 2013a; b).

Three types of functional response have been identified (Real 1977). In a Type I functional response, resource consumption is directly proportional to resource availability (Abrams 1987) up to the point where the organism can consume no more prey (Real 1977) (Figure 4.1a). Unlike type I response organisms, the type II response takes some time between ingestion and catching new prey as they are not filter feeders like type I organisms (Real 1977) (Figure 4.1b). Type III functional response usually occurs when the organisms are not familiar with the

resource (Real 1977). At first, they consume less prey, but once they get used to the resource, prey consumption increases until the organism cannot consume any more prey and this is known as a learning behaviour (Real 1977) (Figure 4.1c).

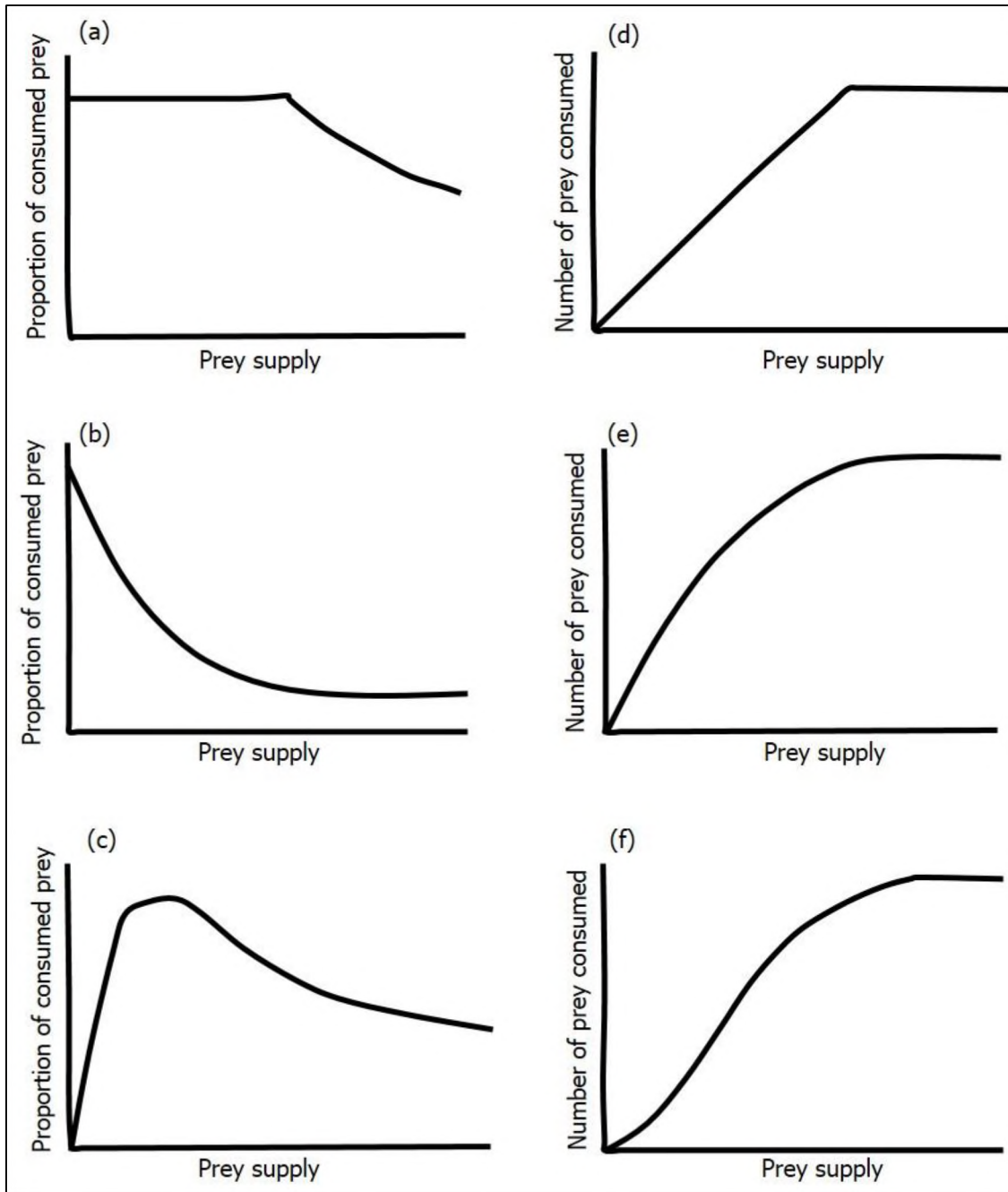


Figure 4.1: Functional response types showing the proportion of eaten prey in relation to number of prey supplied, whereby a, b and c represent Type I, Type II and Type III functional responses respectively. Corresponding graphs show the number of consumed prey in relation to the number of prey supplied, whereby d, e and f represent Type I, Type II and Type III functional responses.

The type of functional response of an organism has implications, in theory, for aspects of the biology and ecology of that organism, such as its growth rate or how it competes for resources (Abrams 1980). The patterns of niche overlap may be determined by functional response of competitors (Abrams 1980). With regard to implications for competition, it is lower when there are plenty of resources in the area (Abrams 1980), and prey consumption by predators increases with prey availability (Verity 1991 and Alexander et al. 2014). While the ability of predators to consume more prey increases with the increase in prey densities (Abrams 1980), consumption also depends on their hunger levels which are essentially dictated by aspects of handling times, such as digestion (Jeschke et al. 2002). When the saturation point is reached, less or no prey will be consumed (Real 1977) resulting in the decrease in handling time (Collins et al. 1981). As such, attack rates and handling times are important considerations of predator-prey interaction outcomes and this information can be derived by determining the functional response of a predator.

The entire Kariega River system is heavily invaded with multiple fish species. During the fish distribution component of the larger study (Chapter 2), it was found that the system is dominated by four invasive species, namely; *Tilapia sparrmanii* Smith, 1840; *Pseudocrenilabrus philander* Weber, 1897; *Lepomis macrochirus* Rafinesque, 1819 and *Micropterus salmoides* Lacepède, 1802. *Micropterus salmoides* and *L. macrochirus* belong to the family Centrarchidae, native to eastern and central North America (De Moor and Bruton 1988) and are both categorised as established and wide spread in South Africa (Ellender and Weyl 2014). The diet of *M. salmoides* includes insects and aquatic vertebrates (Skelton 2001; Wasserman et al. 2011). Similarly, *L. macrochirus* also feeds on small fish and invertebrates, although it is generally considered less of a piscivore than *M. salmoides* (Keast 1985). These two species are regarded as problematic in other parts of the world and have been shown to change community structure in invaded environments by reducing or even removing certain native fishes and invertebrates (Maezono et al. 2005; Maezono and Miyashita. 2003; Whittier and Kincaid 1999).

Tilapia sparrmanii and *P. philander* belong to the family Cichlidae (Skelton 2001). While these species are native to parts of South Africa, they have trans-located to sites outside their natural distribution. *Pseudocrenilabrus philander* is currently categorised as established, while *T. sparrmanii* is categorised as established and wide spread where they occur extraliminally in South Africa (Ellender and Weyl 2014). Small fish, plants, algae and insects constitute the diet of *T. sparrmanii* (Skelton 2001) while that of *P. philander* includes small fish, invertebrates

and algae (Polling et al. 1995). There is, however, no available information on the impacts of these species where they have been introduced. Using a functional response approach, as outlined by Dick et al. (2014), the aim of this study was to compare the potential predatory impact of these four non-native fish species from the Kariega River system Eastern Cape, South Africa. We specifically predicted that the functional responses, and therefore predatory impact of the centrarchids, would be higher than that of the cichlids.

Methods

For the functional response experiment, bluegill *L. macrochirus*, largemouth bass *M. salmoides*, southern mouthbrooder *P. philander* and banded tilapia *T. sparrmanii*, were collected from various impoundments on the Kariega River system. These predators were selected because they are the four dominant fishes in the river system and the purpose was to compare their impact on prey consumption, focusing specifically on *L. macrochirus* as this was the species of concern for the larger study. All fish were collected in April 2015 with *M. salmoides* collected from Yarrow Dam (S33°24'54.66"; E26°22'39.74") and Mosslands farm dams (S33°24.183'; E26°27.159') and *P. philander*, *L. macrochirus* and *T. sparrmanii* collected from Craige Doone farm dam (S33°21.327'; E26°27.998'). Once in the laboratory, all fish used in the experiment were size-matched based on total length (TL) (Table 4.1). These fish were housed in separate 600 l cylindrical housing tanks for a period of three weeks prior to indoor experimentation, during which time they were maintained on a diet of earthworms. Predators were then starved for three days before conducting the experiment.

Predators were size-matched based on total length (TL) following comparative procedures employed by Alexander et al. (2014). Mozambique tilapia, *Oreochromis mossambicus* fry (10 ± 0.5 mm TL) were used as prey in the functional response experiment. The fry were supplied by the aquaculture facility, Aquaculture Innovations. Prey and predators were selected based on total length, following the methods used by Alexander et al. (2014) and Soluk (1993). The mouth gape size was not considered when conducting the experiment as gape differs considerably across fish species of similar lengths. As such, the focus of this study was on predation rates based on fish size which has been shown to be more important for encounter rates between predators and prey in pairwise interactions (Mittelbach 1981).

Table 4.1: The mean standard deviation of total lengths (mm) for *Micropetrius salmoides*, *Pseudocrenilabrus philander*, *Lepomis macrochirus* and *Tilapia sparrmanii*.

Predator	Length (mm) (Mean \pm SD)
<i>M. salmoides</i>	73.2 \pm 2.2
<i>P. philander</i>	76.4 \pm 2.6
<i>L. macrochirus</i>	75.1 \pm 1.9
<i>T. sparrmanii</i>	76.7 \pm 2.2

The experiment was conducted during day-light hours to allow prey to be visible to the predators, in 300 l tanks that were part with a closed circulating water system (Figure 4.2; 4.3). The experiments were conducted in 26 l cages, each floated in a single 300 l square fibre glass tanks (Figure 4.2; 4.3). Predators were randomly assigned to tanks and were allowed to acclimate for a period of 1 hour, prior to the introduction of prey. Prey were supplied at six separate densities (two, four, eight, sixteen, thirty-two and sixty-four) per species of predator with a minimum of three replicates and maximum of six replicates per treatment density (Alexander et al. 2014), depending on predator species availability. Predators were removed from the cages 60 min after they were presented with prey and the number of remaining prey counted. Control trials were run at the same time: six prey densities with no predators to account for any prey deaths, not related to predation, that may have occurred.

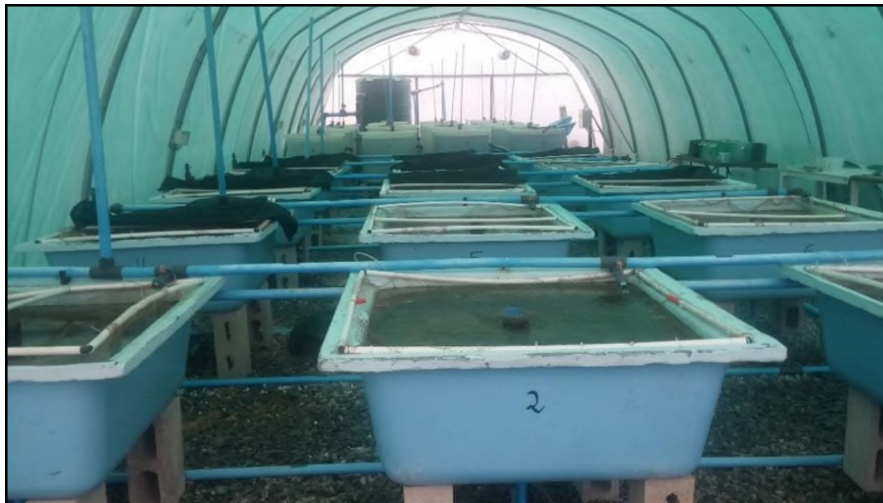


Figure 4.2: Experimental tanks that comprised the closed circulating water system. Each tank housed one 26 l floating cage within which experiments were conducted.

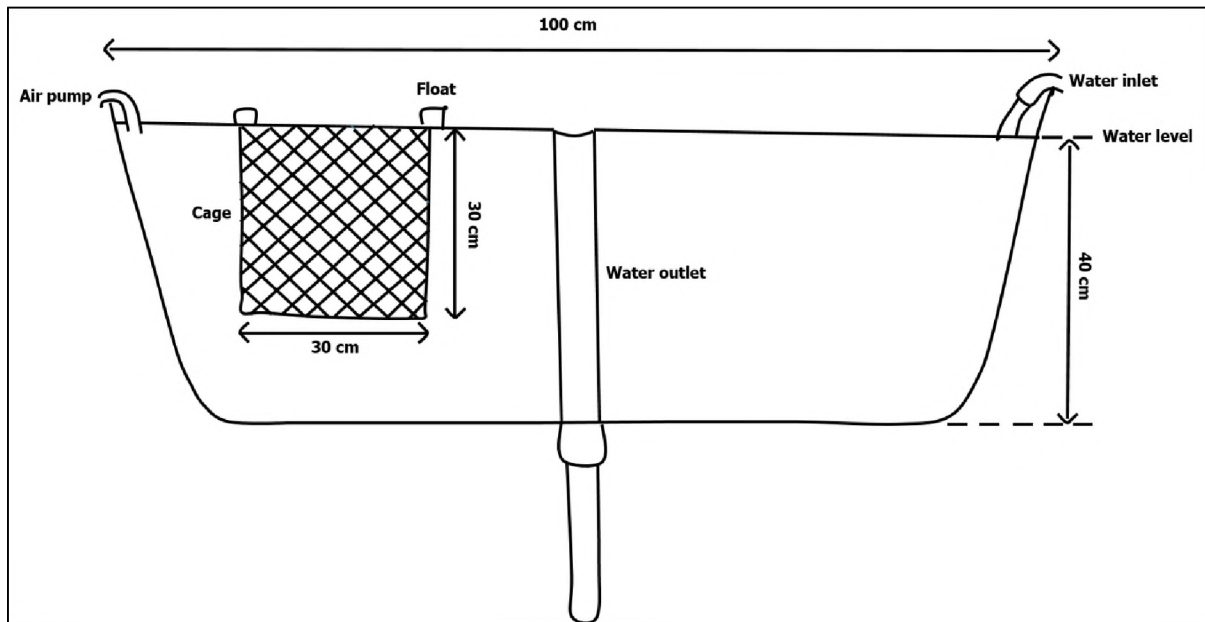


Figure 4.3: Diagram of side view of an experimental tank housing the floating cage. Experimental trials were within the cage and only one cage was used in each 300 l tank.

All statistical analysis was conducted following the methods used by Alexander et al. (2014) and Barrios-O'Neill et al. (2014) using the R statistical environment. A generalised linear model was used for assessing the differences in consumed prey by the different predators. Logistic regressions were used to determine the functional response types, providing information on the shape of the relationship between proportion of prey consumed and the density for each data set (Figure 4.4).

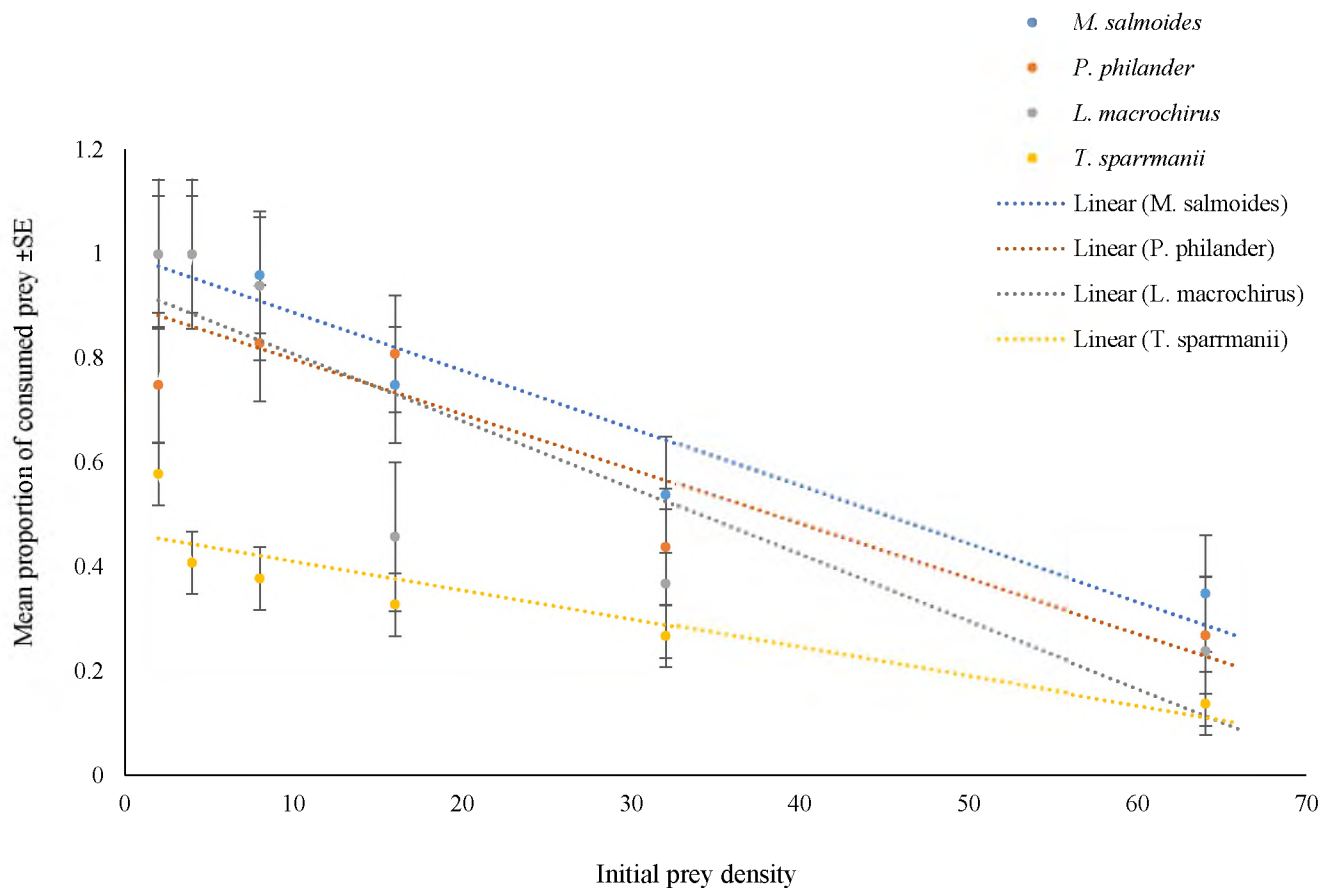


Figure 4.4: *Oreochromis mossambicus* proportional mortality under predation by *Micropterus salmoides*, *Pseudocrenilabrus philander*, *Lepomis macrochirus* and *Tilapia sparrmanii*.

As such, all data were found to represent Type II responses. The data were modelled using the Rogers random predator equation for Type II responses, which takes into account that prey density declines as predators eat them (also referred to as a non-replacement design).

$$Ne = N0 (1 - \exp (a(Nch - T)))$$

Where Ne = number of prey eaten, $N0$ = initial prey density, a = attach rate, h = handling time and T is the time.

Data was bootstrapped ($n = 2000$) to compare the attack rate (a) and the handling time (h). After bootstrapping, Roger's (1972) random predator equation was applied for each data set to construct 95 % confidence interval. Using the bootstrapping approach allowed data to be considered in terms of populations. As such, if the confidence intervals did not overlap, functional response parameters were considered significantly different (Barrios-O'Neill et al.

2014). Generalised Linear Models for Poisson distribution were used to compare prey consumption by predators using raw data.

Results

No prey deaths were observed in any of the control trials, with 100% survival of *O. mossambicus* recorded at each prey density from the one hour trials in the absence of predation pressure. All prey deaths in the study, therefore, were attributed to predation by fish, which was also directly observed in many instances for each of the model predator species. The mean number of consumed prey is shown in Table 4.2. Logistic regressions indicated that all four predatory fish species exhibited a Type II functional response (Table 4.3). In all four predators, the proportion of prey consumption decreases with prey density (Figure 4.4).

Table 4.2: Mean number of consumed prey at different prey densities

Initial prey density	Mean number of prey consumed			
	<i>M. salmoides</i>	<i>L. macrochirus</i>	<i>P. philander</i>	<i>T. sparrmanii</i>
2	2	2	1.5	1.2
4	4	4	4	1.6
8	7.7	7.2	6.6	3
16	12	7.3	13	5.2
32	17.3	11.8	14	8.6
64	22.5	15.3	17.5	9

Table 4.3: Parameter estimates with significant levels of the four predators derived from logistic regression of consumed prey in relation to prey supply.

Species	Intercept (p value)	Supply (p value)	Functional response type
<i>M. salmoides</i>	2.150713 (< 2e-16)	-0.044831 (< 2e-16)	II
<i>L. macrochirus</i>	1.179909 (1.28e-09)	-0.038792 (< 2e-16)	II
<i>P. philander</i>	1.631008 (5.01e-14)	-0.042837 (< 2e-16)	II
<i>T. sparrmanii</i>	-0.220417 (0.256)	-0.024955 (9.44e-08)	II

The overall consumption of *O. mossambicus* differed in all four predators. *Micropterus salmoides* exhibited the highest overall functional response, followed by *P. philander* as evidenced by their increased levels of feeding on prey when not limited and therefore, decreased handling times. The functional response of *L. macrochirus*, however, was only greater than that of *T. sparrmanii* (Figure 4.5 and 4.6).

Predators with lower attack rates exhibited higher handling times as they consumed less prey (Figure 4.7). There was an overlap in the attack rates for *M. salmoides*, *P. philander* and *L. macrochirus* indicating no significant difference. Attack rate for *T. sparrmanii*, however, did not overlap with any of the other predators and was significantly lower than that of any of the other predators. No significant differences in handling times were observed between *M. salmoides* and *P. philander* or between *T. sparrmanii* and *L. macrochirus*. The handling time of *M. salmoides* was, however, significantly different from that of *L. macrochirus* and *T. sparrmanii*, while the handling time of *P. philander* was only significantly different from the latter (Figure 4.6 and 4.7). The relationship between handling time and attack rate is often linked. Predators with small attack rates have high handling time and those with high attack rates have a low handling time (Figure 4.6 and 4.7).

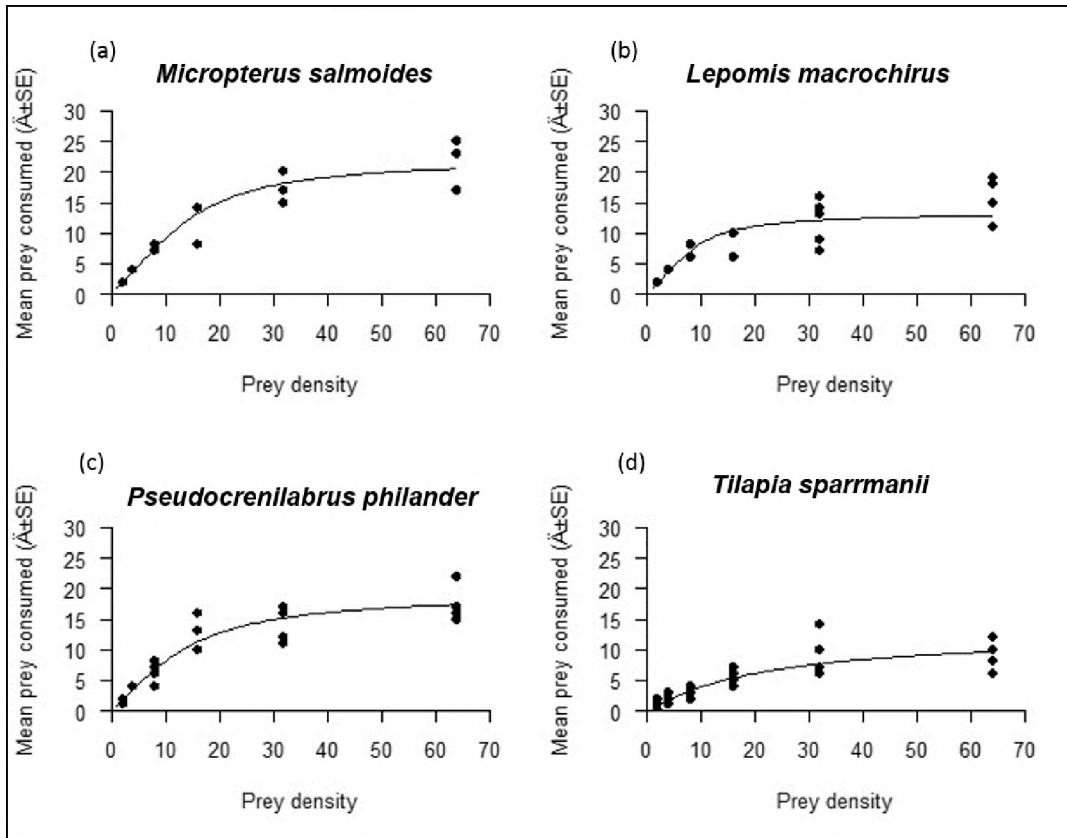


Figure 4.5: Type II functional responses (solid lines) of the model predators *Micropterus salmoides* (a), *Lepomis macrochirus* (b), *Pseudocrenilabrus philander* (c) and *Tilapia sparrmanii* (d), towards the prey, *Oreochromis mossambicus*, provided at densities of 2, 4, 8, 16, 32, and 64. Solid dots represent raw data values of prey consumption.

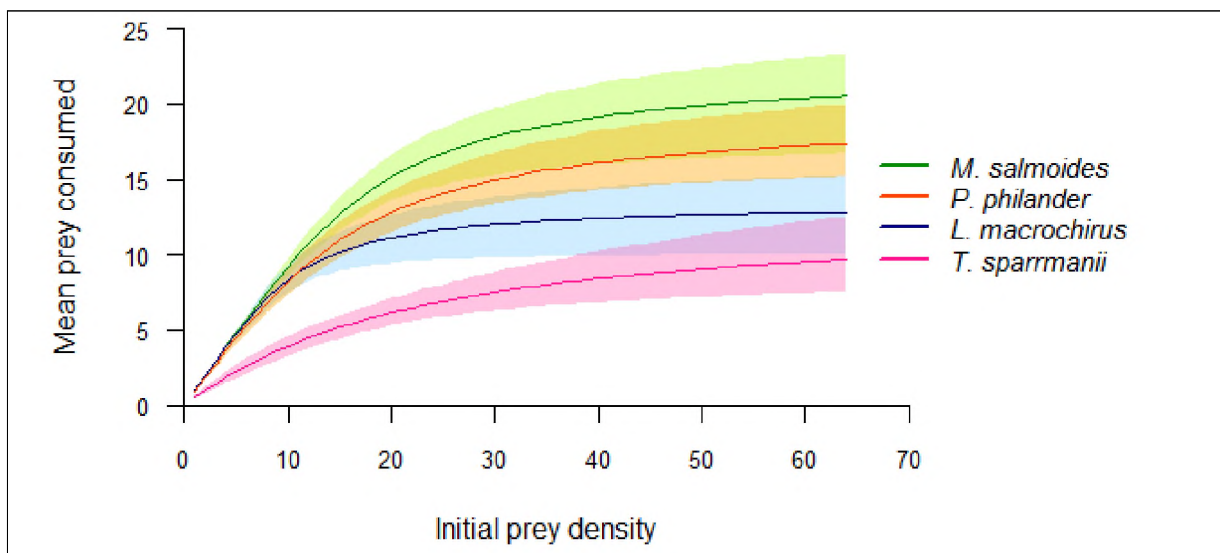


Figure 4.6: Functional responses of *Micropterus salmoides*, *Pseudocrenilabrus philander*, *Lepomis macrochirus* and *Tilapia sparrmanii* against a common prey day-old *Oreochromis mossambicus*. Solid lines represent the model curves (Figure 4.5) while shaded areas represent the 95% confidence intervals as calculated via a bootstrapping procedure.

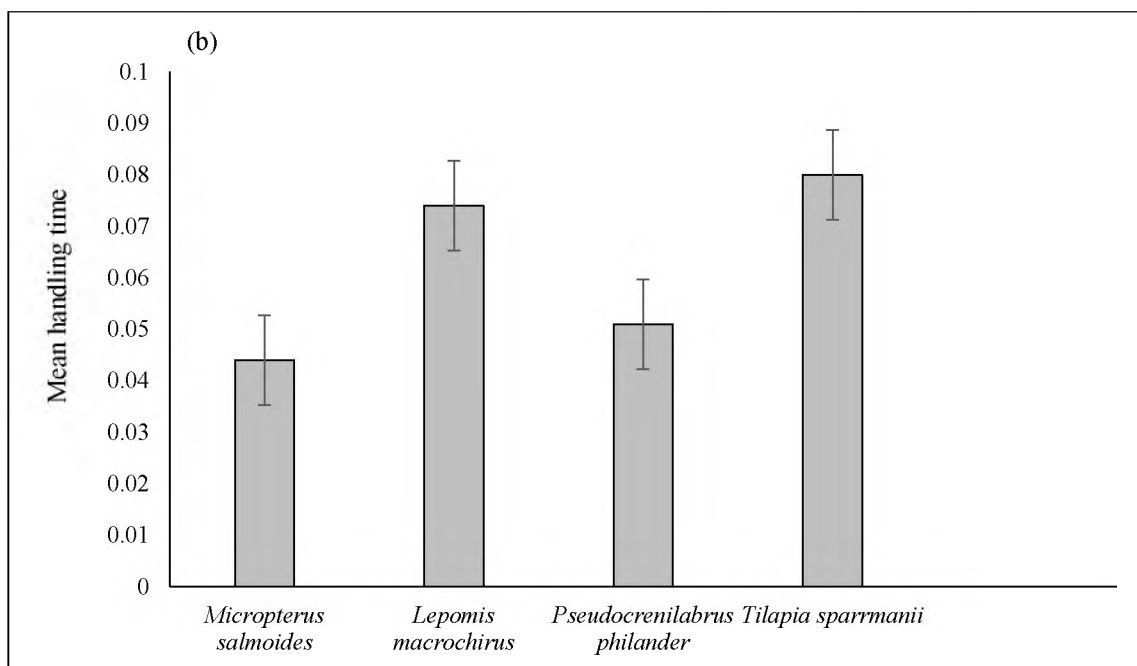
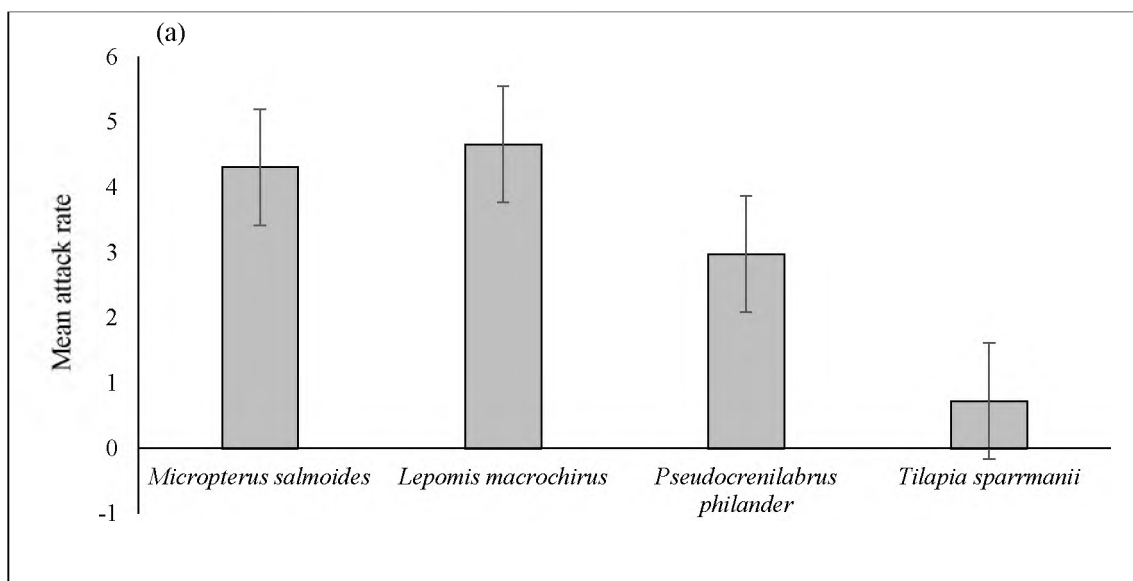


Figure 4.7: (a) Mean attack rate and (b) handling time for the derived from bootstrapping ($n = 2000$).

Discussion

The current study demonstrated that prey consumption by a predator is variable and that each predator-prey system is likely to be unique. The four predatory fish species represented a gradient of functional responses which suggests that each of these species would have different levels of impact in environments in the Kariega River and other systems. While the overall functional responses differed, all four predators exhibited a Type II functional response. Type II functional responses are thought to have potential implications for local prey extinction, given that prey are consumed even when at low density when the encounter rate is largely reduced. This is not surprising, given that fish are highly mobile and often rely on vision for prey detection, making them efficient at seeking out prey, even at low prey densities, as has been shown by other authors (Shoup and Wahl 2009; Werner and Hall 1974). Taxonomic relatedness was, however, not a good indicator of functional response similarity, given that *M. salmoides* and *P. philander* exhibited the most similar functional responses, while the *L. macrochirus* functional response fell between those of *P. philander* and *T. sparrmanii*.

Micropterus salmoides had a heightened functional response when compared with the other fish species. Given that this species is highly invasive throughout much of its introduced range, this has implications for potential prey within those receiving environments, such prey are likely to be more vulnerable in the presence of the efficient predator *M. salmoides*. Surprisingly, *P. philander* had the second highest overall functional response although it was not significantly lower than that of *M. salmoides*. This research represents some of the first work quantifying the potential effects of *P. philander* within the invasion context and suggests that this cichlid may also be a potentially harmful predator in novel environments, given that it is efficient at consuming prey when they are present at both high and low densities. *Lepomis macrochirus*, the focal species for this thesis, did not have a significantly lower functional response than that of *P. philander*, but was significantly lower than that of *M. salmoides*, suggesting that it would have an intermediate impact. *Tilapia sparrmanii* had the lowest functional response, suggesting that it would have a limited predatory impact in novel environments.

For all four predatory species, all prey were consumed at low densities, but as the number of prey increased, predatory activity varied. Christensen (1996) postulated that the maximum number of prey an organism can consume depends on the gape size of the predator, with overall prey consumption increasing with an increase in gape size. In addition to the mouth gape, aspects of the dietary characteristics of the predators are also important (and most likely

linked). *Micropterus salmoides* is a known piscivore and therefore the prey choice selected in the study is ideal for this species. *Pseudocrenilabrus philander* is also considered largely predatory and, while it feeds predominantly on invertebrates, it also feeds on small fish and algae (Muller et al. 2015; Polling et al. 1995). Both *L. macrochirus* and *T. sparrmanii* are, however, considered omnivorous, and of these two species, the latter incorporates the most plant material in its diet. These dietary characteristics reflect the observed functional responses of the species, where the highest functional responses were those of the more piscivory *M. salmoides* and *P. philander*. *Tilapia sparrmanii*, the species that was shown to incorporate the least animal material in its diet, had the lowest functional response. In addition, this species was the poorest at consuming prey at low densities, suggesting that higher densities of prey are needed to stimulate a predatory response in the omnivorous *T. sparrmanii*. Given that *T. sparrmanii* is an omnivore (Zengeya and Marshal 2007), it does not have high preference for protein in its diet. This could explain why this species exhibited the largest handling time in the present study. In the same way, *M. salmoides* have previously been directly shown to have low handling times (Collar et al. 2009), as reflected in this study, where handling time was derived from a functional response model. This biological feature, combined with the known high attack rates and swimming speeds of *M. salmoides* promotes its feeding success (Collar et al. 2009) and therefore, its functional response. Even though *L. macrochirus* is known to practice suction feeding like *M. salmoides*, their smaller mouth (Carroll et al. 2004) is likely an indication of their preference for aquatic invertebrates and a more omnivorous diet (see Chapter three).

The present chapter represents a laboratory investigation on a series of pairwise interactions between one species of predator and one species of prey. These artificial conditions are highly unlikely to represent anything experienced by the predators under natural conditions. It could, therefore, be argued that such studies have little relevance for real ecological scenarios. Simplification, has, however, been identified as important for a mechanistic understanding of various processes in ecology, where confounding factors need to be either catered for or eliminated. Simple experiments such as this can, therefore, provide insight into how predators would theoretically interact with prey under various conditions in the wild. For example, *M. salmoides* has been documented to have large impacts on prey community structure (Maezono and Miyashita 2003). It has been suggested that this species outcompetes native species because of its predatory efficiency. Studies such as this one reflect this finding and offers insight into how this may play out. *Micropterus salmoides* is also particularly efficient at

finding prey, even when prey are present in very low densities. In another functional response study directed specifically at *M. salmoides*, Alexander et al. (2015) showed that the species is capable of finding prey even at low densities in complex habitat. Given these findings, I suggest that the top predator in the Kariega River system is *M. salmoides*. This may also explain why the small native minnow, *Enteromius anoplus*, was not sampled from sites where *M. salmoides* were present (see Chapter Two). In the current study, size-matched *L. macrochirus* and *T. sparrmanii* had lower functional responses and this implies that they may depend less on fish in their diets. With regard to native fish fauna, it is therefore highly likely that *L. macrochirus* and *T. sparrmanii* are of less concern as invaders in the system than *M. salmoides* and *P. philander*. *Lepomis macrochirus* does, however, grow larger than either *T. sparrmanii* and *P. philander*. Future research should therefore assess the influence of body size on functional response. In addition, impacts of the four species on invertebrate communities have not yet been assessed.

It has been made clear that there is not sufficient information on many of the invasive species in South Africa (Ellender et al. 2010). This chapter contributes to our understanding of the impact potential of four introduced species: *M. salmoides*, *P. philander*, *L. macrochirus* and *T. sparrmanii*. In addition to identifying the most problematic species in the Kariega River system, from a functional response perspective, the study is also among the first to assess potential impacts of *P. philander* and *T. sparrmanii* within an invasion context.

CHAPTER 5: General discussion

Lepomis macrochirus is widely distributed in South Africa and is categorised as alien and invasive in South Africa (Ellender and Weyl 2014). This suggests that there is a need for the management of this species. Results of this study contributed to better understanding of the establishment success and impacts of this species in an invaded South African River system in order to better understand and document its potential impacts. This was done by assessing the distribution and relative abundance of fish species in the Kariega River system, Eastern Cape; determining the diet of *L. macrochirus* in an impoundment and by using functional response experiments to assess whether *L. macrochirus* has heightened predatory capabilities when compared to fishes with which it co-occurs, in this case *Micropterus salmoides*, *Tilapia sparrmanii* and *Pseudocrenilabrus philander*.

Results showed that the Kariega River is heavily invaded by *L. macrochirus* and other non-native fishes. These non-native fishes restrict the distribution of native fishes to the upper reaches of the river system and there were few uninvaded habitats. The introduced Centrarchids *M. salmoides* and *L. macrochirus* appear to exert higher impact on the native fishes than the extralimittally introduced *P. philander* and *T. sparrmanii*. This is because small native fish occasionally co-occurred with *T. sparrmanii* and *P. philander* but never with *M. salmoides* and *L. macrochirus*. To try to separate these impacts, the next step was to try to assess the individual impacts of *M. salmoides* and *L. macrochirus* on small fishes. The first step was to assess the diet of *L. macrochirus* (Chapter three) as this has not previously been assessed in South Africa.

This assessment demonstrated that *L. macrochirus* have a similar feeding ecology in South Africa as in their native range with their diet shifting from small to large prey organisms with an increase in body size. In addition, seasonal differences in the diets of *L. macrochirus* in the system were evident. Overall, *L. macrochirus* are generalist feeders with crustacea and insects comprising most of the diet but also including fish and fish eggs in their diet. *Lepomis macrochirus* are known to consume their fish eggs during the mating season as they do not have time to search for food because they provide parental care to their developing fry (Neff 2003). According to the literature, *T. sparrmanii* (Winemiller and Kelso-Winemiller 2003) and *P. philander* (Polling et al. 1995) are also known to be omnivorous and sometimes include fish in their diets (Table 5.1).

The diet of *L. macrochirus* was compared to that of *M. salmoides*, *T. sparrmanii* and *P. philander* which were the other non-native fish common in the river system (Table 5.1). Overall, *M. salmoides* is carnivorous (Taylor 2012; Wasserman et al. 2011; Weyl et al. 1998) while *L. macrochirus*, *T. sparrmanii* and *P. philander* have an omnivorous diet (Muller et al. 2015; Polling et al. 1995; Winemiller and Kelso-Winemiller 2003). There is, however, evidence for dietary overlap between *L. macrochirus* and the co-occurring predators, which may result in competition for resources and cause a considerable predation pressure on a variety of aquatic invertebrates. The presence of invertebrates in the diets of all four species also suggest that the four species do not only have negative impacts on native fish only, they may also have a negative predation pressure on aquatic invertebrates. As aquatic insects and fish were the common prey items in all the predators, fish were used to compare the potential impacts of the four species in a functional response experiment (Chapter four).

Table 5.1: The comparison of *Lepomis macrochirus* diet with the other non-native fishes it co-occurs with in the Kariega River system.

Food item	<i>Lepomis macrochirus</i>	<i>Micropterus salmoides</i>	<i>Tilapia sparrmanii</i>	<i>Pseudocrenilabrus philander</i>
Aquatic Insects	Present	Present	Present	Present
Terrestrial insects	Absent	Present	Absent	Present
Crabs	Absent	Present	Absent	Absent
Zooplankton	Present	Present	Absent	Present
Plants	Present	Absent	Present	Present
<u>Fish</u>	<u>Present</u>	<u>Present</u>	<u>Present</u>	<u>Present</u>
Reference	Results from present study (Van Someren 1946; Olson et al. 2003; Neff 2003; Diggins et al. 1979)	(Weyl et al. 1998; Wasserman et al. 2011; Taylor 2012)	(Winemiller and Kelso-Winemiller 2003)	(Polling et al. 1995; Muller et al. 2015; Zengeya and Marshall 2007)

Functional response experiments provided an insight into how predators would theoretically interact with prey in the wild. Results showed that, for all four predatory species, all prey were consumed at low densities, but as the prey density increased, predatory activity varied depending on the species. *Lepomis macrochirus* had a similar impact to that of *P. philander* and *T. sparrmanii*, but lower than that of *M. salmoides*. At low prey densities, *Tilapia sparrmanii* was the poorest at consuming prey suggesting that higher densities of prey are

needed to stimulate its predatory response. *Tilapia sparrmanii*, is known to incorporate less animal material in its diet (Winemiller and Kelso-Winemiller 2003) therefore, it had the lowest functional response. *Micropterus salmoides* had the highest functional response of all the fish, suggesting that it has more predatory effect on native fishes than the other predators.

Non-native fishes were present in the river sites where they were introduced and the river sites below those sites of introduction. The disappearance of native fish in sites where *L. macrochirus* and *M. salmoides* is present can be most attributed to *M. salmoides* as it had a higher functional response and high preference for fish in their diet (Taylor 2012). Only large sized native fish (*Anguilla mossambica* and *Labeo umbratus*) could manage to co-occur with the piscivorous *M. salmoides*, but they have a limited distribution range. *Lepomis macrochirus* also contributes to fish predation as fish were present in their diet (see Chapter three) but less so than *M. salmoides*. *Tilapia sparrmanii* was present in all three sections, but likely had a limited negative predatory impact on native fish as it had the lowest functional response of the predators. This species is known to have less preference for animals in its diet (Winemiller and Kelso-Winemiller 2003), and could explain why small bodied native fish were still present in sites occupied by *T. sparrmanii*. Similarly, in *P. philander* fish is not a dominant prey item (Muller et al. 2015; Polling et al. 1995) which might explain its co-occurrence with small bodied native fish.

In conclusion, *L. macrochirus* is well established in the Kariega River system with the presence of juvenile and adult fish indicating a self-sustaining population. There is the possibility for competition for resources between these predators as dietary overlap was observed when comparing them. *Lepomis macrochirus* had a similar impact to that of *T. sparrmanii* and *P. philander*, but lower than that of *M. salmoides*. This suggests that the non-native fish do not only have predation impacts on native fish they may also compete with the native fishes in the river system. Future research should focus on quantifying the impacts of these invaders on the ecosystem.

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Index

Appendix 1: Presence (1) and absence (0) of fish species at 96 sites sampled on the Kariega River, Eastern Cape South Africa sampled using electrofishing, seine netting, gill netting, fyke netting and hook and line fishing from 15/01-15/12/2015. Fish species: TS = *Tilapia sparrmanii*, PP = *Pseudocrenilabrus philander*, LMa = *Labeobarbus marequensis*, LM = *Lepomis macrochirus*, MS = *Micropterus salmoides*, EA = *Enteromius anoplus*, GC = *Glossogobius callidus*, LU = *Labeo umbratus*, AM = *Anguilla mossambica*, EP = *Enteromius pallidus*, MF = *Monodactylus falciformis*, MC = *Myxus capensis*, GA = *Gilchristella aestuaria*.

Site #	Coordinates		Fish species												
	Latitude	Longitude	TS	PP	LMa	LM	MS	EA	GC	LU	AM	EP	MF	MC	GA
1	S33.368733 ⁰	S26.477150 ⁰	0	0	0	0	0	1	0	0	0	0	0	0	0
2	S33.369567 ⁰	E26.477933 ⁰	0	0	0	0	0	1	0	0	0	0	0	0	0
3	S33.370350 ⁰	E26.479483 ⁰	0	0	0	0	0	1	0	0	0	0	0	0	0
4	S33.370083 ⁰	E26.478750 ⁰	1	1	0	0	0	1	0	0	0	0	0	0	0
5	S33.370700 ⁰	E26.477033 ⁰	1	1	0	0	0	1	0	0	0	0	0	0	0
6	S33.37117 ⁰	E26.476700 ⁰	1	1	0	0	0	0	0	0	0	0	0	0	0
7	S33.369650 ⁰	E26.476050 ⁰	0	0	0	0	0	1	0	0	0	0	0	0	0
8	S33.369800 ⁰	E26.474950 ⁰	0	0	0	0	0	1	0	0	0	0	0	0	0
9	S33.369350 ⁰	E26.474567 ⁰	0	0	0	0	0	0	0	0	0	0	0	0	0
10	S33.369200 ⁰	E26.474583 ⁰	0	0	0	0	0	0	0	0	0	0	0	0	0
11	S33.355917 ⁰	E26.514050 ⁰	0	0	0	0	0	0	0	0	0	0	0	0	0
12	S33.355167 ⁰	E26.513583 ⁰	0	0	0	0	0	0	0	0	0	0	0	0	0
13	S33.362950 ⁰	E26.514850 ⁰	1	1	0	0	0	1	0	0	0	0	0	0	0

14	S33.358714 ⁰	E26.513964 ⁰	1	1	1	0
15	S33.360917 ⁰	E26.483350 ⁰	1	1	0	0
16	S33.360600 ⁰	E26.484000 ⁰	0	0	0	0
17	S33.357767 ⁰	E26.487417 ⁰	0	0	0	0
18	S33.355917 ⁰	E26.471950 ⁰	0	0	0	0
19	S33.425594 ⁰	E26.432861 ⁰	1	1	0	0
20	S33.357867 ⁰	E26.474850 ⁰	0	0	0	0
21	S33.358050 ⁰	E26.475400 ⁰	0	1	0	0
22	S33.359883 ⁰	E26.478483 ⁰	1	1	0	0
23	S33.355450 ⁰	E26.466633 ⁰	0	0	0	0
24	S33.360550 ⁰	E26.488783 ⁰	0	0	0	0
25	S33.353433 ⁰	E26.471667 ⁰	0	0	0	0
26	S33.403050 ⁰	E26.452650 ⁰	0	0	0	1
27	S33.358618 ⁰	E26486017 ⁰	0	0	0	0
28	S33.424586 ⁰	E26431706 ⁰	1	0	0	0
29	S33.425081 ⁰	E26.428639 ⁰	1	0	0	0
30	S33.425058 ⁰	E26.428672 ⁰	1	0	0	0
31	S33.415183 ⁰	E26.377706 ⁰	1	0	0	0
32	S33.40910 ⁰	E026.50051 ⁰	0	1	0	1
33	S33.386836 ^{0"}	E26.484506 ⁰	0	0	0	1
34	S33.31045 ⁰	E26.51951 ⁰	1	0	0	1

0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	1	1	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	1	1	0	0	0	0	0
0	1	1	1	0	0	0	0	0
0	1	1	1	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	1	0	0	0	0	0	0
0	0	0	0	1	0	0	0	0

35	S33.38966°	E26.48739°	1	1	0	1
36	S33.39100°	E26.48812°	0	1	0	0
37	S33.39104°	E26.48847°	0	0	0	0
38	S33.448700°	E26.456233°	1	0	0	0
39	S33.460733°	E26.485883°	1	0	0	0
40	S33.451200°	E26.464017°	0	0	0	0
41	S33.448381°	E26.452067°	1	0	0	0
42	S33.456422°	E26.483453°	1	0	0	0
43	S33.455217°	E26.479844°	0	0	0	0
44	S33.457725°	E26.478961°	1	0	0	0
45	S33.463336°	E26.477456°	1	0	0	0
46	S33.461000°	E26.481217°	1	0	0	0
47	S33.461633°	E26.481600°	1	0	0	0
48	S33.486283°	E26.526167°	1	0	0	0
49	S33.483778°	E26.525933°	0	0	0	0
50	S33.507200°	E26.624017°	0	0	0	0
51	S33412783°	E26.533250°	1	0	0	0
52	S33.413100°	E26.533083°	0	0	0	0
53	S33.413283°	E26.532850°	0	0	0	0
54	S33.413517°	E26.578317°	1	0	0	1
55	S33.416333°	E26.582067°	0	0	0	0

0	0	0	0	1	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
1	0	0	1	0	0	0	0	0
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0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0

56	S33.416800°	E26.582683°	0	0	0	0
57	S33.25.161°	E26.593883°	0	0	0	0
58	S33.28.853°	E26.632783°	1	0	0	0
59	S33.480883°	E26.628533°	0	0	0	0
60	S33.607383°	E26.632367°	0	0	0	0
61	S33.599033°	E26.631883°	0	0	0	0
62	S33.472583°	E26.606567°	0	0	0	1
63	S33.458300°	E26.602633°	0	0	0	0
65	S33.452550°	E26.597350°	1	0	0	0
66	S33.452717°	E26.597450°	1	0	0	0
67	S33.440167°	E26.592014°	1	0	0	0
68	S33.438517°	E26.591850°	1	0	0	0
69	S33.433033°	E26.603467°	0	0	0	0
70	S33.352533°	E26.496875°	0	0	0	0
71	S33.353081°	E26.496769°	0	0	0	0
72	S33.351708°	E26.497428°	0	0	0	0
73	S33.569200°	E26.637150°	0	0	0	0
74	S33.593950°	E26.634100°	0	0	0	1
75	S33.551533°	E26.610983°	0	0	0	1
76	S33.551317°	E26.611800°	0	0	0	0
77	S33.542800°	E26.604033°	0	0	0	0

0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	1	1	0
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0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0

78	S33.513050°	E26.608817°	1	0	0	0
79	S33.505667°	E26.594383°	1	0	0	0
80	S33.371983°	E26.422133°	0	0	0	1
81	S33.368461°	E26.429408°	0	0	0	1
82	S33.373647°	E26.451242°	0	0	0	1
83	S33.399303°	E26.421425°	0	0	0	1
84	S33.351550°	E26.497567°	0	0	0	0
85	S33.351400°	E26.497617°	0	0	0	0
86	S33.351267°	E26.497783°	0	0	0	0
87	S33.351075°	E26.497644°	0	0	0	0
88	S33.350717°	E26.497550°	0	0	0	0
89	S33.350567°	E26.497450°	0	0	0	0
90	S33.350267°	E26.497400°	0	0	0	0
91	S33363533°	E26.497667°	0	0	0	0
92	S33.350133°	E26.497717°	0	0	0	0
93	S33.349750°	E26.49773°	0	0	0	0
94	S33.349633°	E26.497533°	0	0	0	0
95	S33.521786°	E26.616278°	1	0	0	1
96	S33.526886°	E26.608811°	1	0	0	0

0	0	0	0	1	0	0	0	0
1	0	0	0	1	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
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0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0

Appendix 2: Estimates of abundance for TS= *Tilapia sparrmanii*, PP= *Pseudocrenilabrus philander*, LMar= *Labeobarbus marequensis*, EA= *Enteromius anoplus*, MS= *Micropterus salmoides*, LM= *Lepomis macrochirus*, GC= *Glossogobius callidus*, LU= *Labeo umbratus*, AM= *Anguilla mossambica*, EP= *Enteromius pallidus*, MF= *Monodactylus falciformis*, MC= *Myxus capensis* and GA= *Gilchristella aestuaria* caught using different gears during field surveys in the Kariega River system, South Africa.

	TS	PP	LMar	EA	MS	LM	GC	LU	AM	EP	MF	MC	GA
Electrofishing													
Mean	0.95	1.41	0.00	1.61	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Std error	0.48	1.18	0.00	0.57	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00
DR	0.13	0.13	0.00	0.34	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
N (Sampled sites)	56.00	56.00	56.00	56.00	56.00	56.00	56.00	56.00	56.00	56.00	56.00	56.00	56.00
Fyke netting													
Mean	1.36	0.13	0.00	0.00	0.08	0.50	0.11	0.14	0.02	0.00	0.01	0.00	0.00
Std error	0.49	0.06	0.00	0.00	0.02	0.07	0.04	0.05	0.01	0.00	0.01	0.00	0.00
DR	0.16	0.02	0.00	0.00	0.06	0.24	0.04	0.04	0.02	0.00	0.001		
N (fyke net nights)	256.00	256.00	256.00	256.00	256.00	256.00	256.00	256.00	256.00	256.00	256.00	256.00	256.00
Gill netting													
Mean	0.17	0.00	0.02	0.00	0.37	0.17	0.00	13.26	0.00	0.00	0.00	0.00	0.00
Std error	0.12	0.00	0.02	0.00	0.12	0.06	0.00	6.69	0.00	0.00	0.00	0.00	0.00
DR	0.07	0.00	0.02	0.00	0.26	0.15	0.00	0.09	0.00	0.00	0.00	0.00	0.00
N (gill net nights)	46.00	46.00	46.00	46.00	46.00	46.00	46.00	46.00	46.00	46.00	46.00	46.00	46.00
Hook and line													
Mean	0.00	0.00	0.00	0.00	6.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Std error	0.00	0.00	0.00	0.00	4.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
DR	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

N (number of sites)	4.00	4.00	4.00	4.00	4.00	4.00
Seine netting						
Mean	12.73	1.45	0.00	0.05	0.92	2.78
Std error	7.76	1.22	0.00	0.04	0.45	1.85
DR	0.43	0.10	0.0	0.03	0.13	0.08
N (number of pulls)	60.00	60.00	60.00	60.00	60.00	60.00

4.00	4.00	4.00	4.00	4.00	4.00	4.00
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0.75	0.00	0.00	0.00	0.02	0.03	0.05
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0.39	0.00	0.00	0.00	0.02	0.03	0.05
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0.13	0.00	0.00	0.00	0.02	0.02	0.02
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60.00	60.00	60.00	60.00	60.00	60.00	60.00
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Appendix 3: Number of fish species sampled in each site on the Kariega River, Eastern Cape South Africa using different gears. Fish species: TS = *Tilapia sparrmanii*, PP = *Pseudocrenilabrus philander*, LMa = *Labeobarbus marequensis*, LM = *Lepomis macrochirus*, MS = *Micropterus salmoides*, EA = *Enteromius anopus*, GC = *Glossogobius callidus*, LU = *Labeo umbratus*, AM = *Anguilla mossambica*, EP = *Enteromius pallidus*, MF = *Monodactylus falciformis*, MC = *Myxus capensis*, GA = *Gilchristella aestuaria*.

Site No	Section	GPS S	GPS E	Gear	TS	PP	Lma	EA	MS	LM	GC	LU	AM	EP	MF	MC	GA
1	1	S33.368733 ⁰	S26.477150 ⁰	Electro fishing	0	0	0	2	0	0	0	0	0	0	0	0	0
2	1	S33.369567 ⁰	E26.477933 ⁰	Electro fishing	0	0	0	3	0	0	0	0	0	0	0	0	0
3	1	S33.370350 ⁰	E26.479483 ⁰	Electro fishing	0	0	0	4	0	0	0	0	0	0	0	0	0
4	1	S33.370083 ⁰	E26.478750 ⁰	Electro fishing	14	2	0	2	0	0	0	0	0	0	0	0	0
4	1	S33.370083 ⁰	E26.478750 ⁰	Electro fishing	0	0	0	3	0	0	0	0	0	0	0	0	0
5	1	S33.370700 ⁰	E26.477033 ⁰	Electro fishing	4	3	0	3	0	0	0	0	0	0	0	0	0
6	1	S33.37117 ⁰	E26.476700 ⁰	Electro fishing	2	1	0	0	0	0	0	0	0	0	0	0	0
7	1	S33.369650 ⁰	E26.476050 ⁰	Electro fishing	0	0	0	6	0	0	0	0	0	0	0	0	0
8	1	S33.369800 ⁰	E26.474950 ⁰	Electro fishing	0	0	0	4	0	0	0	0	0	0	0	0	0
9	1	S33.369350 ⁰	E26.474567 ⁰	Electro fishing	0	0	0	0	0	0	0	0	0	0	0	0	0
10	1	S33.369200 ⁰	E26.474583 ⁰	Electro fishing	0	0	0	0	0	0	0	0	0	0	0	0	0
11	1	S33.355917 ⁰	E26.514050 ⁰	Electro fishing	0	0	0	0	0	0	0	0	0	0	0	0	0
12	1	S33.355167 ⁰	E26.513583 ⁰	Electro fishing	0	0	0	0	0	0	0	0	0	0	0	0	0
13	1	S33.362950 ⁰	E26.514850 ⁰	Electro fishing	22	1	0	1	0	0	0	0	0	0	0	0	0
14	1	S33.358714 ⁰	E26.513964 ⁰	Fyke net	1	0	0	0	0	0	0	0	0	0	0	0	0
14	1	S33.358714 ⁰	E26.513964 ⁰	Fyke net	32	7	0	0	0	0	0	0	0	0	0	0	0
14	1	S33.358714 ⁰	E26.513964 ⁰	Fyke net	82	8	0	0	0	0	0	0	0	0	0	0	0
14	1	S33.358714 ⁰	E26.513964 ⁰	Fyke net	20	0	0	0	0	0	0	0	0	0	0	0	0
14	1	S33.358714 ⁰	E26.513964 ⁰	Fyke net	5	5	0	0	0	0	0	0	0	0	0	0	0
14	1	S33.358714 ⁰	E26.513964 ⁰	Fyke net	0	0	0	0	0	0	0	0	0	0	0	0	0

14	1	S33.358714 ⁰	E26.513964 ⁰	Fyke net
14	1	S33.358714 ⁰	E26.513964 ⁰	Fyke net
14	1	S33.358714 ⁰	E26.513964 ⁰	Gill net
14	1	S33.358714 ⁰	E26.513964 ⁰	Gill net
14	1	S33.358714 ⁰	E26.513964 ⁰	Gill net
14	1	S33.358714 ⁰	E26.513964 ⁰	Sein net
14	1	S33.358714 ⁰	E26.513964 ⁰	Sein net
14	1	S33.358714 ⁰	E26.513964 ⁰	Sein net
15	1	S33.360917 ⁰	E26.483350 ⁰	Electro fishing
16	1	S33.360600 ⁰	E26.484000 ⁰	Electro fishing
17	1	S33.357767 ⁰	E26.487417 ⁰	Electro fishing
18	1	S33.355917 ⁰	E26.471950 ⁰	Electro fishing
19	2	S33.425594 ⁰	E26.432861 ⁰	Fyke net
19	2	S33.425594 ⁰	E26.432861 ⁰	Fyke net
19	2	S33.425594 ⁰	E26.432861 ⁰	Sein net
19	2	S33.425594 ⁰	E26.432861 ⁰	Sein net
19	2	S33.425594 ⁰	E26.432861 ⁰	Sein net
19	2	S33.425594 ⁰	E26.432861 ⁰	Sein net
20	1	S33.357867 ⁰	E26.474850 ⁰	Electro fishing
21	1	S33.358050 ⁰	E26.475400 ⁰	Electro fishing
22	1	S33.359883 ⁰	E26.478483 ⁰	Fyke net
22	1	S33.359883 ⁰	E26.478483 ⁰	Fyke net
22	1	S33.359883 ⁰	E26.478483 ⁰	Sein net
23	1	S33.355450 ⁰	E26.466633 ⁰	Electro fishing

0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	1	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0
11	3	0	0	0	0	0	0	0	0	0	0	0
17	4	0	0	0	0	0	0	0	0	0	0	0
11	3	0	0	0	0	0	0	0	0	0	0	0
1	66	0	0	0	0	0	0	0	0	0	0	0
0	0	0	17	0	0	0	0	0	0	0	0	0
0	0	0	26	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	1	0	0	0	0	0
0	0	0	0	0	0	0	1	0	0	0	0	0
3	1	0	0	0	0	2	0	0	0	0	0	0
3	0	0	0	0	0	5	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	5	0	1	0	0	0	0	0	0	0	0	0
85	9	0	0	0	0	0	0	0	0	0	0	0
22	3	0	0	0	0	0	0	0	0	0	0	0
422	73	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0

24	1	S33.360550 ⁰	E26.488783 ⁰	Electro fishing
25	1	S33.353433 ⁰	E26.471667 ⁰	Electro fishing
26	2	S33.403050 ⁰	E26.452650 ⁰	Fyke net
26	2	S33.403050 ⁰	E26.452650 ⁰	Fyke net
26	2	S33.403050 ⁰	E26.452650 ⁰	Fyke net
26	2	S33.403050 ⁰	E26.452650 ⁰	Fyke net
26	2	S33.403050 ⁰	E26.452650 ⁰	Fyke net
26	2	S33.403050 ⁰	E26.452650 ⁰	Fyke net
26	2	S33.403050 ⁰	E26.452650 ⁰	Fyke net
26	2	S33.403050 ⁰	E26.452650 ⁰	Fyke net
26	2	S33.403050 ⁰	E26.452650 ⁰	Fyke net
26	2	S33.403050 ⁰	E26.452650 ⁰	Fyke net
26	2	S33.403050 ⁰	E26.452650 ⁰	Fyke net
26	2	S33.403050 ⁰	E26.452650 ⁰	Fyke net
26	2	S33.403050 ⁰	E26.452650 ⁰	Fyke net
26	2	S33.403050 ⁰	E26.452650 ⁰	Fyke net
26	2	S33.403050 ⁰	E26.452650 ⁰	Fyke net
26	2	S33.403050 ⁰	E26.452650 ⁰	Gill net
26	2	S33.403050 ⁰	E26.452650 ⁰	Gill net
26	2	S33.403050 ⁰	E26.452650 ⁰	Gill net
26	2	S33.403050 ⁰	E26.452650 ⁰	Gill net
26	2	S33.403050 ⁰	E26.452650 ⁰	Gill net
26	2	S33.403050 ⁰	E26.452650 ⁰	Gill net
26	2	S33.403050 ⁰	E26.452650 ⁰	Gill net
26	2	S33.403050 ⁰	E26.452650 ⁰	Gill net
26	2	S33.403050 ⁰	E26.452650 ⁰	Hook and Line Fishing
26	2	S33.403050 ⁰	E26.452650 ⁰	Sein net
26	2	S33.403050 ⁰	E26.452650 ⁰	Sein net

0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	1	5	0	0	0	0	0	0	0
0	0	0	0	2	2	0	0	0	0	0	0	0
0	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	2	0	0	0	0	0	0	0	0
0	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	1	1	0	0	0	0	0	0	0
0	0	0	0	1	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	20	0	0	0	0	0	0	0	0
0	0	0	0	19	102	0	0	0	0	0	0	0
0	0	0	0	3	43	0	0	0	0	0	0	0

0	0	0	7	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	2	0	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	22	0	0	0	0	0	0
0	0	0	0	0	0	6	0	0	0	0	0	0
5	0	0	0	0	0	0	3	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	3	0	0	0	0	0	0
0	0	0	1	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	2	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	2	0	0	0	0	0
0	0	0	0	0	0	0	3	0	0	0	0	0
0	0	0	0	0	0	1	0	0	0	0	0	0
1	0	0	0	0	0	4	0	0	0	0	0	0
1	0	0	2	0	0	0	0	0	0	0	0	0
0	0	0	0	1	0	0	0	0	0	0	0	0
0	0	0	0	3	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0

31	3	S33.415183 ⁰	E26.377706 ⁰	Gill net
31	3	S33.415183 ⁰	E26.377706 ⁰	Gill net
31	3	S33.415183 ⁰	E26.377706 ⁰	Gill net
31	3	S33.415183 ⁰	E26.377706 ⁰	Gill net
31	3	S33.415183 ⁰	E26.377706 ⁰	Sein net
31	3	S33.415183 ⁰	E26.377706 ⁰	Sein net
31	3	S33.415183 ⁰	E26.377706 ⁰	Sein net
31	3	S33.415183 ⁰	E26.377706 ⁰	Sein net
31	3	S33.415183 ⁰	E26.377706 ⁰	Sein net
32	2	S33.40910 ⁰	E026.50051 ⁰	Fyke net
32	2	S33.40910 ⁰	E026.50051 ⁰	Fyke net
32	2	S33.40910 ⁰	E026.50051 ⁰	Fyke net
32	2	S33.40910 ⁰	E026.50051 ⁰	Fyke net
32	2	S33.40910 ⁰	E026.50051 ⁰	Fyke net
32	2	S33.40910 ⁰	E026.50051 ⁰	Fyke net
32	2	S33.40910 ⁰	E026.50051 ⁰	Fyke net
32	2	S33.40910 ⁰	E026.50051 ⁰	Fyke net
32	2	S33.40910 ⁰	E026.50051 ⁰	Fyke net
32	2	S33.40910 ⁰	E026.50051 ⁰	Fyke net
32	2	S33.40910 ⁰	E026.50051 ⁰	Fyke net
32	2	S33.40910 ⁰	E026.50051 ⁰	Fyke net
32	2	S33.40910 ⁰	E026.50051 ⁰	Fyke net
32	2	S33.40910 ⁰	E026.50051 ⁰	Fyke net
32	2	S33.40910 ⁰	E026.50051 ⁰	Gill net
32	2	S33.40910 ⁰	E026.50051 ⁰	Gill net
32	2	S33.40910 ⁰	E026.50051 ⁰	Gill net

0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	4	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	1	0	0	0	0	0	0	0	0
1	0	0	0	1	0	0	0	0	0	0	0	0
4	0	0	0	4	0	0	0	0	0	0	0	0
1	0	0	0	4	0	0	0	0	0	0	0	0
11	0	0	0	4	0	0	0	0	0	0	0	0
2	0	0	0	19	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	3	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	1	0	0	0	0	0	0	0	0

0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	3	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	1	0	0	0	0	0	0	0	0
0	0	0	0	2	0	0	0	0	0	0	0	0
0	3	0	0	0	18	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	1	1	0	0	0	0	0	0	0
0	0	0	0	0	4	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	0	3	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0

0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	6	0	0	0	0	0	0	0
0	0	0	0	0	3	0	0	0	0	0	0	0
0	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	4	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	3	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	3	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	1	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	2	0	0	0	0	0	0	0

0	0	0	0	0	3	0	0	0	0	0	0	0
0	0	0	0	0	6	0	0	0	0	0	0	0
0	0	0	0	0	3	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	3	0	0	0	0	0	0	0
0	0	0	0	0	4	0	0	0	0	0	0	0
0	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0

33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Fyke net
33	2	S33.386836°"	E26.484506°	Gill net
33	2	S33.386836°"	E26.484506°	Gill net
33	2	S33.386836°"	E26.484506°	Gill net
33	2	S33.386836°"	E26.484506°	Gill net

0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	3	0	0	0	0	0	0	0
0	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	4	0	0	0	0	0	0
0	0	0	0	0	0	3	0	0	0	0	0	0
0	0	0	0	0	0	3	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	2	0	0	0	0	0	0
0	0	0	0	0	0	2	0	0	0	0	0	0
0	0	0	0	0	0	7	0	0	0	0	0	0
0	0	0	0	0	0	3	0	0	0	0	0	0
0	0	0	0	0	0	1	0	0	0	0	0	0
0	0	0	0	0	0	3	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	1	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	1	0	0	0	0	0	0	0	0

33	2	S33.386836°"	E26.484506°	Gill net
33	2	S33.386836°"	E26.484506°	Gill net
33	2	S33.386836°"	E26.484506°	Gill net
33	2	S33.386836°"	E26.484506°	Gill net
33	2	S33.386836°"	E26.484506°	Gill net
33	2	S33.386836°"	E26.484506°	Gill net
33	2	S33.386836°"	E26.484506°	Gill net
33	2	S33.386836°"	E26.484506°	Gill net
34	2	S33.31045°	E26.51951°	Electro fishing
34	2	S33.31045°	E26.51951°	Fyke net
34	2	S33.31045°	E26.51951°	Fyke net
34	2	S33.31045°	E26.51951°	Fyke net
34	2	S33.31045°	E26.51951°	Fyke net
34	2	S33.31045°	E26.51951°	Fyke net
34	2	S33.31045°	E26.51951°	Fyke net
35	2	S33.38966°	E26.48739°	Electro fishing
35	2	S33.38966°	E26.48739°	Fyke net
35	2	S33.38966°	E26.48739°	Fyke net
35	2	S33.38966°	E26.48739°	Fyke net
36	2	S33.39100°	E26.48812°	Electro fishing
36	2	S33.39100°	E26.48812°	Fyke net
36	2	S33.39100°	E26.48812°	Fyke net
36	2	S33.39100°	E26.48812°	Fyke net
37	2	S33.39104°	E26.48847°	Electro fishing

0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	1	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	1	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	1	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	1	0	0	0	0
0	1	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0

37	2	S33.39104°	E26.48847°	Fyke net
37	2	S33.39104°	E26.48847°	Fyke net
37	2	S33.39104°	E26.48847°	Fyke net
38	3	S33.448700°	E26.456233°	Fyke net
38	3	S33.448700°	E26.456233°	Fyke net
39	3	S33.460733°	E26.485883°	Fyke net
39	3	S33.460733°	E26.485883°	Fyke net
40	3	S33.451200°	E26.464017°	Fyke net
40	3	S33.451200°	E26.464017°	Fyke net
41	3	S33.448381°	E26.452067°	Fyke net
41	3	S33.448381°	E26.452067°	Fyke net
41	3	S33.448381°	E26.452067°	Fyke net
41	3	S33.448381°	E26.452067°	Fyke net
41	3	S33.448381°	E26.452067°	Fyke net
41	3	S33.448381°	E26.452067°	Fyke net
41	3	S33.448381°	E26.452067°	Gill net
41	3	S33.448381°	E26.452067°	Gill net
41	3	S33.448381°	E26.452067°	Gill net
41	3	S33.448381°	E26.452067°	Gill net
42	3	S33.456422°	E26.483453°	Fyke net
42	3	S33.456422°	E26.483453°	Fyke net
43	3	S33.455217°	E26.479844°	Fyke net
43	3	S33.455217°	E26.479844°	Fyke net
44	3	S33.457725°	E26.478961°	Fyke net

0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	1	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0
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1	0	0	0	0	0	0	7	0	0	0	0	0
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44	3	S33.457725°	E26.478961°	Fyke net
45	3	S33.463336°	E26.477456°	Fyke net
45	3	S33.463336°	E26.477456°	Fyke net
46	3	S33.461000°	E26.481217°	Fyke net
47	3	S33.461633°	E26.481600°	Fyke net
48	3	S33.486283°	E26.526167°	Fyke net
48	3	S33.486283°	E26.526167°	Fyke net
48	3	S33.486283°	E26.526167°	Fyke net
49	3	S33.483778°	E26.525933°	Fyke net
49	3	S33.483778°	E26.525933°	Fyke net
50	2	S33.507200°	E26.624017°	Fyke net
50	2	S33.507200°	E26.624017°	Fyke net
50	2	S33.507200°	E26.624017°	Fyke net
51	2	S33412783°	E26.533250°	Fyke net
51	2	S33412783°	E26.533250°	Fyke net
52	2	S33.413100°	E26.533083°	Fyke net
53	2	S33.413283°	E26.532850°	Fyke net
54	2	S33.413517°	E26.578317°	Fyke net
54	2	S33.413517°	E26.578317°	Fyke net
54	2	S33.413517°	E26.578317°	Fyke net
54	2	S33.413517°	E26.578317°	Fyke net
54	2	S33.413517°	E26.578317°	Sein net
55	2	S33.416333°	E26.582067°	Fyke net
55	2	S33.416333°	E26.582067°	Fyke net

55	2	S33.416333°	E26.582067°	Sein net
56	2	S33.416800°	E26.582683°	Fyke net
56	2	S33.416800°	E26.582683°	Sein net
57	2	S33.25.161°	E26.593883°	Fyke net
57	2	S33.25.161°	E26.593883°	Fyke net
57	2	S33.25.161°	E26.593883°	Sein net
58	2	S33.28.853°	E26.632783°	Fyke net
58	2	S33.28.853°	E26.632783°	Fyke net
58	2	S33.28.853°	E26.632783°	Sein net
59	2	S33.480883°	E26.628533°	Fyke net
59	2	S33.480883°	E26.628533°	Fyke net
59	2	S33.480883°	E26.628533°	Sein net
60	2	S33.607383°	E26.632367°	Fyke net
60	2	S33.607383°	E26.632367°	Fyke net
60	2	S33.607383°	E26.632367°	Fyke net
60	2	S33.607383°	E26.632367°	Sein net
60	2	S33.607383°	E26.632367°	Sein net
61	2	S33.599033°	E26.631883°	Fyke net
61	2	S33.599033°	E26.631883°	Fyke net
61	2	S33.599033°	E26.631883°	Fyke net
61	2	S33.599033°	E26.631883°	Sein net
61	2	S33.599033°	E26.631883°	Sein net
62	2	S33.472583°	E26.606567°	Fyke net
62	2	S33.472583°	E26.606567°	Fyke net

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62	2	S33.472583°	E26.606567°	Fyke net
63	2	S33.458300°	E26.602633°	Fyke net
63	2	S33.458300°	E26.602633°	Fyke net
63	2	S33.458300°	E26.602633°	Fyke net
63	2	S33.458300°	E26.602633°	Sein net
63	2	S33.458300°	E26.602633°	Sein net
65	2	S33.452550°	E26.597350°	Fyke net
65	2	S33.452550°	E26.597350°	Fyke net
65	2	S33.452550°	E26.597350°	Sein net
65	2	S33.452550°	E26.597350°	Sein net
66	2	S33.452717°	E26.597450°	Fyke net
66	2	S33.452717°	E26.597450°	Sein net
66	2	S33.452717°	E26.597450°	Sein net
67	2	S33.440167°	E26.592014°	Fyke net
67	2	S33.440167°	E26.592014°	Sein net
68	2	S33.438517°	E26.591850°	Fyke net
68	2	S33.438517°	E26.591850°	Sein net
68	2	S33.438517°	E26.591850°	Sein net
69	2	S33.433033°	E26.603467°	Fyke net
69	2	S33.433033°	E26.603467°	Sein net
69	2	S33.433033°	E26.603467°	Sein net
70	1	S33.352533°	E26.496875°	Electro fishing
70	1	S33.352533°	E26.496875°	Electro fishing
71	1	S33.353081°	E26.496769°	Electro fishing

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0	0	0	2	0	0	0	0	0	0	0	0	0
0	0	0	4	0	0	0	0	0	0	0	0	0

71	1	S33.353081°	E26.496769°	Electro fishing
72	1	S33.351708°	E26.497428°	Electro fishing
72	1	S33.351708°	E26.497428°	Electro fishing
73	2	S33.569200°	E26.637150°	Fyke net
73	2	S33.569200°	E26.637150°	Fyke net
74	2	S33.593950°	E26.634100°	Fyke net
74	2	S33.593950°	E26.634100°	Fyke net
74	2	S33.593950°	E26.634100°	Sein net
74	2	S33.593950°	E26.634100°	Sein net
75	2	S33.551533°	E26.610983°	Fyke net
75	2	S33.551533°	E26.610983°	Fyke net
75	2	S33.551533°	E26.610983°	Fyke net
75	2	S33.551533°	E26.610983°	Fyke net
75	2	S33.551533°	E26.610983°	Sein net
75	2	S33.551533°	E26.610983°	Sein net
76	2	S33.551317°	E26.611800°	Fyke net
76	2	S33.551317°	E26.611800°	Sein net
77	2	S33.542800°	E26.604033°	Fyke net
77	2	S33.542800°	E26.604033°	Sein net
78	2	S33.513050°	E26.608817°	Fyke net
78	2	S33.513050°	E26.608817°	Fyke net
78	2	S33.513050°	E26.608817°	Sein net
79	2	S33.505667°	E26.594383°	Fyke net
79	2	S33.505667°	E26.594383°	Fyke net

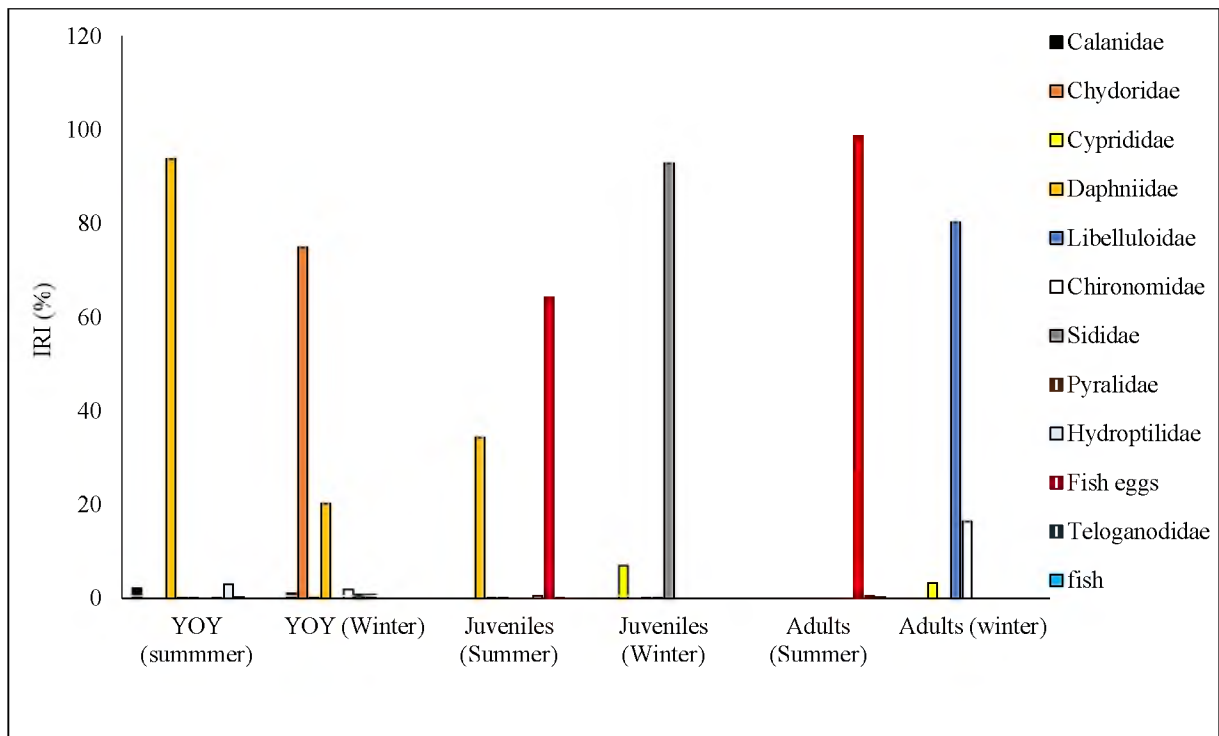
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83	1	S33.399303°	E26.421425°	Fyke net
83	1	S33.399303°	E26.421425°	Fyke net
83	1	S33.399303°	E26.421425°	Gill net
83	1	S33.399303°	E26.421425°	Gill net
83	1	S33.399303°	E26.421425°	Gill net
83	1	S33.399303°	E26.421425°	Gill net
83	1	S33.399303°	E26.421425°	Gill net
83	1	S33.399303°	E26.421425°	Gill net
83	1	S33.399303°	E26.421425°	Gill net
83	1	S33.399303°	E26.421425°	Gill net
83	1	S33.399303°	E26.421425°	Hook and Line Fishing
84	1	S33.351550°	E26.497567°	Electro fishing
84	1	S33.351550°	E26.497567°	Electro fishing
85	1	S33.351400°	E26.497617°	Electro fishing
85	1	S33.351400°	E26.497617°	Electro fishing
86	1	S33.351267°	E26.497783°	Electro fishing
86	1	S33.351267°	E26.497783°	Electro fishing
87	1	S33.351075°	E26.497644°	Electro fishing
87	1	S33.351075°	E26.497644°	Electro fishing
88	1	S33.350717°	E26.497550°	Electro fishing
88	1	S33.350717°	E26.497550°	Electro fishing
89	1	S33.350567°	E26.497450°	Electro fishing
89	1	S33.350567°	E26.497450°	Electro fishing
90	1	S33.350267°	E26.497400°	Electro fishing

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90	1	S33.350267°	E26.497400°	Electro fishing
91	1	S33363533°	E26.497667°	Electro fishing
91	1	S33363533°	E26.497667°	Electro fishing
92	1	S33.350133°	E26.497717°	Electro fishing
92	1	S33.350133°	E26.497717°	Electro fishing
93	1	S33.349750°	E26.49773°	Electro fishing
93	1	S33.349750°	E26.49773°	Electro fishing
94	1	S33.349633°	E26.497533°	Electro fishing
94	1	S33.349633°	E26.497533°	Electro fishing
95	2	S33.521786°	E26.616278°	Fyke net
95	2	S33.521786°	E26.616278°	Fyke net
95	2	S33.521786°	E26.616278°	Fyke net
95	2	S33.521786°	E26.616278°	Sein net
95	2	S33.521786°	E26.616278°	Sein net
96	2	S33.526886°	E26.608811°	Fyke net
96	2	S33.526886°	E26.608811°	Fyke net
96	2	S33.526886°	E26.608811°	Sein net
96	2	S33.526886°	E26.608811°	Sein net

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0	0	0	0	0	0	0	0	0	0	0	0	0



Appendix 4: Importance rating index (IRI) in percentages of prey items in three size classes of bluegill caught at Howisons Poort dam in Summer and Winter period.