ASSESSING THE STATUS OF THE BAROTSE FLOODPLAIN FISHERY AND THE IMPLICATIONS OF AUSTRALIAN REDCLAW CRAYFISH CHERAX QUADRICARINATUS INVASION ON THE FISHERY

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GENERAL ABSTRACT

Inland capture fisheries play an important role of supporting livelihoods of people in developing countries. Despite their significance these fisheries are often poorly monitored resulting in them being undervalued and often missing from policy and decision-making relating to food security and water use, particularly in third world countries. The Anthropocene has given rise to increased pressure on these systems, further justifying the need for monitoring activities to determine the ecosystem service provision status and the levels of existing and emerging threats to such services. This thesis focuses on the Barotse floodplain fishery of the Upper Zambezi system and the potential implications of the recent *Cherax quadricarinatus* invasion on the floodplain fishery. The thesis specifically assesses the current status of the fishery (Chapter 3), invasion dynamics of *C. quadricarinatus* (Chapter 4), economic impact of *C. quadricarinatus* on the fishery (Chapter 5) and fishers' knowledge, awareness and perception of *C. quadricarinatus* (Chapter 6). To evaluate the current status of the fishery (Chapter 3), fisheries dependant surveys were conducted. The study revealed a multi-gear multi-species fishery with average catch rates of 5.83 kg per fisher per day and estimated annual harvest of 3123 tonnes per annum. The decline in catch rate, low mean sizes of species harvested, change in species composition, and predominant use of illegal fishing gear compared to previous surveys, suggested further overexploitation of fishery resources. The invasive *C. quadricarinatus* was identified as the most dominant by-catch species and more prevalent among fishers at the invasion core and in dry season. Analysis of the invasion dynamics of *C. quadricarinatus* (Chapter 4) involved extensive survey of the Barotse floodplain using collapsible promar traps. The study revealed significant up and down-stream spread from the 2019 range on the floodplain. Relative abundance was higher at the invasion core compared to the invasion edge while male to female sex ratio was not different between these zones, implying both sexes were acting as dispersers. Signals of environmental filtering were not detected while density dependent spatial sorting, and hydrological variation had a strong influence on *C. quadricarinatus* spread. To quantify economic impact *C. quadricarinatus* (Chapter 5) creel surveys were conducted during wet and dry season across the invasion range. The study showed that fish damage due to crayfish was limited to gillnets at the invasion core during the dry season and equated to the monetary loss of ~ US$ 21,000 per annum. In addition, gear damage and loss of time due to crayfish was experienced for various fishing gears but most prevalent at the invasion core and more so in dry season. Assessment of fishers' awareness, knowledge and perception (Chapter 6) involved the use of social surveys administered at the invasion core. This component revealed that most of the respondents were aware of, but not knowledgeable about *C. quadricarinatus*. Respondents were not aware of any management information relating to *C. quadricarinatus* and consequently did not follow any management practices. The respondents were supportive of management interventions due to their perceived threat of *C. quadricarinatus* to the fishery. Age, education, and residence of respondents significantly influenced knowledge and perceptions of *C. quadricarinatus*. Findings from this study have important implications for the conservation of floodplain wetlands as it informs policy makers to put in place measures that address both overexploitation and aquatic invasive species dynamics to better facilitate sustainability of fisheries and conservation of biodiversity.

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PREFACE

This thesis is comprised of a general introduction (Chapter 1), a study area chapter (Chapter 2), four data chapters (Chapter 3, 4, 5 and 6) and a general discussion and conclusion (Chapter 7). The data chapters are organised in the form of scientific papers, one of which is under review (see below). The general introduction and a combined reference list at the end of the thesis has ensured limited repetition.

- Nawa N, Ellender BR, Pegg J, Chalmers R, Wasserman RJ. Assessment of the multi-species Barotse floodplain fishery of the Upper Zambezi system.
- Nawa N, South J, Ellender BR, Pegg J, Madzivanzira TC, Wasserman RJ. (under Review). Edge-core invasion dynamics of the Australian redclaw crayfish *Cherax quadricarinatus* on the Barotse floodplain of the Upper Zambezi System. *Freshwater Biology*.
- Nawa N, South J, Ellender BR, Pegg J, Wasserman RJ. Quantifying the economic impact of Australian redclaw crayfish *Cherax quadricarinatus* on the Barotse floodplain artisanal fishery.
- Nawa N, South J, Ellender BR, Pegg J, Bradbeer SJ, Wasserman RJ. Fishers' awareness, knowledge and perception of the invasive Australian redclaw crayfish *Cherax quadricarinatus* on the Barotse floodplain of the Upper Zambezi system.

DECLARATION

I, Nawa Nawa, hereby declare that this thesis submitted to the Department of Zoology and Entomology represents my original work and has not been previously submitted to any other academic institution. I have acknowledged the authorship of any external ideas, phrases, passages or illustrations utilised within this thesis.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Global inland capture fisheries

Inland capture fisheries involve the exploitation of wild fishery resources in inland waters such as rivers, floodplains, lakes, canals, reservoirs and other land locked waters (FAO 2014; Funge-Smith and Bennett 2019). In 2020, the global capture fisheries production (excluding algaes) was estimated at 90.3 million metric tonnes per annum and of this, global inland capture fisheries accounted for about 12.7% (~ 11.5 metric million tonnes) (FAO 2022). Although the inland capture fisheries yield has increased compared to the average for the 1990s (FAO, 2022), the yields are still thought to be underestimated by up to 50% (Fluet-Chouinard et al. 2018; Funge-Smith and Bennett 2019). About 92% of the global inland capture fisheries production comes from Asia and Africa (FAO 2022). In Asia, some of the countries with high fisheries production includes India (1.84 million tonnes), China (1.46 million tonnes) and Bangladesh (1.25 million tonnes) while in Africa, Uganda (0.57 million tonnes), Tanzania (0.41 million tonnes) and Nigeria (0.35 million tonnes) are the leading countries (FAO 2022). The major species groups of inland captures accounting for over 75% of the total inland catches are cyprinids, cichlids and crustaceans (FAO 2022).

Inland capture fisheries range from small-scale artisanal units operating in small water bodies to large scale commercial enterprises using motorised boats in large lakes and rivers (Neiland et al. 2005; Youn et al. 2014; Funge-Smith and Bennett 2019). Although commercial fisheries (e.g., Laurentian Greak Lakes trawl fishery, Myanmar inn fishery, Lake Victoria Nile perch fishery, Lake Tanganyika Kapenta light fishery etc.) make significant contribution to fisheries production they only represent 10-13% of global inland fisheries production (Funge-Smith et al. 2018). The majority of the inland capture fisheries are characterised by small scale operations whose catch is typically meant for household consumption and local trade or barter (Bartley et al. 2015). Small-scale inland fisheries are an important source of food and nutritional resources especially in rural communities of low-income countries (Welcomme et al. 2010; Lynch et al. 2016). Low-income food-deficit (LIFD) countries constitute 80% of the total harvest from capture fisheries (Kapetsky 2003). In these countries, small scale fisheries are particularly crucial in addressing malnutrition by providing protein, vitamins (i.e., vitamin A, B, D) and mineral elements (i.e., calcium, iron, zinc) where alternative sources of nutrition are unavailable or cost-prohibitive (Roos et al. 2007; Youn et al. 2014).

In addition to being a source of food, small scale inland capture fisheries are an important source of livelihood and economic security through provision of income (Youn et al. 2014). The income is generated from direct employment for fishers engaged in fish harvesting as well as indirect employment to others involved in the fisheries industry (i.e., fish processing and trade, transportation and gear manufacturing) (Youn et al. 2014). According to the 2012 World Bank report, inland capture fisheries employed close to 17 million fishers while more than 8 million workers were engaged in post-harvest activities of which more than half are women (World Bank 2012) mostly involved in processing and fish trade (Funge-Smith and Bennett 2019). In Asia, in the lower Mekong basin women dominate trade in 5,000 to 6,000 fish markets while in Africa, women constitute 67% of the inland fishery processing sector (DeGraaf and Garibaldi 2014). In Sub-Saharan Africa, small scale fisheries are particularly important for female headed households whose livelihood options tend to be limited (Kyaw 2009). The income generated from small scale inland capture fisheries enables households to acquire food and various products either through purchase or barter. As a result, inland capture fisheries make a direct and indirect contribution to human wellbeing, quality of life and overall food security (Youn et al. 2014).

Despite the importance of inland capture fisheries, obtaining accurate and consistent information regarding catch statistics is inherently challenging due to their small-scale and highly dispersed nature (Allan et al. 2005; Welcomme et al. 2010; Youn et al. 2014; Lynch et al. 2016). Poor monitoring of these small-scale fisheries has resulted in under reporting of fishery production (Welcomme 2010; Fluet-Chouinard et al. 2018; Funge-Smith 2018). Inland harvest for small-scale fisheries are particularly under-reported in South America, Asia and Africa (Fluet-Chouinard et al. 2018). A total of 42 countries from these regions collectively have an aggregated net under-reporting of 64.8%. Bangladesh, Democratic Republic of Congo and Zambia account for 42% of the total unreported (hidden) harvest (Fluet-Chouinard et al. 2018). The under reporting of fishery harvest has contributed to the continued undervaluing of inland fisheries in policy decisions involving food security, economic growth and sustainable management (De Graaf et al. 2012; Cooke et al. 2016; Bartley et al. 2015; Funge-Smith and Bennett 2019). The inland fisheries are given less priority and perceived as of low value compared to other freshwater services such as hydropower, municipal use and agricultural irrigation (Dugan et al. 2006; Youn et al. 2014). Given the poor data availability, reliable and timely assessment of small-scale inland capture fisheries is required to accurately reflect the magnitude of capture harvests and highlight their significance to human livelihoods.

1.1.1 Floodplain fisheries

Some of the most important small-scale inland capture fisheries occur on floodplain systems such as on river floodplains (Welcomme 2008). The river-floodplain systems are highly productive freshwater environments that are closely linked to seasonal changes in water level known as the ‘flood pulse’ (Junk et al. 1989). The flood pulse enhances the productivity of fish populations by offering feeding and reproductive opportunities within the floodplains (Welcomme 1979; Agostinho et al. 2004). Due to their high productivity, floodplain-based fisheries contribute significantly to global inland capture fisheries production (Welcomme 2008; Mosepele et al. 2022). These dynamic environments typically support multi-species artisanal fisheries that sustain the livelihoods of millions of people, particularly in tropical and sub-tropical regions (Turpie 2008; Welcomme et al. 2010).

1.1.1.1 Floodplain fisheries in Africa

African’s major river basins are host to some of the largest floodplains (~ over 400, 000 square kilometers) in the world which contribute significantly to global inland capture fisheries production (Table 1.1; ANRMIC 2022). These floodplain fisheries are typically multi-species and multi-gear in nature as local communities use a wide range of fishing gears designed to exploit diverse fish resources in various aquatic habitats and at different stages of the flood cycle (Hoggarth and Utomo, 1994; Lohmeyer, 2002). These fisheries sustain rural communities (ANRMIC 2022). For example, in Sudd, South Sudan about 1.7 million people depend on the floodplain fishery with an average fish per capita consumption of 17kg per year which is three times the national average (Fluet-Chouinard et al. 2018). In the Congolese Cuvette, fishing which takes place at the end of flood period provide enough fish for consumption and income to cover all household expenses for the rest of the year (Comptour 2016). In the Okavango delta, Botswana, 44% of the household considered fish as most reliable food source during period of food shortage (Mosepele and Ngwenya 2006). On the Barotse floodplain of Zambia, fish forms part of the diet for 99% of households and the per capita consumption on the floodplain is five times the national average (Turpie et al. 1999).

Despite their substantial contribution, fisheries production from floodplains in Africa are underestimated as many catches go unrecorded (ANRMIC, 2022). According to findings from a recent FAO survey aimed at re-assessing small-scale inland fisheries to illuminate hidden harvest, fisheries data from river-floodplain systems is poorer than that of lake-based fisheries (ANRMIC 2022). This is due to the highly disbursed nature of river-floodplain systems coupled with the difficulty in accessing fishers during the flood period (Lohmeyer, 2002) resulting in some of the catches going unrecorded (ANRMIC 2022). To accurately estimate the scale of floodplain fisheries production, there is need for catch monitoring programs that consider seasonality and geographical extent of fishing operations.

Table 1.1 Main river basins in Africa and some fisheries in their floodplains (Adapted from African Natural Resources and Investment Center 2022)

River basins	**Main floodplains**	**Surface (km^2)**	**Estimated Max production** (tonnes)	**Number of fishers**
Nile	Sudd	88 300	140 -200 000	>100 000
Congo	Cuvette	142 000	-	180 000
Lake Chad	Chari – Logone - Yaeres	63 000	>45 000	>40 000
Niger	Inner Delta	43 000	100 000	35 000
Zambezi	Kafue flats + Barotse plain	17 250	15-45 000	>45 000
West African basins	Senegal	12 000	18-24 000	-
East African basin	Kilombero, Rufiji, Tana	8 600	-	-
Central African basin	Okavango	28 000	1500	3 000

Floodplain fisheries in Africa are, however, under threat from various pressures. Growth in the human population has exerted increased pressure on river-floodplain ecosystem services. This is through direct activities such as over-exploitation of fish stocks, but also indirectly through large-scale modifications of these aquatic environments (ANRMIC, 2022; Mosepele 2022). For example, agriculture irrigation, dam construction for hydropower generation (Welcomme 2008) and pollution from municipalities and manufacturing industries (Tockner and Stanford 2002). More recently, however, as with many other ecosystems globally, floodplains have experienced another form of pressure; that of biological invasions (Rauro et al. 2020; Thomaz 2021; Pegg et al. 2022). Biological invasions are a human-mediated process involving the introduction of species into new environments where they may become established and subsequently spread (Richardson et al. 2000; Pyšek and Richardson 2010; Blackburn et al. 2011). The increase in human movement has facilitated the transportation (intentional and unintentional) of many species beyond their native range, resulting in the break of the geographical barrier as the first major filter for species distributions (Theoharides and Dukes al. 2007; Simberloff et al. 2009; Blackburn et al. 2011). In many instances, species adversely impact on the recipient native community and ecosystem (Richardson et al. 2000; Ricciardi et al. 2013; Simberloff et al. 2013; Pyšek et al. 2020).

1.2 Biological invasion

According to the unified framework for biological invasion, the invasion processes comprise of four keys stages (i.e., transport, introduction, establishment and spread) and at each stage there are barriers that must be overcome by an introduced species before proceeding to the next stage (Fig 1.1). For an introduced species to become invasive it must successfully pass through all four stages (Blackburn et al. 2011). Most species that are introduced do not pass all four barriers and fail to become invasive (Theoharides and Duke 2007; Blackburn et al. 2011). The transport and introduction stages are associated with geographical barrier and captivity barrier respectively and an alien species' ability overcome both barriers is aided by human action (i.e., transportation) either intentionally or unintentionally. At the establishment stage, alien species can fail to survive (i.e., overcome survival barrier) and/or reproduce (i.e., overcome reproduction barrier) (Blackburn et al. 2011). The species' capacity to establish is also dependent on other factors such as propagule pressure, abiotic conditions and biotic resistance (Theoharides and Duke 2007;

Blackburn et al. 2011). At the spread stage, an alien species must overcome the dispersal barriers to spread into new location where individuals must overcome new environmental barriers (i.e., survive and reproduce) (Blackburn et al. 2011). The capacity of alien species to overcome barriers at each stage is influenced by species traits such as phenotypic plasticity, abiotic tolerance, fast growth, fecundity, competitive ability etc. (Theoharides and Duke 2007; Statzner et al. 2008; Whitney and Gabler 2008). By identifying traits that enable alien species to successfully complete the invasion process, invasions with adverse impact can be predicted and managed more effectively (Kolar and Lodge 2001; van Kuijk et al. 2021)

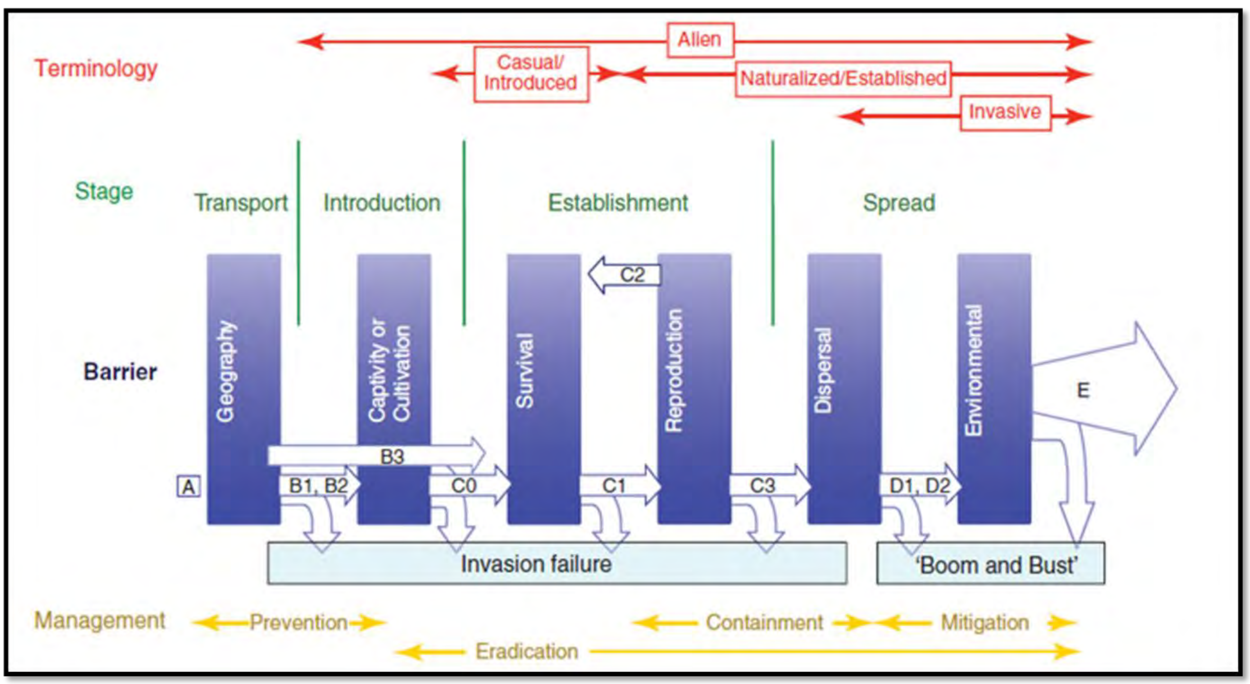

Figure 1.1 A unified framework for biological invasion showing four key stages of the invasion processes and associated barriers needed to be overcome by an introduced species at each stage. Letters A = not transported beyond limits of native range; B1 = individual transported beyond limits of native range, and in captivity; B2 = individuals transported beyond limits of native, and in cultivation; B3 = individuals transported beyond limits of native range, and directly released into novel environment; C0 = individuals released into wild in location where introduced, but incapable of surviving for a significant period; C1 = individuals surviving in the wild in location

were introduced, no reproduction in location where introduced; C2 = individuals surviving in the wild in location where introduced, reproducing occurring but populations not self-sustaining; C3 = individuals surviving in the wild location where introduced, reproducing occurring, and population self-sustaining; D1 = self-sustaining population in the wild, with surviving a significant distance from the original point of introduction; D2 = self-sustaining populations in the wild, with individuals surviving and reproducing a significant distance from the original point of introduction; E = fully invasive species, individuals dispersing, surviving and reproducing at multiple sites (Extracted from Blackburn et al. 2011).

Invasive alien species (IAS) can cause negative ecological and socio-economic impacts (Pyšek and Richardson 2010; Simberloff et al. 2013; Pyšek et al. 2020). With the rate of biological invasion closely tied to rising globalization (Bonnamour et al. 2021) and expected to continue increasing in the future (Seebens et al. 2020), the impacts of IAS on ecosystems and human well-being are poised to escalate. As a result, IAS are now recognised as one of the leading causes of native species extinction (Bellard et al. 2016; Blackburn et al. 2019), degradation of ecosystem function and services (Vilà and Hulme 2017) and economic cost estimated at over US$1 trillion globally (Diagne et al. 2021a). Freshwater ecosystems have and are projected to continue as some of the most vulnerable environments to biological invasions (Strayer and Findley 2010; Moorhouse and Macdonald 2015; Darwall et al. 2018).

1.2.1 Biological invasion in freshwater ecosystems

Freshwater ecosystems are considered one of the most threaten ecosystems worldwide (Reid et al. 2019) due to their sensitivity to climate change effects (Woodward et al. 2010) and range of other human-induced stresses (Darwall et al. 2018), including invasive species (Strayer 2010; Poulin et al. 2011). The extensive use of non-native freshwater species for food provisioning and recreation by humans had led to their introduction in freshwater ecosystems such as lakes, rivers and other wetlands (Lodge et al. 1998; Gherardi et al. 2007). Non-native species introduced in freshwater systems are taxonomically diverse and include fish, crustaceans, molluscs, vascular plants, algae etc. (Strayer 2010; Dawson et al. 2017). Pathways for introduction of non-native freshwater species are also diverse but typically involve intentional stocking of impoundment and lakes for aquaculture or sport angling (Cuvin-Aralar 2016), stocking for biocontrol (Dawson et al. 2017), disposal of unwanted aquarium pets (Chan et al. 2019) as well as accidental introductions through release of ballast water, biosecurity lapses in ornamental trades, transfer of propagule from shipping and boating activities (Gozlan et al. 2010; Britton et al. 2023). Freshwater ecosystems are more susceptible to biological invasion than terrestrial ecosystems due to the relatively ease of dispersal resulting from the flow and connectivity of water within freshwater systems (Strayer and Findlay 2010; Darwall et al. 2018). Anthropogenic activities such as construction of impoundments and canals which facilitates establishment and dispersal of non-native species respectively further exacerbated the vulnerability of freshwater systems to invasion (Craig et al. 2017).

Although non-native freshwater species can provide substantial socio-economic benefits, they also cause adverse ecological impacts which occur through various processes (competition, predation, genetic introgression, pathogens and environmental modification) across different levels of biological organization (Ellender and Weyl 2014; Ellender et al. 2014; Coetzee et al. 2018; Britton et al. 2023). The impacts of aquatic invasive species (AIS) often result in irreversible changes in invaded communities, influencing ecosystem functioning, biodiversity and local extinction of species (Strayer 2010; Catford et al. 2012). In addition, freshwater invasive species cost global economies billions of US dollars through damage and management (Cuthbert et al. 2021; Haubrock et al. 2021b; Haubrock et al. 2022). However, the economic costs associated with freshwater invasive species are largely under-reported in Africa and Asia

(Cuthbert et al. 2021). The limited reporting of costs in Africa is particularly concerning as biological invasions in developing countries may disproportionately affect livelihoods, given the high poverty levels, limited resources for management and lack of preparedness to address challenges that come with IAS (Early et al. 2016). In the African freshwater fisheries context, this is particularly relevant for floodplain river ecosystems given their crucial contributions to food security, nutrition and livelihood of rural communities on the continent (ANRMIC 2022).

Floodplain ecosystems are regarded as hotspots for freshwater biodiversity as their diverse habitats support various aquatic flora (Piedade et al. 2022), invertebrates (Dube et al. 2022) fish (Reichard 2022) and complex food webs (Cuthbert et al. 2022). However, these biodiversity-rich wetlands are under threat from invasive species (Rauro et al. 2020; Pegg et al. 2022). Like other freshwater ecosystems, floodplains have been subjected to several non-native species introductions such as plants/macrophytes, invertebrates, fish and amphibians (Thomaz 2021). But of particular interest in African river floodplains, are invasive alien crayfish species. Freshwater crayfish have been introduced globally for capture fisheries, aquaculture, and aquarium trade as well as accidentally through release of unused baits or unwanted aquarium pets (Gherardi 2006; Lodge et al. 2012; Twardochleb et al. 2013; Madzivanzira et al. 2020; Haubrock et al. 2021a). However, mainland Africa has no native freshwater crayfish species, thus introduced crayfish currently represent a phylogenetically novel invasion (Madzivanzira et al. 2020), which may have implications for biotic resistance dynamics.

1.3 Non-indigenous freshwater crayfish

Crayfish predominantly occupy the benthic zone within freshwater systems and prefer lentic or slow-moving waters (Nyström 2002: Crandall and Buhay 2008). With a generalist omnivorous diet, crayfish are considered opportunistic feeders feeding on a wide range food resource such as aquatic plants, invertebrates, decaying organic matter, fish eggs and small fish (Nyström 2002; Jones et al. 2016). Through their feeding and burrowing activities, crayfish cause changes to both abiotic and biotic materials which directly or indirectly affects the availability of resources to organisms (Jone et al. 2016). The majority of freshwater crayfish species reproduce sexually while other also reproduce asexually by parthogenesis (Jones et al. 2009; Souty-Grosset 2016). In addition, crayfish exhibit tolerance to a wide range of environmental variables with tolerance levels differing between families (Nyström 2002). Freshwater crayfish have been widely translocated by humans beyond their native range (Hobbs and Lodge 2010). The introduction freshwater crayfish into novel areas has been motivated by their high socio-economic value in several regions around the world (Reynolds and Souty-Grosset 2012).

The ability of freshwater crayfish to adapt to a wide range of environmental conditions has made them one of the most successful aquatic invasive alien species (Lodge et al. 2012). Of the 692 documented freshwater crayfish species (Crandall and De Grave 2017), 28 have been successfully introduced with viable populations established (Gherardi 2010). Due to their omnivorous nature and ability to attain large sizes and high population density, the non-indigenous crayfish species (NICS) can cause severe ecological impacts through strong trophic interactions (i.e., predation, competition, vector of pathogens, and hybridisation) and ecosystem engineering (Hobbs and Lodge 2010; Twardochleb et al., 2013). Non-indigenous crayfish species also cause adverse socio-economic effects through their impact on ecosystem services such as food provisioning and increased expenses for agriculture and water management (Lodge et al. 2012; Madzivanzira et al. 2020). Economic cost attributed to NICS impact is estimated to be more than US$ 1 billion however the costs are mostly attributed to Europe while elsewhere the cost remains largely unreported (Kouba et al. 2021).

A total of nine non-native crayfish species have been translocated to Africa and these include the smooth marron *Cherax cainii*, noble crayfish *Astacus astacus*, yabby *Cherax destructor* and white river crayfish *Procambarus zonangulus*. Others are redclaw crayfish *C. quadricarinatus*, spiny-cheek crayfish *Faxonius limosus*, signal crayfish *Pacifastacus leniusculus*, red swamp crayfish *Procambarus clarkii* and marbled crayfish *Procambarus virginalis* (Madzivanzira et al. 2020). In Africa, NICS were primarily introduced for aquaculture, fisheries and the pet trade (Weyl et al. 2020). However, deliberate releases, escape from captivity and unaided spread have led to the establishment of five NICS (*P. clarkii*, *C. quadricarinatus*, *F. limosus*, *A. astacus* and *P. virginalis*) in several freshwater bodies (Madzivanzira et al. 2020). The presence of NICS in Africa's freshwater system is of great concern given the evidence of their impact on recipient ecosystem elsewhere (Lodge et al. 2012; Twardochleb et al. 2013). In Southern Africa, *Cherax quadricarinatus* is the most problematic invasive species, having been identified as invasive in seven river systems, including the major river systems of the Zambezi and Limpopo, both of which support important freshwater subsistence fisheries that transcends national borders (Madzivanzira et al. 2020).

1.3.1 Australian redclaw crayfish Cherax quadricarinatus

The Australian redclaw crayfish *Cherax quadricarinatus* is a parastacid crayfish (Decapoda: Astacidea: Parastacidae). The crayfish is native to tropical and subtropical region of north-eastern Queensland, the Northern Territory of Australia and southern Papua New Guinea (Riek 1969). In its native environment, *C. quadricarinatus* inhabits a wide range of aquatic habitats such as lentic habitats which include slow flowing rivers, lakes, and lagoons (Jones 1990). Within these habitats *C. quadricarinatus* are bottom dwellers preferring hard substrates such as rocks, submerged logs and leaf matter which they exploit for food and shelter (Ruscoe 2002).

Like the majority of freshwater crayfish species, *C. quadricarinatus* exhibits opportunistic and polytrophic omnivorous behaviour feeding various plant materials ranging from periphyton to aquatic macrophytes (Momot 1995) as well as animal proteins such as invertebrates (Abrahamsson 1966), frog and fish eggs (Lodge et al. 1985), and carrion (Momot 1995).

Cherax quadricarinatus is adapted to a broad range of climatic and environmental conditions (Jones 1990). It has an optimal water temperature range of between 23°C and 31°C, however its capable of enduring broader temperatures from 11°C to as high as 35°C (Jones 1990). Adult *C. quadricarinatus* exhibit tolerance to pH levels ranging from 6.5 to 9 and can withstand dissolved oxygen (DO) levels as low as 1.0 mg/L (Masser and Rouse 1997; Wingfield 2000). *Cherax quadricarinatus* can tolerate ammonia concentrations of up to 1.0 mg/L and nitrite levels as high as 0.5 mg/L for brief periods (Masser and Rouse 1997).

Cherax quadricarinatus is a faster growing crayfish species achieving body weight of 50 to 90 g within a year (Wingfield 2002). Its maximum lifespan spans 4 to 5 years and can attain an average mass of approximately 300 g over that period (Jones 1990; Masser and Rouse 1997). Under optimal conditions *C. quadricarinatus* reaches sexual maturity at the age of 6 to 9 months (Jones 1990; Wingfield 2002). *Cherax quadricarinatus* exhibit sexually dimorphism in growth pattern, with males displaying faster growth and reaching a larger final size compared to females (Cortés-Jacinto et al. 2004). Mature male *C. quadricarinatus* develop red or orange patch on the outer margin of their propodus or claw. Individuals without the reddish patches are generally identified as females (Fig. 1.2: Masser and Rouse 1997). However, a more accurate determination of an individual's sex involves examining the genital openings on the underside of the cephalothorax at the base of the walking legs (Masser and Rouse 1997). Male crayfish are characterised by two short projections resembling acorns on the bases of the last pair of walking legs, while females have openings at the base of the second pair of walking legs (McLay and van den Brink 2016). In this species, various combination intersex individuals with both female and male genital openings can also be found (Sagi et al. 2002; Parnes et al. 2003).

Figure 1.2 Male and Female Australian redclaw crayfish *C. quadricarinatus* (Photograph: Nawa Nawa taken from the Barotse floodplain, Upper Zambezi Floodplains Ecoregion, Zambia; Date: 31/07/2021).

Reproduction in *C. quadricarinatus* is contingent upon water temperature being above 23ºC. Females typically produce a range of 300 to 800 eggs per brood, which they actively brood for a duration of 6 to 10 weeks (Jones 1990). Like other crayfish species, female *C. quadricarinatus* affix the eggs to the swimmerets beneath their tail, where they remain attached throughout the incubation period (4 to 6-week). Females carrying eggs are known as 'berried' females and are easily identifiable as they tend to curl their tail under the body in the initial 3 weeks after spawning. They also exhibit reduced activity during this phase. After hatching, the offsprings remains connected to the mother's swimmerets for about a week after which they become independence (Jones 1990; Masser and Rouse 1997).

Due to its physical and biological characteristics *C. quadricarinatus* has been heralded as an excellent species for aquaculture (Jones et al. 2000; Rigg et al. 2020) and therefore stands as the second most cultured and harvested crayfish species worldwide (Haubrock et al. 2021a). Its significance in aquaculture and popularity within the aquarium trade has led to numerous species translocations (Haubrock et al. 2021a). As a result of escapes from aquaculture facilities and pet trade and unauthorized releases by recreational fishers, populations of *C. quadricarinatus* have become established in the wild (Lodge et al. 2012; Madzivanzira et al. 2020). In Southern Africa, *C. quadricarinatus* has been introduced in South Africa, Eswatini, Zimbabwe and Zambia with populations established in several freshwater bodies (Madzivanzira et al. 2020). *Cherax quadricarinatus* has been extensively studied in captive settings for its biology, physiology, aquaculture, and production, however its ecology and invasion impact in the wild are still inadequately understood (Furse et al. 2015).

1.4 Present study

The potential implications of the recent *Cherax quadricarinatus* invasion on the Barotse floodplain fishery has yet to be assessed and as such represents a major knowledge gap, hindering associated fisheries management considerations. This study, therefore, deals with discrete aspects of the Barotse floodplain fishery, but is centred on the role *C. quadricarinatus* plays in these fisheries dynamics. The thesis is comprised of a general introduction (Chapter 1-present chapter), a study site overview (Chapter 2), four discrete data chapters (Chapters 3, 4, 5 and 6) and a general synthesis (Chapter 7). The data chapters are complementary, cumulatively providing a more holistic understanding of the *C. quadricarinatus* invasion and associated implications for the floodplain fishery. More specifically, Chapter 3 evaluates the sustainability of the Barotse floodplain fishery with regards to the exploitation patterns of the fishery resources and contribution of *C. quadricarinatus* and other invasive species. The distribution of *C. quadricarinatus* on the Barotse floodplain and factors driving its range expansion dynamics are then assessed (Chapter 4). Chapter 5 then evaluates the economic cost incurred by artisanal fishers on the floodplain due to the *C. quadricarinatus* invasion. Finally, Chapter 6 assesses fishers' awareness, knowledge and perception regarding *C. quadricarinatus* invasions on the Barotse floodplain.

Understanding both the current level of fishery resources exploitation as well as the threat posed by *C. quadricarinatus* to fishery is crucial to ensuring sustainability of fishery resources and conservation of biodiversity of this important wetland. Also key to this understanding is the inclusion of socio-economic dynamics surrounding the *C. quadricarinatus* invasion on the Barotse floodplain. The present study incorporates fisheries, ecological, economic and perception components which together offer much insight for the potential management of fisheries on the floodplain.

CHAPTER 2

STUDY AREA

The study was conducted on the Barotse floodplain of the Upper Zambezi system (Ecoregion 556, Abell et al. 2008) in the Western Province of Zambia (13°50′S–22°45′ E, 16°40′S–23°45′E) (Fig. 2.1 A). The main floodplain area covers approximately 550, 000 hectares while the total wetland extends around 1.2 million hectares (Turpie 1999). The Barotse floodplain is an extensive low-lying flat land composed of Kalahari sands interspersed with dambo areas (Timberlake 1997). The floodplain mainly consists of grassland with several small, wooded areas on elevated ground (van Gils 1998) and swamp forest scattered across (IUCN 2003). The floodplain is a designated Ramsar site of high conservation value supporting considerable biodiversity (Timberlake 1997). The floodplain undergoes seasonal inundation due to increased discharge of the Zambezi River caused by rainfall of over 1400mm experienced over the headwater catchment areas in south-eastern Angola and north-western Zambia (Cai et al. 2017). The flood period generally occurs between February and April before receding between May and July (Fig. 2.2 A; B) (Zimba et al. 2018). The floodplain comprises the main river channel, several small rivers, streams, lagoons, swamps, and canals which support diverse flora and fauna (Turpie et al. 1999). During the flood period various water bodies become interconnected into a large single expanse of water (Fig. 2.1 B; Fig. 2.2 A). As the floods recede the many water bodies become disconnected and isolated once again.

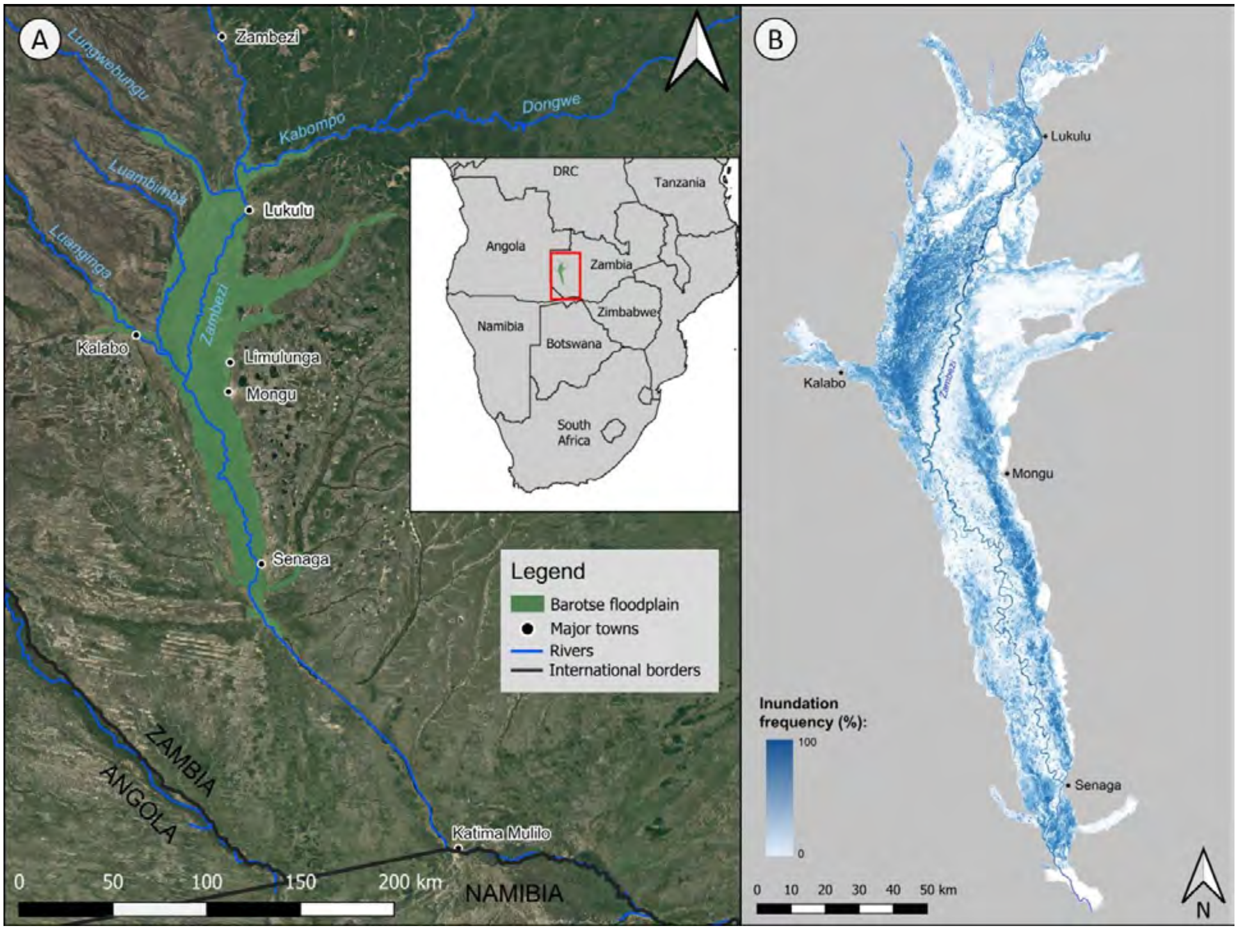

Figure 2.1 Map showing: A) the Barotse floodplain of the Upper Zambezi system located in Western part of Zambia and B) the satellite imagery indicating inundation frequency of the floodplain.

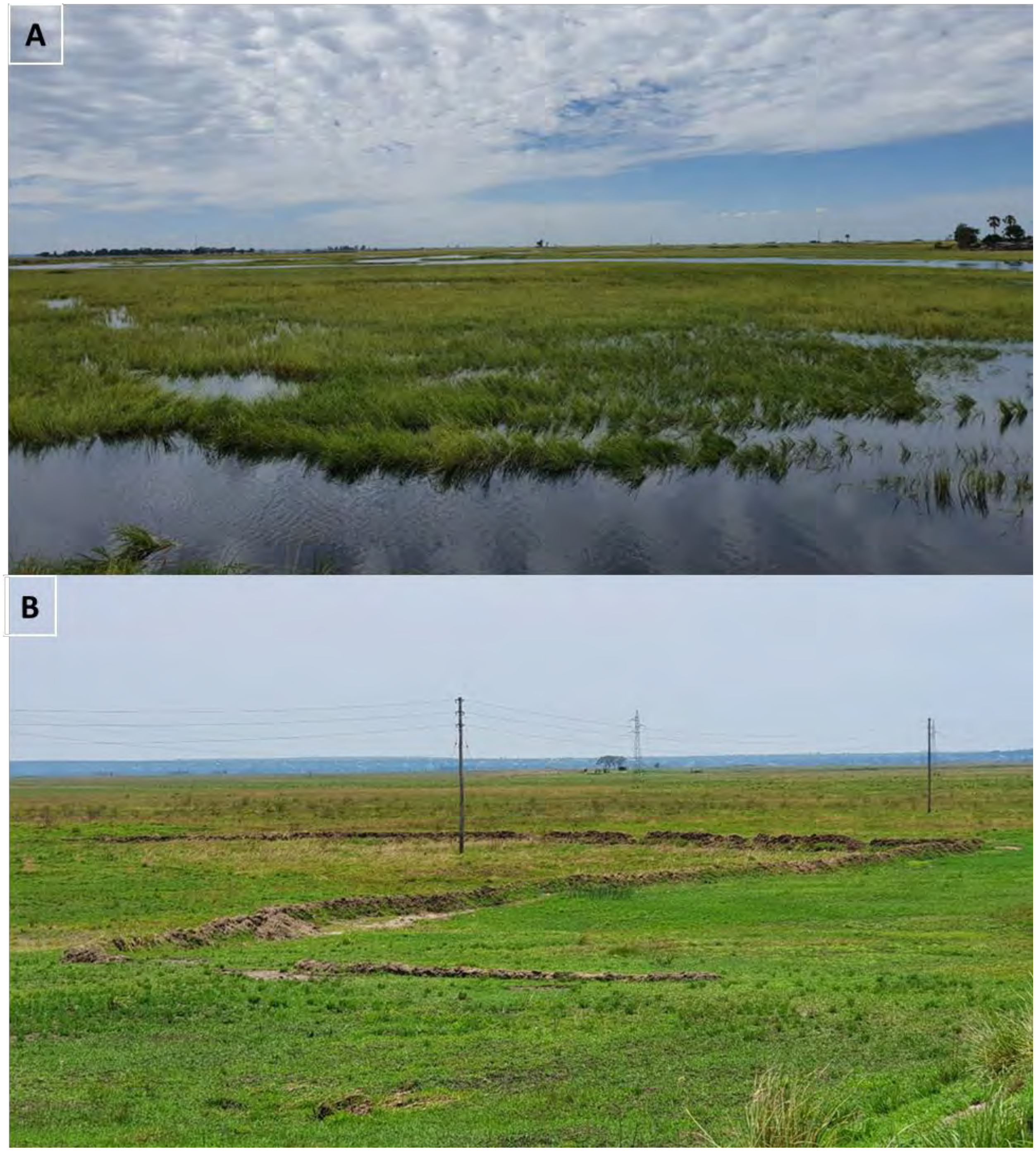

Figure 2.2 The Barotse floodplain during the A) flood period (wet season; Date: 16/04/2021) and B) dry period (dry season; Date: 14/11/2021) (Photograph: Nawa Nawa).

There are about 111 fishing villages on the floodplain inhabited by over 14 000 people from various ethnic groups (DOF 2019). Local people on the floodplain utilise a mixed livelihood strategy consisting of crop farming, livestock keeping, fishing, and exploitation of other natural resources (IUCN 2003). The floodplain fishery is an important economic activity providing food, income and employment to ~ 70, 000 people on the floodplain (CGIAR 2013). The total number of fishers on the floodplain is about 2800 (DOF 2019). Fishers utilise a wide range of fishing gears which includes gillnets, seine nets, hook and line, traps, baskets, spears, and weirs (van Gils 1988; Turpie et al. 1999). Men, women, and children all participate in the fishery (Turpie 1999), however, men generally use canoes to access better fishing grounds and utilise nets and hook and line (Cole et al. 2015; Rajaratnam et al. 2015; 2016), while women and children typically fish small or shallow water bodies using baskets, traps, and small nets (Fig. 2.3 A; B) (Rajaratnam et al. 2015; 2016). The low participation of women in fish harvesting is due to their gendered role as caretakers of families and limited access to fishing grounds (Cole et al. 2015). As a result, the benefits derived by women from fishing are relatively small compared to men (Cole et al. 2015; Rajaratnam et al. 2015). Most women's catch is usually consumed at household level while fish catch for men is mainly for sale (Pitamber 2006). Women are predominantly involved in other nodes of the value chain such as fish processing and fish trade (Fig. 2.4 A; D) (Rajaratnam et al. 2016). Women's involvement in fish trading helps them to generate income to secure food and other basic needs for their households (Rajaratnam et al. 2016).

Figure 2.3 Photographs showing A) men fishing using a gillnet (Date: 02/08/2021) and B) women fishing using traditional baskets (Date:16/11/2021) on the Barotse floodplain (Photograph: Nawa Nawa).

Figure 2.4 Women selling A) fresh and B) dried fish by the roadside on the Barotse floodplain (Photograph: Nawa Nawa; Date: 30/07/2021).

Despite the significance of the fishery, the fisheries resources are under threat from overexploitation due to increase in fishing pressure and use of unsustainable fishing methods (CGIAR 2013; DOF 2014, 2019; Tweddle et al. 2015). The Barotse floodplain has also been subjected to the introduction of the non-native Australian redclaw crayfish *C. quadricarinatus*. The crayfish were illegally introduced on the floodplain in 2012 (Douthwaite et al. 2018) through escapes from an informal aquaculture pond for road constructions workers (Madzivanzira et al. 2020). Since the crayfish introduction, reports have emerged of crayfish being caught in fishing gears (Fig. 2.5 A; D) (N Namasiku, pers. Com.) and it is not yet clear what the implications of the presence of *C. quadricarinatus* may have on the fishery.

Fig 2.5 Photograph showing A) a local fisherman removing crayfish entangled in a gillnet and B) crayfish discarded by fisherman on the banks of a water body on the Barotse floodplain (Photograph: Nawa Nawa; Date: 30/07/2021).

CHAPTER 3

ASSESSMENT OF THE MULTI-SPECIES BAROTSE FLOODPLAIN FISHERY OF THE UPPER ZAMBEZI SYSTEM

Abstract

River-floodplain systems support multi-species fisheries which sustain millions of people in south-central Africa. The Barotse floodplain fishery on the upper Zambezi River system is one of the largest fisheries areas in the region and over the years has been subject to increased anthropogenic impact including exploitation and introduction of non-native species. To assess the current status of the fishery, fisheries dependant surveys were undertaken using a set of key indicators; catch rates, species composition, size structure and gear use with specific reference to the contribution of invasive species. Catch rates were higher in wet than dry season and highest in Senanga stratum while the total annual fish yield was lower than previously estimated. Species composition was similar between seasons and across strata. The most common species harvested are *Clarias* spp., Alestidae – *Micralestes acutidens*, *Brycinus lateralis*, *Coptodon rendalli*, Mixed Small Fish (Cyprinidae, Mormyridae and juveniles of Cichlidae) while *O. niloticus* also formed part of the catch. The mean length at capture of four out of five species examined was below the length at 50% maturity. The fishery was dominated by gillnets, hook and line and seine nets but gear use did not differ between seasons and across strata. The use of illegal fishing gear was different between seasons and across strata. The use of illegal mesh size (< 3 inches) was not different between seasons but was highest in Senanga while usage of monofilament gillnet was higher in wet season and highest in Senanga. Non-native *Cherax quadricarinatus* by-catch was higher in dry than wet season and highest at the invasion core (Mongu, central Barotse floodplain). Decline in catch rate, fishes predominantly selected for below their Lm_{50}, change in species composition, and widespread use of illegal fishing gear all signal collapse of the Barotse floodplain fishery. The occurrence of non-native species *O. niloticus* and *C. quadricarinatus* further threaten the fishery. Effective management measures addressing both overexploitation and invasive species need to be implemented to ensure sustainability of fishery resources and conservation of biodiversity. This study highlights the importance of resource assessment to improve fisheries management.

Keywords

Zambezi floodplain, CPUE, *Cherax quadricarinatus* by-catch, catch rate declines, gear creep, sustainable fishery resources.

3.1 Introduction

The Barotse floodplain of the Upper Zambezi is one of the largest wetlands in the Zambezi basin and over 70,000 people (CGIAR, 2013) derive part of their livelihood from the wetland's multi-species artisanal fishery (Turpie et al. 1999; IUCN, 2003). The fishery is based on a wide range of fish species, providing food and income to the local community (CGIAR, 2013). Some of the commonly harvested species include Cichlids, Catfish (*Clarias* spp.) Tigerfish (*Hydrocynus vittatus*), African Pike (*Hepsetus cuvieri*), Robbers (*Micralestes acutidens, Brycinus lateralis, Rhabdalestes maunensis*), Mormyrids (*Heteromomyrus szaboi, Petrocephalus longicapitis, Pollimyrus marianne*), and Squeakers (*Synodontis* spp.) (Baidu-Forson et al. 2014; DOF 2014). Fish harvested comprise part of the diet of 99.3% of the households on the floodplain (Turpie et al. 1999). Most of the fish caught are sold within the Western province of Zambia, providing much-needed protein in the region (IUCN 2003), with fish consumption in the province estimated at around 5 times that of the national average (Turpie et al. 1999).

A mixture of modern and traditional fishing gears is used to exploit diverse fishery resources on the Barotse floodplain. The fishing gears used include gillnets, seine nets, hook and line, traps, baskets, spears, and weirs (van Gils 1988; Turpie et al. 1999). Gillnets have been reported to be the most important fishing gear in the fishery accounting for most of the fish catch, which is mainly cichlids (van Gils 1988; Peel et al. 2014). Gillnets and seine nets are predominantly used in lagoons and along the edges of river channels during low water period while traditional fishing gears like weirs, spears and traps are commonly used on the floodplain when it is inundated (Turpie 1999).

The Barotse floodplain fishery has grown markedly over time. In the 1970s, it was considered under-exploited (Bell-Cross 1974). In the 1980s, the total number of fishermen operating on the floodplain was estimated to be 912 equating to 0.18 fishermen/km^2 which was comparatively lower than most of the floodplains in Africa (Welcomme 1985). A 1994 frame survey revealed an increase in the number of fishers to 2159 (DOF 1994) which further increased to 3378 in 2013 (DOF 2013) and then recently declined to 2807 in 2019 (DOF 2019). Fishing pressure on the floodplain has been observed to be particularly high in areas with dense populations, especially major towns like Mongu and Senanga (Tweddle et al. 2004). Between 1990 and 2010, the annual fishery yield for the Barotse floodplain averaged 6972 tonnes. yr^{-1} with the most recent data in 2014 indicating a yield of 7714 tonnes. yr^{-1} (DOF 2015). Although the data shows a relatively stable yield for this period, the accuracy is questionable due to inadequacies in data collection (Tweddle 2010). Over the past 20 years, the Barotse floodplain fishery has increasingly been subjected to over-exploitation as fishing effort and the use of illegal fishing methods has risen significantly with concern about declining yield (Tweddle et al. 2004; 2015). The use of illegal fishing methods such as of mosquito nets, small-meshed (< 3 inches, or 76.2 mm) gillnets and seine nets has become widespread on the floodplain (Tweddle et al. 2004). Most of the gillnets are used actively in either a dragging or drifting method (Peel et al. 2014). The drifting gillnets are commonly associated with water beating aimed at driving fish from vegetation cover (Mwandima and Mwima 2005; Tweddle et al. 2010). Both the active gillnets and large seine nets have exerted pressure on larger-sized juveniles of cichlids species (Tweddle et al. 2004; 2010; Peel et al. 2014). This has resulted in a shift from large economically valuable cichlids species to small low value species (Tweddle et al. 2015). If over-exploitation of fisheries continues some of the remaining fish species risk collapsing as has already happened to other commercially valuable cichlids (Peel et al. 2014; Tweddle et al. 2015).

The Barotse floodplain fishery has also been subjected to the introduction of the non-native Australian redclaw crayfish *Cherax quadricarinatus*, with anecdotal reports indicating that crayfish now form part of fishers' catch (N Namasiku, pers. Com.). The introduction of *C. quadricarinatus* elsewhere in Africa has impacted fisheries by causing damage to fishers' catch through partial consumption of fish caught with gillnets (Lowery and Mendes 1977; Weyl et al. 2017; Chakandinakira et al. 2023). The damage caused can have cascading impact throughout the value chain (Madzivanzira et al. 2022). In addition, *C. quadricarinatus* gillnet catch often results in entanglement, damaging the net and reducing their fishing efficiency (Weyl et al. 2017). The potential impact of *C. quadricarinatus* on the Barotse floodplain fishery is a major food security concern given the high poverty level in the region (ZSA, 2023).

The Barotse floodplain fishery has not been consistently assessed over the years. The most recent assessment of the fishery was a frame survey conducted in 2019. The last catch assessment surveys on the floodplain were conducted in 2014 and, as such, the current status of the fishery is unknown (DOF 2014; Peel et al. 2014). This, in combination with previous reports of overexploitation and emergent anecdotal information of *C. quadricarinatus* prompted the present investigation whereby aspects of the sustainability of the Barotse floodplain fishery were assessed. In particular, we aimed to determine 1) the catch per unit effort (CPUE) across dry and wet seasons and across three strata, with comparisons to historic total annual fish yield, 2) if species composition would differ between season and across strata with mean length of five species falling below the length at 50% maturity, 3) if fishing methods and use of illegal fishing gears would differ between season and across strata, and 4) if crayfish (*C. quadricarinatus*) by-catch would be evident and if so, would it be higher in dry season than wet season and higher in

Mongu stratum (invasion core) compared to Senanga (downstream invasion edge) and Lukulu (upstream invasion edge) strata.

3.2 Materials and Method

3.2.1 Study site

The study was conducted on the Barotse floodplain (see Chapter 2, Fig. 2.1), which is located on the upper Zambezi River system (Fig. 3.1). At peak inundation, the floodplain has a maximum width of 50 km and stretches about 230 km in length from the North in Lukulu (upstream) to the South in Senanga (downstream) (Cai et al. 2017). The floodplain is home to several water bodies (i.e., rivers, lagoons, man-made canals) that support artisanal fisheries (Turpie et al. 1999; Tweddle et al. 2004). Fishing activities on the floodplain are closely linked to seasonal flooding with low fishing activities during the flood period and then intensifying as water recedes. The fishery is subjected to a three-month fish ban from December to February as part of the nationwide fisheries management strategy (GRZ, 2011). The Barotse floodplain fishery is managed as a common property resource through a dual governance system consisting of the traditional authority, the Barotse Royal Establishment and the Zambian Government through the Department of Fisheries (Turpie 2008; Madzudzo et al. 2013). (See chapter 2 for detailed study site description).

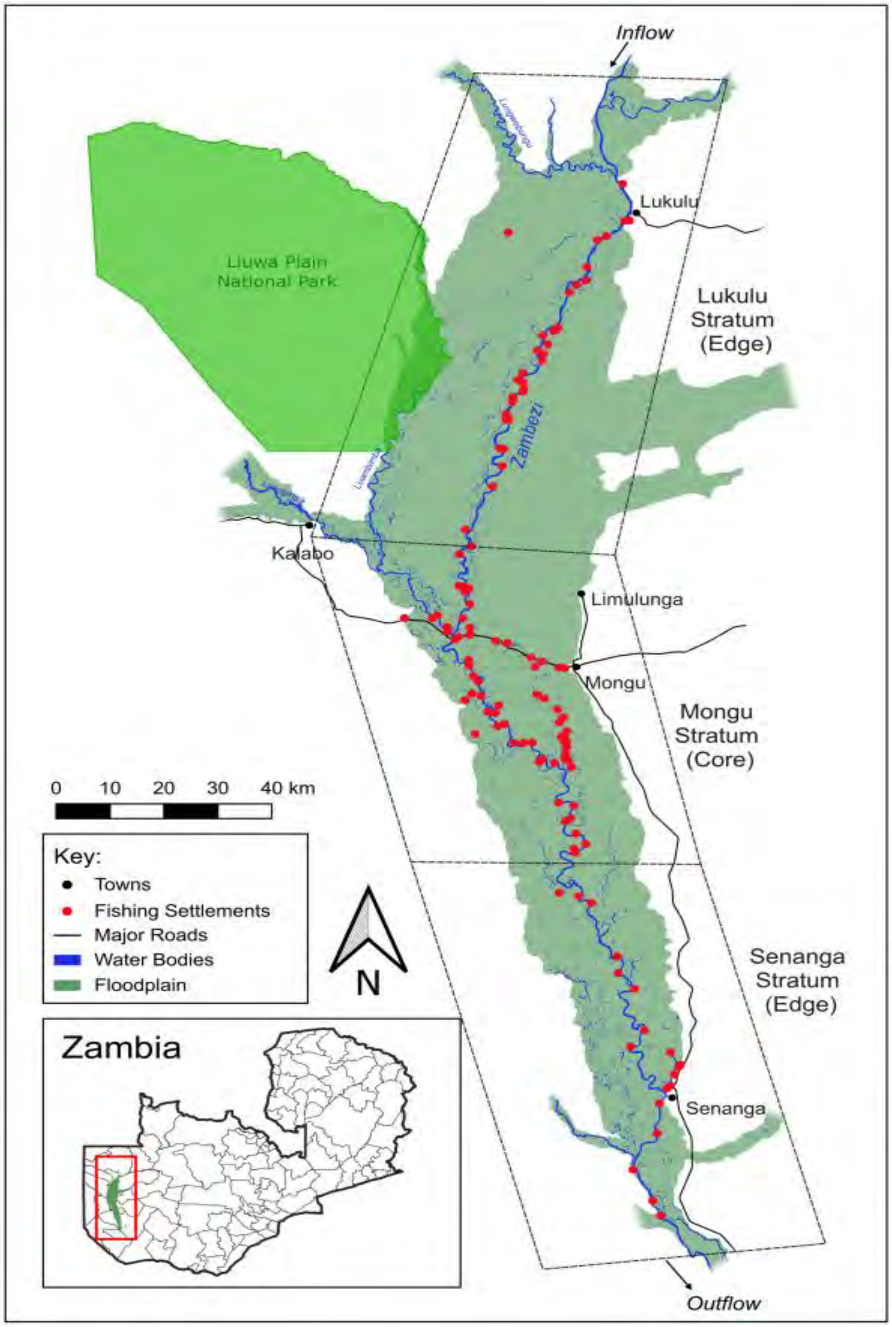

Figure 3.1 The three strata (Senanga, Mongu and Lukulu) on the Barotse floodplain where sampling was conducted.

3.2.2 Sampling

Data was collected using catch assessment surveys (CAS), specifically the roving creel survey method. The roving creel method is used for estimating catch and effort data for geographically disbursed fisheries where fishers do not come through a specific entry point (Pollock et al. 1994). This involves enumerators moving daily through their sampling strata and interviewing all fishers encountered. The surveys were conducted bi-annually in 2021, targeting the wet season/high water period (April to May) and dry season/low water period (October to November). Each survey was conducted for 30 consecutive days across three strata (Senanga, Mongu and Lukulu) (Fig. 3.1). The survey was implemented using an electronic-based CAS questionnaire accessed via the ODK collect App installed on Lenovo tablets. The questionnaire was structured consisting of open-ended and closed-ended questions (Appendix 3.1).

Prior to the implementation of the surveys, field enumerators with a minimum of a Grade 12 education were recruited from each stratum (2 in Senanga, 3 in Mongu and 2 in Lukulu). The enumerators were trained for 7 days on how to administer the electronic-based questionnaire. Upon completion of the training, enumerators were deployed in their respective stratum. Enumerators were designated specific substratum where they randomly administered the questionnaire to active fishers in different water bodies as well as those returning from fishing at landing sites and villages (Fig 3.2). The interviews were conducted in the morning (6am to 11am) and late afternoon (15pm to 18 pm) as this is the time when most of the fishing activities takes place. Field backstop visits to enumerators were conducted regularly to ensure quality control and assurance. A one-week refresher training was conducted prior to the implementation of each subsequent survey.

Figure 3.2 An enumerator conducting the interview with one of the fishers on the Barotse floodplain (Photograph: Nawa Nawa; Date: 18/10/2021).

During each interview, the catch was sorted based on individual species or species groups based on pre-determined categories used by local fishers (AES and WWF 2017). A total of twenty-one species or species groups were used with identification by field enumerators facilitated by a picture identification guide based on images from Skelton (2001) and through training prior to the commencement of each survey. The pre-determined fish species or species categories were: Catfish (*Clarias gariepinus, Clarias ngamensis, Clarias stappersii, Clarias theodorae*), African Pike (*Hepsetus cuvieri*), Tigerfish (*Hydrocynus vittatus*), Redbreast Tilapia (*Coptodon rendalli*), Threespot Tilapia (*Oreochromis andersonii*), Nembwe (*Serranochromis jallae*) Purpleface Largemouth (*Serranochromis macrocephalus*), Other Largemouths (*Serranochromis altus*, *Serranochromis angusticeps*), Sargochromines (*Sargochromis* spp.), Nile Tilapia (*Oreochromis niloticus*), Other Large Breams, Small Breams (<10cm – any bream under 10cm, such as

Pharyngochromis acuticeps, Pseudocrenilabrus philander and any juveniles of large species), Yellowfish (*Labeobarbus codringtonii*), Silver Catfish (*Schilbe intermedius*), Small Mixed Mormyrids (*Heteromomyrus szaboi, Petrocephalus longicapitis, Pollimyrus marianne*), Bulldog (*Marcusenius altisambesi*), Western Bottlenose (*Mormyrus lacerda*), Squeakers (*Synodontis spp*), Climbing Perch (*Ctenopoma multispine, Microctenopoma intermedium*), Robbers/ Alestidae (*Micralestes acutidens, Brycinus lateralis, Rhabdalestes maunensis*), Mixed Small Fish (Cyprinidae, Mormyridae and juveniles of Cichlidae usually sold as a unit in hand, bucket or scoop) and an option of Other Species allowing additional species to be entered if they are frequently recorded.

For each species or species group, the entire catch was weighed in kilograms (kg) giving the total weight per species category. A maximum of 20 individuals per species (excluding species groups) was measured for length data (i.e. recording fork length or total length) in centimetres (AES and WWF 2017). To estimate the activity rate (fishing effort) of fishers, they were asked about their recent fishing activity in the past week (i.e. did they fish yesterday, day before yesterday and how many days in the past week). Information on the type of fishing gear used and bycatch species was also recorded from each fisher (Appendix 3.1). Additional information on fishing effort was obtained from the 2019 Frame Survey (DOF 2019). Frame surveys are conducted by the Zambia Department of Fisheries every five years to gather information on the total number of people, number of fishers, number of boats, and type of fishing gear as well as information on other livelihood activities (AES and WWF 2017). Data on level of participation (population of fishers) was used to estimate total harvest of the fishery. To assess illegal fishing use of mesh size less than 3 inches and monofilament nets were considered illegal as these are prohibited according to the Zambian Fisheries Act No. 22 of 2011.

3.3 Data Analysis

3.3.1 Catch and Effort

Daily catch rate was expressed as individual catch per unit effort (CPUE) for all fishing gears and adapted from AES and WWF (2017) as follows.

$$(1)\ \text{CPUE} = kg.\ fisher^{-1}.\ d^{-1}$$

When quantifying annual fish yield from creel surveys, the calculation of CPUE is generally a recommended method (Brouwer et al. 1997; Pollock et al. 1997). A generalised linear model with a log link function was used to test the effect of season and stratum on individual CPUE values. Individual CPUE were upscaled based on reported effort or how far they had gone in their fishing at the time of the interview (i.e., effort less than half = total kg+(total kg x 3), effort half = total kg+(total kg x 1), effort more than half = total kg+(total kg x 0.5) and effort complete = total kg. Fishing effort was expressed as mean number of days fished per week during a sampling period. The effect of season and stratum on fishing effort was analysed using a generalised linear model with quasipoisson distribution. Differences in factors for both models were examined post-hoc using the emmeans package (Lenth 2020).

3.3.2 Total catch

To estimate total annual harvest for the fishery, CPUE and effort values were used. The calculation was adapted from AES and WWF (2017) as follows:

$$(2)\ \text{Total yield} = \text{CPUE}\ (kg.\ fisher^{-1}.\ d^{-1}) \times \text{Effort (days fished)} \times \text{total number fishers}$$

Since CPUE and Effort differed by season and strata calculation was disaggregated accordingly. The effort used was upscaled based on the nine-month fishing period (March to November) considering the three-month fish ban period (December to February). Effort for wet season was based on a three-month fishing period (March to May) while that of dry season was based on a six-month (June to November) fishing period.

3.3.3 Species composition

The relative composition of fish species or species group caught was expressed as a percentage of the total catch by weight (kg) for each stratum. To assess the potential of overfishing, the mean length of five fish species (*C. rendalli*, *O. andersonii*, *H. vittatus*, *S. macrocephalus* and *S. intermedius*) was determined across the three strata as indicators of temporal change in size structure because they are commercially important species on the Barotse floodplain (Baidu-Forson et al. 2014). The mean length obtained for each species was then compared with its length at 50% maturity (Lm_{50}) reported for the fish species. Female Lm_{50} was used a conservative measure except in cases where maturity data was only available in combined form (male and female). The mean length of fish harvested is normally used as a standard measure of overexploitation (Kolding and van Zwieten, 2014).

3.3.4 Gear usage

Gear usage was expressed as the relative percentage frequency of the total number of fishers per stratum. A chi-square test of independence was used to determine the difference in the number of fishing gear types across the strata. To assess the prevalence of illegal fishing, the frequency usage of gillnets with mesh sizes less than 3 inches as well as monofilament gillnets were tested using a Chi-square test of independence.

3.3.5 Crayfish by-catch

To assess the prevalence of *C. quadricarinatus* being caught by fishers, the proportion of fishers catching crayfish was determined and then tested for significant difference using the Chi-square test of independence. The frequency capture of bycatch species by fishers was determined by classifying bycatch species into categories: crabs, crayfish, terrapin, otters and other types. The composition of by-catch was expressed as a percentage of total frequency of bycatch. The frequency of bycatch was then be tested for significant difference across season and strata using Chi-square test.

3.4 Results

A total of 944 interviews were conducted across the floodplain. The highest number of interviews were from Mongu stratum accounting for 39.3% of the total interviews, followed by Senanga and Lukulu strata with 31.4% and 29.3% respectively (Table 3.1).

Table 3.1 Number of fishers interviewed during wet and dry season across three strata (Senanga, Mongu and Lukulu) on the Barotse floodplain.

Stratum	Wet Season	Dry Season	Total interviews
Senanga	125	171	296
Mongu	117	254	371
Lukuku	107	170	277

3.4.1 Catch and effort

Of the fishers interviewed, 98% had caught at least one fish while 2% had not caught a fish at the time of the interview. Analysis of CPUE revealed that both stratum and season had a significant effect on CPUE (Table 3.2). The CPUE for Senanga (wet, 11.63 $kg.fisher^{-1}.day^{-1}$; dry, 9.15 $kg^{-1}.fisher^{-1}.day^{-1}$) and Lukulu (wet, 5.17 $kg.fisher^{-1}.day^{-1}$; dry, 4.15 $kg.fisher^{-1}.day^{-1}$) strata were significantly higher than that for Mongu (wet, 2.92 $kg.fisher^{-1}.day^{-1}$; dry, 3.24 $kg.fisher^{-1}.day^{-1}$) stratum (both, $p < 0.01$; Fig. 3.3), while CPUE for Senanga stratum was higher than that for Lukulu stratum ($p < 0.01$). Overall, CPUE for wet season (6.85 $kg.fisher^{-1}.day^{-1}$) was higher than dry season (5.26 $kg.fisher^{-1}.day^{-1}$) ($p < 0.03$; Fig. 3.3). The mean annual CPUE across the floodplain was 5.86 $kg.fisher^{-1}.day^{-1}$.

Table 3.2 Model terms for all factors from GLM with a gamma distribution used to determine effects of factors “stratum” and “season” on CPUE. Type 2 Anova and χ^2 used to report the effect size of a factor on the dependent variable.

Model term	**Chisq**	**df**	***p*-value**
Stratum	223.63	1	< 0.01
Season	14.82	1	< 0.01

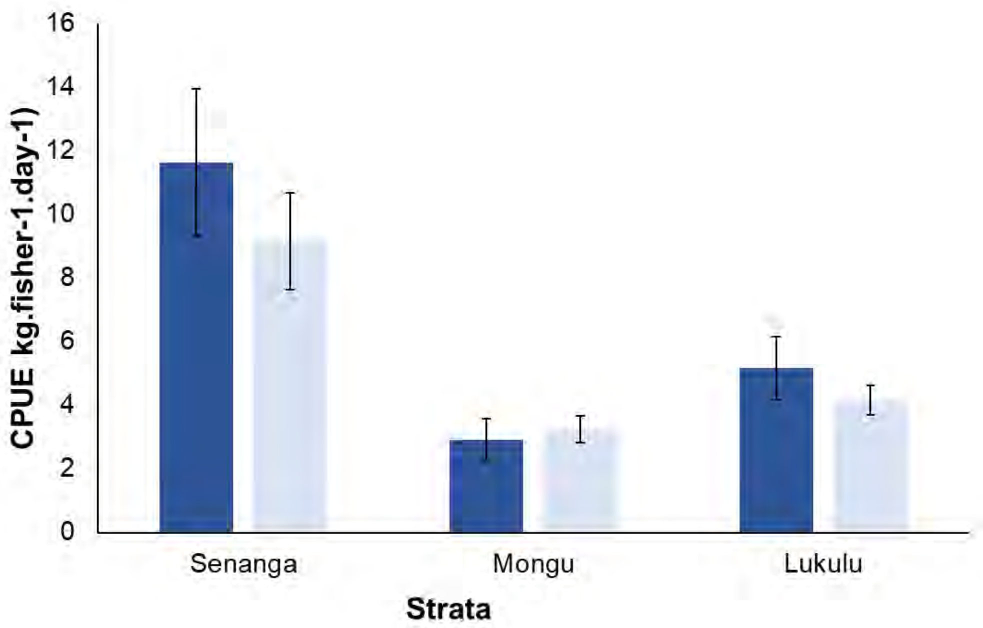

Figure 3.3 CPUE (kg.fisher^{-1}.day^{-1}) for wet (blue) and dry (light blue) season across the three strata (Mongu, Senanga and Lukulu) on the Barotse floodplain. Error bars represent 95% confidence intervals.

Analysis of weekly effort revealed that both stratum and season had a significant main effect (Table 3.3). Weekly effort for Senanga (wet, 6.10 days.week^{-1}; dry, 5.04 days.week^{-1}) and Lukulu (wet, 4.87 days.week^{-1}; dry, 5.0 days.week^{-1}) strata were significantly higher than that for Mongu (wet, 4.98 days.week^{-1}; dry, wet, 4.12 days.week^{-1}) stratum (both, $p < 0.01$; Fig. 3.4), while effort for Senanga stratum was higher than that for Lukulu stratum ($p < 0.01$). Overall, effort for wet season (5.36 days.week^{-1}) was higher than dry season (4.65 days.week^{-1}) ($p < 0.01$; Fig. 3.4). The mean weekly effort across the floodplain was 4.92 days.week^{-1}.

Table 3.3 Model terms for all factors from GLM with a quasipoisson distribution used to determine effects of factors "stratum" and "season" on weekly effort. Type 2 Anova and χ^2 used to report the effect size of a factor on the dependent variable.

Model term	**Chisq**	**df**	***p*-value**
Stratum	33.87	1	< 0.01
Season	21.65	1	< 0.01

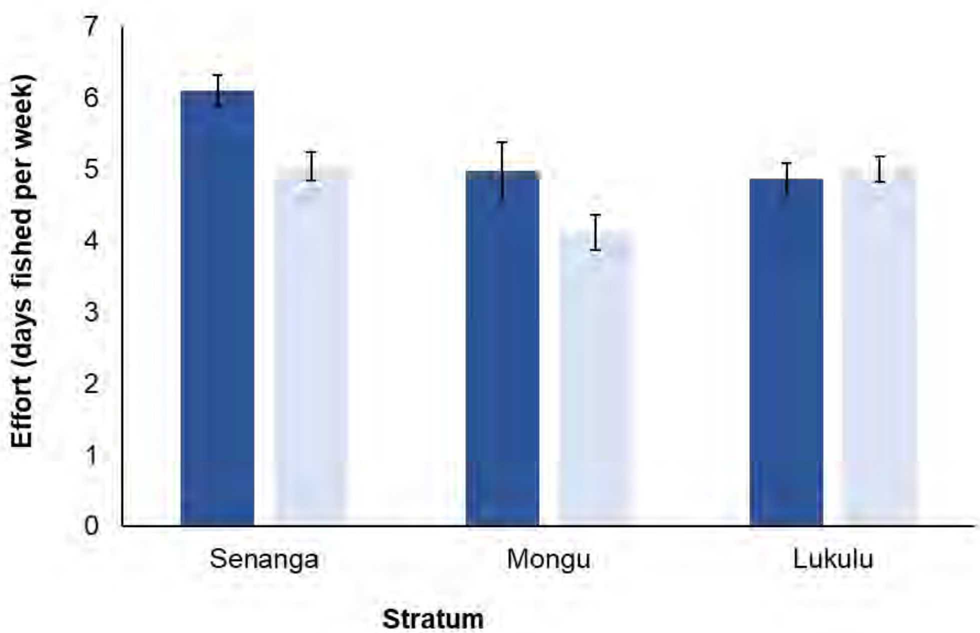

Figure 3.4 Number of days fished per week during wet (blue) and dry (light blue) season across the three strata (Senanga, Mongu and Lukulu) on the Barotse floodplain. Error bars represent 95% confidence intervals.

3.4.2 Total catch

Based on disaggregated data by strata and season, the total annual fish yield for the fishery was 3123 tonnes. year ^{1} (Table 3.4). The highest yield came from Senanga stratum which accounted for 66.5% of the total yield followed by Mongu and Lukulu strata with 28.9% and 4.6% respectively.

Table 3.4 Annual fish yield (kgs) of the Barotse floodplain disaggregated by strata and season.

Stratum	Season	Mean CPUE	Days fished	Number of fishers	Yield
Senanga	Wet	11.63	80	972	904,348.80
	Dry	9.15	132	972	1,173,981.60
Mongu	Wet	2.92	65	1672	317,345.60
	Dry	3.24	108	1672	585,066.24
Lukulu	Wet	5.17	64	163	53,933.44
	Dry	4.15	131	163	88,614.95
Total Yield					**3,123,290.63**

3.4.3 Species composition

Species/species group composition did not differ significantly across season ($\chi2$= 0.01, df = 1, *p* = 0.94) and strata ($\chi2$= 0.04, df = 2, *p* = 0.98). However, there were proportional variation in composition across seasons and strata. In Senanga stratum the wet season catch was dominated by *Clarias* spp. and Robbers while the dry season mostly comprised of Robbers, *Clarias* spp., *M. altisambesi* and *C. rendalli* (Table 3.5). In Mongu stratum *Clarias* spp., and Robbers were more dominant during wet season whereas *Clarias* spp., *C. rendalli* and *S. macrocephalus* were the most species in dry season (Table 3.5). In Lukulu, *Clarias* spp., Mixed Small Fish, and *H. vittatus* dominated the wet season catch while *Clarias* spp., *C. rendalli*, and Mixed Small Fish accounted for a higher proportion of the catch in dry season (Table 3.5). Overall, the species composition across the entire fishery was dominated by *Clarias* spp., Robbers, *C. rendalli*, Mixed Small Fish, *M. altisambesi* and *H. vittatus* together accounting for 80.37% of the total catch (Table 3.5).

Table 3.5 Percentage composition of species/group by weight during wet and dry season across three strata (Senanga, Mongu and Lukulu) on the Barotse floodplain. The last column indicates overall percentage composition by weight.

Common name/group	**Scientific name (s)**	**Senanga**		**Mongu**		**Lukulu**		**Overall**
		Wet	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**	
Catfishes - all types	*Clarias* spp. (e.g., *C. gariepinus, C. ngamensis,* etc.)	69.30	17.34	26.09	46.29	27.32	29.66	37.17
Robbers	*M. acutidens, B. lateralis, R. maunensis*	17.95	28.04	14.95	6.61	9.14	16.85	17.91
Redbreast Tilapia	*C. rendalli*	1.69	11.89	9.54	14.21	10.96	16.68	10.39
Mixed Small Fish <10cm	*Enteromius* spp. and juveniles of various bream species	2.89	4.56	9.70	2.99	18.57	2.88	5.69
Bulldog	*M. altisambesi*	1.07	12.20	3.72	0.45	0.15	5.18	4.87
Tigerfish	*H. vittatus*	1.91	1.63	8.09	0.15	13.32	7.10	4.34
Small Breams <10cm	Any bream < 10cm e.g., *P. acuticeps, P. philander*	1.00	6.52	5.58	4.71	1.23	3.39	3.70
Purpleface Largemouth	*S. macrocephalus*	0.26	1.87	5.32	12.39	1.51	3.34	3.18
Squeakers	*Synodontis* spp.	0.34	6.12	1.16	2.73	2.88	2.58	3.01
Sargos	*Sargochromis* spp.	0.06	2.92	1.07	6.74	0.17	1.65	2.02
Other Largemouths	*Serranochromis* spp.	0.74	1.32	0.38	0.38	2.36	4.98	1.83
Threespot Tilapia	*O. andersonii*	0.15	4.45	2.78	1.56	0.12	0.88	1.79
Silver Catfish	*S. depressirostris*	1.43	0.39	4.84	-	5.92	0.05	1.46
Nile Tilapia	*O. niloticus*	-	-	0.33	0.04	2.55	4.30	1.14
Climbing Perch	*C. multispine*	0.66	0.26	4.32	-	2.03	-	0.72
Small Mixed Mormyrids	*H. ansorgii, P. okavangensis, P. marianne*	0.55	0.28	1.26	0.30	0.36	-	0.36
Western Bottlenose	*M. lacerda*	0.01	0.04	0.23	0.23	1.39	0.36	0.30
Nembwe	*S. jallae*	-	0.13	0.08	-	-	0.12	0.06
African Pike	*H. cuvieri*	-	0.03	0.47	0.06	-	-	0.04
Other Large Breams	-	-	-	-	0.16	-	0.01	0.02
Yellowfish	*L. codringtonii*	0.00	0.00	0.10	0.00	0.00	0.00	0.01

The mean length at capture of *C. rendalli*, *O. andersonii*, *H. vittatus* and *S. intermedius* were all below the length at 50% maturity reported for each fish species (Table 3.6). Out of the total measurements taken for each species, 91.1% of the *C. rendalli*, 89.8% of *O. andersonii* 90.9% of

H. vittatus, and 90.0% of *S. intermedius* were below length at 50% at maturity (Fig. 3.5 A to E). The mean length at capture of *S. macrocephalus* was higher than the length at 50% maturity estimated for the fish species (Table 3.6). Based on the total measurement 26.0% of *S. macrocephalus* were below 140 mm length at 50% maturity. (Fig. 3.5 D).

Table 3.6 Mean length (mm) of 5 species in the catch and length at 50% maturity (***Lm_{50}***). TL = total length, SL standard length. Value in parentheses represent 95% confidence intervals.

Common name	Scientific name	Mean Length	Length at Maturity (*Lm_{50}*)
Redbreast Tilapia	*C. rendalli*	150 (±1.80) mm TL	214 mm TL, combined male & female (Peel 2012)
Threespot Tilapia	*O. andersonii*	155 (±5.43) mm TL	240 mm TL, combined male & female (Peel 2012)
Tigerfish	*H. vittatus*	171 (±5.52) mm SL	270 mm SL, female (Magqina et al. 2021)
Purpleface Largemouth	*S. macrocephalus*	159 (±2.65) mm TL	140 mm TL, female (van der Waal 1984)
Silver catfish	*S. intermedius*	132 (±1.12) mm SL	173 mm SL, female (Merron and Mann 1995)

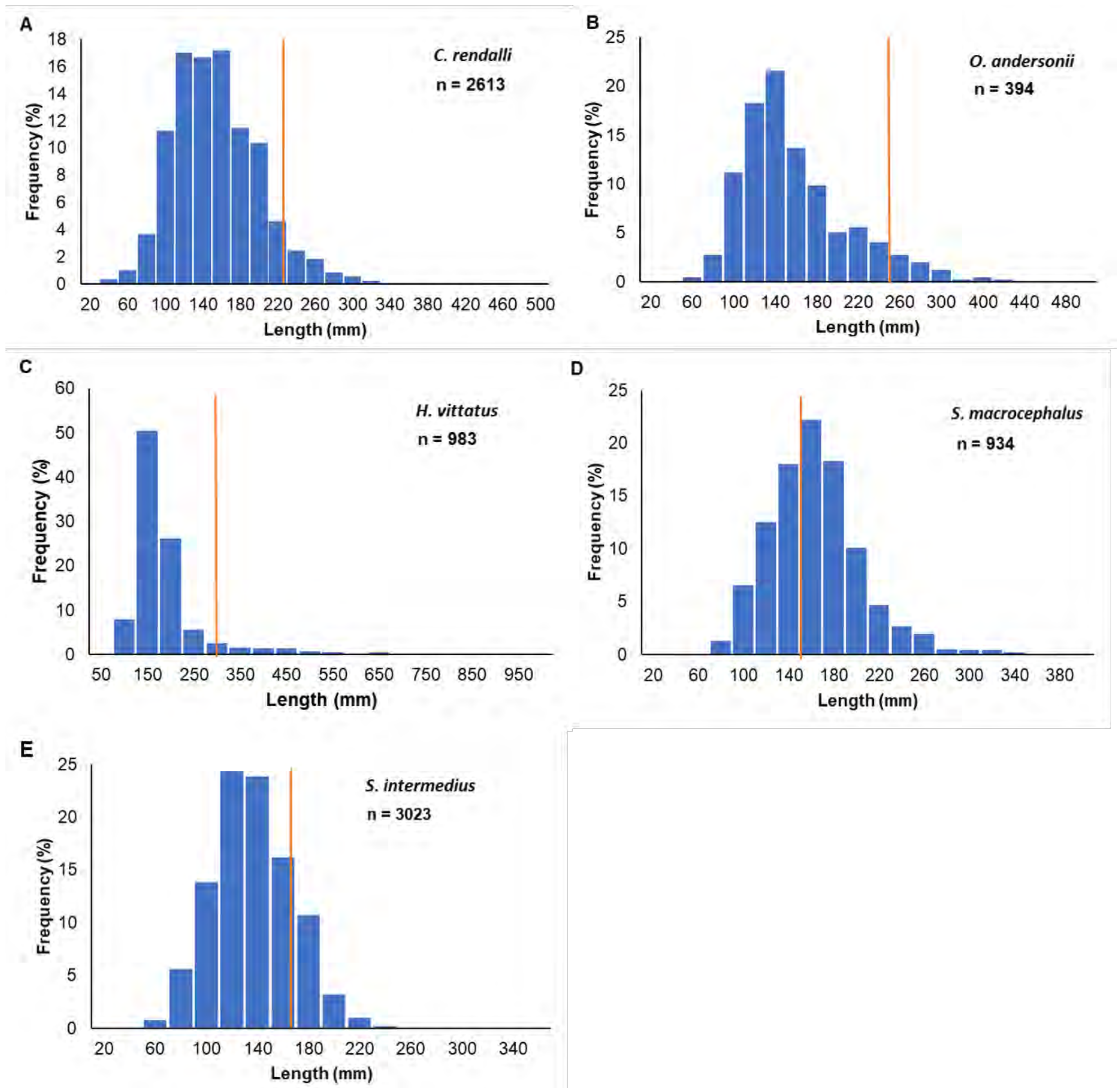

Figure 3.5 Length frequency distribution of (A) *C. rendalli*, (B) *O. andersonii*, (C) *H. vittatus*, (D) *S. macrocephalus* and (F) *S. intermedius* in all fishing gears during wet and dry season across three strata (Senanga, Mongu and Lukulu) on the Barotse floodplain. The letter 'n' stands for sample size while the red line represents length (mm) at 50% maturity for each species indicated in Table 3.6.

3.4.4 Gear usage

Overall, the five most common fishing gears were gillnet, hook and line, seine net, large hooks on pole and mosquito seine together accounting for 75.42% of the total gear usage across the floodplain (Table 3.7). The types of fishing gear used did not differ significantly across season ($\chi2$= 0.01, df = 1, p = 0.93) and strata ($\chi2$= 0.04, df = 2, p = 0.98). However, proportional usage varied considerably. In Senanga stratum the most common gear types during wet season were gillnets, large hooks on poles and longline while in dry season seine net, hook and line and gillnet were more dominant (Table 3.7). In Mongu stratum gillnet, hook and line and mosquito seine were the most important fishing methods in wet season whereas the use of hook and line, seine net and gillnet were prominent in dry season (Table 3.7). In Lukulu stratum, gillnet, reed baskets scoop and mosquito seine nets were commonly used in wet season while seine nets, large hooks on poles and cast nets were dominant fishing gears in dry season (Table 3.7). An estimated 22.35% of the fishing gear used is legal (Multifilament gillnets > 3 and hook and line gears) while 77.65% is illegal (monofilament nets; mesh size <3 and the rest of the fishing gears).

Table 3.7 Percentage usage of fishing gear during wet and dry season across three strata (Senanga, Mongu and Lukulu) on the Barotse floodplain. Last column shows overall percentage usage.

Fishing gear	**Senanga**		**Mongu**		**Lukulu**		**Overall**
	Wet	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**	
Gillnet	36.00	15.20	47.01	16.54	25.23	8.82	22.25
Hook and line	12.80	30.41	17.09	35.43	11.21	10.59	22.03
Seine net	0.80	33.92	11.11	23.23	-	25.88	18.54
Large hooks on poles	25.60	3.51	2.56	-	4.67	14.71	7.52
Mosquito seine <5m	-	2.34	11.97	1.57	14.95	5.88	5.08
Hand spear	0.80	5.26	-	12.60	-	1.76	4.77
Reed basket scoop	-	2.34	-	0.79	21.50	6.47	4.24
Drift gillnet	4.00	5.26	1.71	2.76	9.35	1.76	3.81
Cast net	-	1.17	-	3.54	-	11.18	3.18
Small vertical trap	-	-	4.27	1.57	-	10.59	2.86
Longline	18.40	-	-	-	0.93	-	2.54
Large mesh reed trap	0.80	-	1.71	1.57	3.74	2.35	1.59
Small mesh reed fish trap	0.80	-	0.85	-	4.67	-	0.74
Vertical scoop trap	-	0.58	-	-	1.87	-	0.32
Bottle trap	-	-	0.85	0.39	-	-	0.21
Fish weir Floodplain	-	-	-	-	1.87	-	0.21
Scoop net	-	-	0.85	-	-	-	0.11

Overall, 91% of the fishers used illegal mesh size across the entire Barotse floodplain. The proportion of fishers using gillnets with illegal mesh size (< 3 inches) to those with legal mesh size (3 inches and above) was significantly different across the strata ($\chi 2$= 15.92, df = 2, p < 0.01). The use of illegal mesh size in Senanga (97.2%) was significantly higher than that of Mongu (87.6%) ($\chi 2$= 10.44, df = 1, p < 0.01) and Lukulu (88.1%) ($\chi 2$= 9.51, df = 1, p < 0.01) (Fig. 3.6). The use of illegal mesh size was not significantly different between Mongu and Lukulu ($\chi 2$= 0.01, df = 1, p = 0.94) (Fig. 3.6). There was no significant difference in the usage of illegal use mesh size during wet (92.9%) and dry season (88.0%) across the strata ($\chi 2$= 1.5, df = 1, p = 0.22).

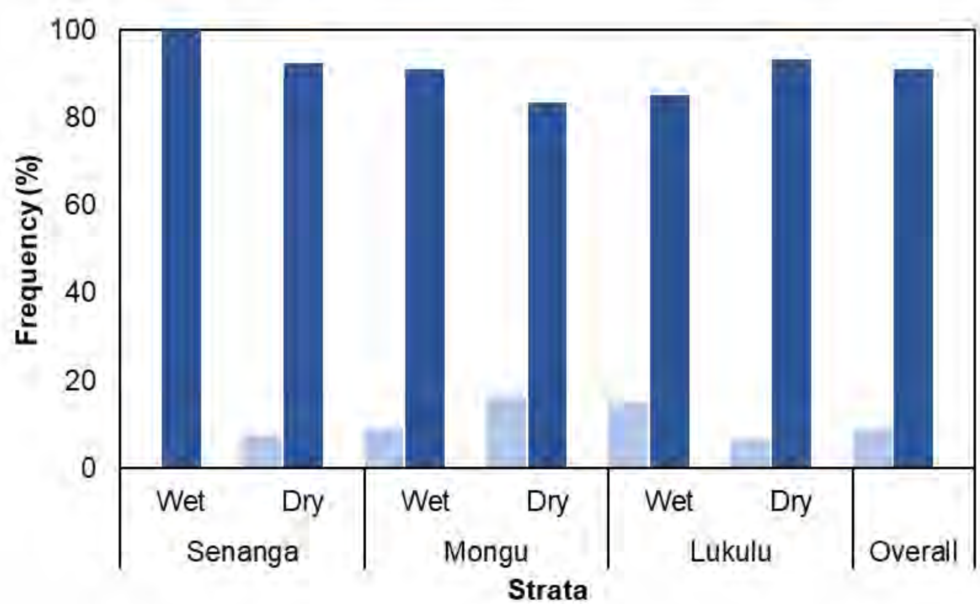

Figure 3.6 Percentage usage of legal mesh size (≥ 3 inches; light blue) and illegal mesh size (< 3 inches; blue) gillnets during wet and dry season across the three strata (Senanga, Mongu and Lukulu) on the Barotse floodplain.

Approximately 84% of fishers used monofilament gillnets across the Barotse floodplain. The proportion of fishers using monofilament gillnets to those using multifilament gillnets was significantly different across the strata ($\chi 2= 34.41$, df = 2, $p < 0.01$). There was a significantly high proportion of fishers using monofilament gillnets in Senanga (95.8%) compared to Mongu (77.3%) ($\chi 2= 25.9$, df = 1, $p < 0.01$) and Lukulu (81.0%) ($\chi 2= 17.13$, df = 1, $p < 0.01$) (Fig. 3.7). The proportional usage of monofilament gillnet was not significantly different between Mongu and Lukulu ($\chi 2= 0.4$, df = 1, $p = 0.53$) (Fig. 3.7). The usage of monofilament gillnets was significantly higher in wet (94.5%) than dry season (68.7%) across the strata ($\chi 2= 39.7$ df = 2, $p < 0.01$) (Fig. 3.7). About 92.9% of fishers used monofilament during wet season compared to 88.0% during dry season.

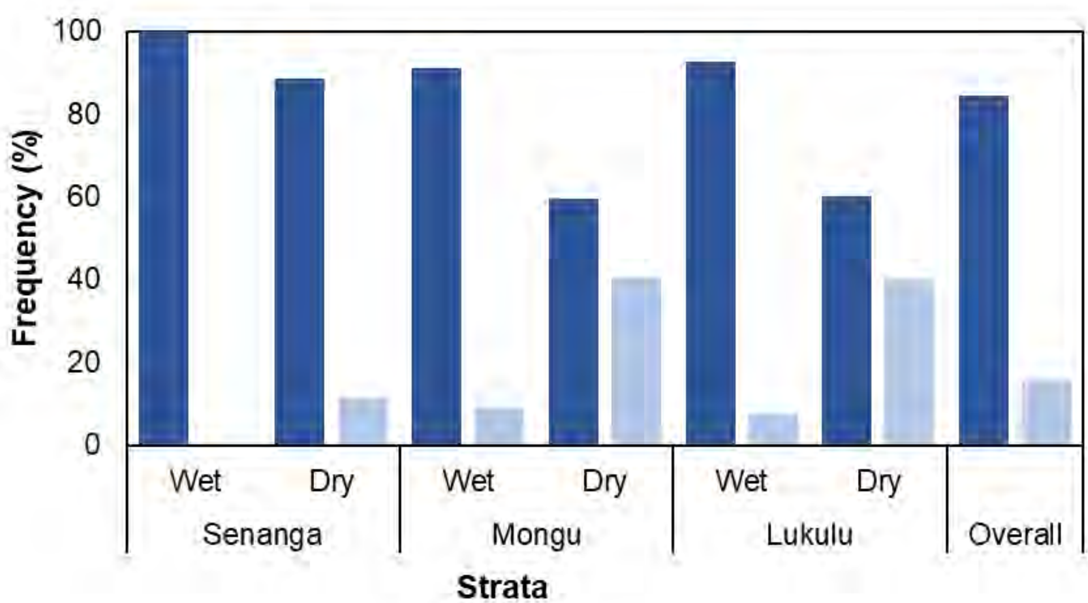

Figure 3.7 Percentage frequency of fishers using monofilament (blue) and multifilament gillnets during (light blue) wet and dry season across three strata (Senanga, Mongu and Lukulu) on the Barotse floodplain.

3.4.5 Crayfish by-catch

Overall, 36.0% of fishers caught by-catch species in their fishing gears across the entire Barotse floodplain. Of fishers with by-catch, the percentage of fishers with crayfish by-catch was the highest followed by those with crabs, otters and terrapin (Table 3.8). The proportion of fishers with crayfish by-catch in Mongu (85.1%) was significantly higher than Senanga (57.8%) ($\chi2$= 2.49, df = 1, $p < 0.01$) and Lukulu (32.9%) ($\chi2$= 34.57, df = 1, $p < 0.01$) while that of Senanga was significantly higher than Lukulu ($\chi2$= 13.34, df = 1, $p < 0.01$) (Table 3.8). The percentage of fishers with crayfish by-catch was significantly higher in dry season (69.0%) compared to the wet season (48.1%) across the strata ($\chi2$= 13.1, df = 1, $p < 0.01$) (Table 3.8).

Table 3.8 Percentage of fishers who caught by-catch species in their fishing gear during wet and dry season across three strata (Senanga, Mongu and Lukulu) on the Barotse floodplain. The letter 'n' represents sample size.

Name of by-catch species	**Senanga**				**Mongu**				**Lukulu**				**Overall**		
	Wet		**Dry**		**Wet**		**Dry**		**Wet**		**Dry**		**Fishers with by-catches**		**All fishers**
	n	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**%**
Crayfish	10	43.5	57	61.3	23	76.7	103	87.3	5	19.2	20	40.0	218	64.1	23.1
Crabs	5	21.7	34	36.6	6	20.0	15	12.7	13	50.0	25	50.0	98	28.9	10.4
Otter	6	26.1	1	1.1	-	-	-	-	5	19.2	-	-	12	3.5	1.3
Terrapin	2	8.7	1	1.1	-	-	-	-	3	11.5	3	6.0	9	2.6	1.0
Others	-	-	-	-	1	3.3	-	-	-	0.0	2	4.0	3	0.9	0.3

3.5 Discussion

Assessment of resource exploitation of river floodplain fisheries is important for determining their sustainability and improving fisheries management. However, like most inland fisheries, river-floodplain fisheries are confronted with a paucity of data impeding their effective management (Isaac et al. 2016). This study provides the first catch assessment of the Barotse floodplain fishery since 2014. Contrary to expectation, CPUE was higher in wet season than dry season and highest in Senanga stratum while total annual fish yield was relatively lower than previously estimated. Species composition was similar between season and across strata with Mean length of four selected indicator species falling below the length at 50% maturity. Fishing methods were not different between seasons and across strata. However, the use of illegal fishing gears was different between seasons and across strata. The use of illegal mesh size (<3 inches) was highest in Senanga while usage of monofilament gillnet was higher in wet season and highest in Senanga. Crayfish (*C. quadricarinatus*) by-catch was higher in dry season than wet season and highest at the invasion core (Mongu - central Barotse floodplain).

The high fish catch rates in Senanga stratum is likely due to high primary productivity associated with downstream inundation of floodplain systems (Ndehedehe et al. 2020). River flows from upstream delivers sediments and nutrients downstream stimulating primary production which supports high density of aquatic organisms such fish and other higher consumers (Junk et al. 1989; Keddy et al. 2009; Ndehedehe et al. 2021). On the other hand, the high number of fishers may have contributed to the low catch rates in Mongu as more fishers compete for finite resources. Frame surveys have reported the highest number of fishers in and around Mongu area (DOF 2013; 2019). Tweddle (2004) also expressed concerns about high fishing pressure in Mongu having localised impact on abundance and diversity of fish stock. Higher catch rates observed during wet season (high water period) contrast with other studies that have found catch rates to be higher during dry season (low water period) when fishing effort is also high (Turpie 1999; Kolding et al. 2003). Considering the number of fishers per boat (1.48 $fisher. boat^{-1}$) in this study the calculated mean annual CPUE of 5.86 $kg.fisher^{-1}.day^{-1}$ equates to 8.67 $kg. boat^{-1}. night^{-1}$ representing a decline from 11.75 $kg. boat^{-1}.night^{-1}$ estimated for the fishery in 2014 (DOF 2015). The decline in fish catches is potentially due to an increase in the fishing population (i.e., fishing pressure) coupled with the use of illegal fishing methods such as small mesh sizes and active use of fishing gears which characterises the fishery.

The annual fish yield of 3123 $tonnes.year^{-1}$ calculated in this study is also considerably lower than 7714 tonnes estimated in 2014 by the Department of Fisheries (DOF 2014; 2015). The low yield is a further reflection of an overall decline in CPUE. However, it is worth noting that the annual fish yield is likely to be underestimated as illegal fishing during the fish ban period is reportedly high (CGIAR 2013). Furthermore, the potential underestimation of the fishing population during the 2019 frame survey may also have contributed to low yield (DOF 2019). The survey reported a decrease in the number of fishers from 3,378 in 2013 to 2,807 in 2019 which was attributed to the untimely implementation of the frame survey as some of the fishers had migrated upland for farming activities (DOF 2019). However, even if the 2013 population data were used, the annual fish yield would still be comparatively low. The yield is also lower than 13,360 to 18, 365 tonnes. $year^{-1}$ estimated for the Kafue floodplain fishery (AES and WWF 2018). When the surface area for the Barotse floodplain (approximately 550 000 hectares) is taken into account (Turpie et al. 1999), the fish yield for this study translates into 5.8 $kg.ha^{-1}$ which is slightly higher than the yield 5.5 $kg.ha^{-1}yr^{-1}$ reported for the Chobe floodplain (Simasiku 2019) but less than 20 to 28 $kg.ha^{-1}yr^{-1}$ reported for Kafue Flats (AES and WWF 2018). Apart from the low CPUE, the characteristic sandy, well-drained, nutrient-poor soils of the Barotse floodplain makes it inherently less productive when compared to other floodplains like the Kafue floodplain (Bell-Cross 1974).

The twenty-one fish species/group harvested confirms the local people's dependence on diverse fishery resources. The five most important species/group during both wet and dry across the floodplain are *Clarias* spp, Robbers, *C. rendalli*, Mixed Small Fish, *M. altisambesi* reflecting a change from the previously dominant large cichlid species. The combined catch composition of large cichlids has dropped to 23.0% from 41.3 % reported in 2014 (DOF 2014). Although the composition of *C. rendalli* in the catch has remained relatively high, other large cichlids like *Serranochromis* spp. have declined considerably. The shift to smaller prolific adult fishes and juveniles of large cichlids is likely due to the indiscriminate use of small mesh size nets re-affirming earlier assertions of over-exploitation in the fishery (Tweddle et al. 2004; 2010; Peel et al. 2014).

Furthermore, the presence of non-native fish species *O. niloticus,* in the catch likely poses a threat to biodiversity and fishery resources due to its ability to hybridise with *Oreochromis* spp. (Bbole et al. 2014; Deines et al. 2014). Although the biomass of *O. niloticus* recorded in this study is relatively low, it is comparable to that of native species *O. andersonii*, an indication of its high adaptability and capacity to outcompete native species (Canonico et al. 2005). The versatility of *O. niloticus* introduction is quite evident on the Kafue Flats where it became well established following its introduction with *Oreochromis* hybrid species forming a significant part of the catch (AES and WWF 2017). Similar observations have been made in Mutukutuku reservoir in Solwezi district where both *O. niloticus* and *O. andersonii* hybrids have become more dominant than native *Oreochromis* spp (Jere et al. 2019). It is not yet clear when and how *O. niloticus* was introduced on the Barotse floodplain but as of the year 2014 the species had not been reported in the fishery (DOF 2014; Peel et al. 2014). The rollout of aquaculture projects nationwide by the Zambia government (Genschick et al. 2017) is likely to have been the main pathway of *O. niloticus* through either intentional or accidental introductions from fish farms/ponds. In view of the aquaculture project expansion due to associated socio-economic benefits (Genschick et al. 2017), measures must be put in place to restrict the culturing of *O. niloticus* to conserve wild genetic resources of native *Oreochromis* species.

Results on size structure indicates that the four fish species (*C. rendalli*, *O. andersonii*, *H. vittatus*, *S. macrocephalus* and *S. Intermedius*) are being harvested before they reach maturity. Harvesting fish prematurely is a sign of overfishing in the fishery as the fish species are not given a chance to breed and re-stock the fish population (Welcomme 1999; Allan et al. 2005). The targeting of juvenile fish was found to have caused the collapse of cichlids in Lake Malawi and Lake Malombe in Malawi (van Zwieten et al. 2003; Tweddle 2010). Overfishing may therefore be responsible for the decline in large cichlids species observed in this study. Species such as *O. andersonii* listed as vulnerable on the IUCN Redlist of Threatened Species (Tweddle and Marshall 2007) risk disappearing from the fishery altogether if over-exploitation and hybridisation from *O. niloticus* continues. It is evident that the Barotse floodplain fishery is undergoing fishing down and this can be attributed to high fishing pressure coupled with unsustainable fishing methods (Tweddle et al. 2010; 2015).

The seventeen fishing gears recorded on the Barotse floodplain fishery is indicative of fishers' ingenuity and adaptability to exploit all available fish resources across habitats and seasons. The broad range of fishing gears has been a prominent feature of the fishery (Bell-Cross 1974; Tweddle et al. 2004; Peel et al. 2014) and explains the diverse fish species/group harvested. The usage of fishing gear among fishers exhibits seasonal variation as fisher target seasonally available fish species (Turpie, 1999; Baidu-Forson et al. 2014). The five most important fishing gears in the fishery are gillnet, hook and line, and seine net, large hooks on poles and mosquito nets. Illegal gillnets (<3 inches mesh size and monofilament) and seine nets are two widely used methods in the upper Zambezi region and are strongly associated with overexploitation of fisheries resources (Tweddle et al. 2015). The usage of these nets may therefore provide an indication of fishery status.

Analysis of illegal fishing gears revealed high usage of small mesh size gillnets and monofilament gillnets during both wet and dry across the Barotse floodplain. This gear creep is much higher than the one reported on the Barotse floodplain in 2014 (Peel et al. 2014). The use of fine-meshed nets and monofilament gillnets has been on the rise in the Zambezi basin since the early 2000s (Simasiku, 2014; Tweddle et al. 2015). High usage of small mesh size is a symptom of overfishing as fishers resort to targeting smaller species to make up for declining number of large valuable species (Allan et al. 2005; Kolding and van Zwieten 2014). The use of small mesh sizes is probably contributing to the presence of juvenile fish species which now make up a large proportion of the catch, a phenomenon also observed by Peel et al. (2014). Continued use of monofilament gillnets and small, meshed gillnets coupled with the use of active fishing methods such as water beating (*mindili* or *kutumpula)*, mosquito nets, and large seine nets (*Sefa Sefa*) (Tweddle et al. 2004; Baidu-Forson et at. 2014) is likely to lead to further decline in CPUE and collapse of remaining economically valuable species.

The occurrence of *C. quadricarinatus* during both wet and dry seasons represents a significant change in the fishery considering that none were recorded during the 2014 survey (DOF 2014) despite their introduction in 2012 (Douthwaite et al. 2018). However, this is not surprising given how widely distributed *C. quadricarinatus* has become on the Barotse floodplain following its introduction (Madzivanzira et al. 2021; Chapter 4). The higher prevalence of crayfish by-catch in Mongu stratum is due to the relatively high abundance of *C. quadricarinatus* as the area is the invasion core while Senanga (downstream) and Lukulu (upstream) are invasion edges where the population is yet to be fully established (Chapter 4). The high crayfish by-catch in the dry season can be attributed to increased catchability of fishing gears as crayfish become densely concentrated in water bodies following water recession (Chapter 4). The full implications of crayfish for the Barotse floodplain fishery are not clear, however, recent studies indicate that crayfish have the potential to have socio-economic implications through damages to fish catch and gillnets (Madzivanzira et al. 2022; Chakandinakira et al. 2023). There is a need therefore to conduct a comprehensive assessment to understand the impact *C. quadricarinatus* may have on the artisanal fishery of the Barotse floodplain.

All fishery indicators, including decline in catch rate, low mean sizes, change in species composition, and predominant use of illegal fishing gear indicative of the collapse of the Barotse floodplain fishery. The occurrence of non-native species *O. niloticus* and *C. quadricarinatus* further threatens the fishery resources. Given the rapidly increasing human population and high levels of poverty and unemployment which characterises the upper Zambezi region (Tweddle 2015), the Barotse floodplain fishery is likely to continue this unsustainable trajectory. Unless these underlying challenges of impoverished communities are dealt with, the collapse of the fishery especially the remaining economically valuable species is imminent. Despite the gloomy forecast, the fishery still stands a chance of recovery provided effective management interventions are implemented (Tweddle et al. 2015; Lorenzen et al. 2016) sooner especially those involving the control of destructive fishing methods. There is also a need to strengthen co-management in the fishery by enhancing collaboration between the Department of Fisheries and traditional authorities. In addition, the management interventions should also incorporate biosecurity measures to address the threat posed by invasive alien species.

CHAPTER 4

EDGE-CORE INVASION DYNAMICS OF THE AUSTRALIAN REDCLAW CRAYFISH *CHERAX QUADRICARINATUS* ON THE BAROTSE FLOODPLAIN OF THE UPPER ZAMBEZI SYSTEM

Abstract

Understanding what facilitates population expansion of non-native invasive species is crucial to implementing management actions. *Cherax quadricarinatus* is invasive in the Barotse floodplain in the Zambezi Floodplains Ecoregion and threatens the Okavango Floodplains and Zambezian Headwaters Ecoregions. This study tests a series of hypotheses to ascertain whether the leading edge of an invasive population of Australian redclaw crayfish *Cherax quadricarinatus* is driven by spatial sorting, environmental filtering, or density dependent processes. The study assessed changes in spread rate, population dynamics and trait variability, with respect to biotic and abiotic factors along a non-linear 200 km invasion gradient. Relative abundance was higher at the core compared to the edge. Male to female sex ratio was not significantly different between core and edge. Signals of environmental filtering were not detected. Geometric mean, chelae length and front leg length were higher at the invasion edge, but body condition decreased, compared to the core, in both sexes. There has been significant up and down-stream spread from the former invasion edges detected in 2019. Presence of male and female individuals at the invasion edge suggest both sexes are acting as dispersers. Lack of environmental filtering suggests high connectivity of fragmented dry season refugia during the wet season. Intense intra-specific competition at the core may be pushing less fit individuals towards the edge. Density dependent spatial sorting, and hydrological variation, appear to have a strong influence on *C. quadricarinatus* spread and traits. Better understanding of the effects of flood regime on spread is needed. Population suppression to reduce spatial sorting and conspecific competition could be a viable management option.

Keywords

Zambezi floodplains ecoregion, biological invasions, aquatic invasive species, population dynamics, range expansion, environmental filtering, spatial sorting.

4.1 Introduction

Success of biological invasions is typically associated with introduced species that manage to transition through all the key stages of the invasion processes from introduction to establishment and spread (Blackburn et al. 2011). During this process, progression from one stage to another requires overcoming abiotic and biotic barriers which is achieved through selection of certain traits (Blackburn et al. 2011). As invasion range expands, individuals dispersing to invasion edges encounter new environmental conditions which exposes them to different selection pressures to those at the core. These selection pressures can lead to the appearance of distinctive phenotypes at the edge to those at the core (Chuang and Peterson 2016). Mounting evidence indicates that non-random processes such as environmental filtering, natural selection, spatial sorting together with density gradient are responsible for traits changes at the edges (Chuang and Peterson 2016). The emergence of these phenotypic changes has been linked to rapid invasion rates (Weiss-Lehman et al. 2017; van Kuijk et al. 2021) and increased impact on invaded ecosystems (Iacarella et al. 2015). Understanding the processes that bring about phenotypic changes may therefore help predict future invasions and their potential impacts on ecosystems. This is a crucial research goal given the multiple interacting stressors acting on freshwater systems and rapidly decreasing biodiversity (Strayer 2010; Birk et al. 2020).

According to the environmental filtering hypothesis, the environment acts as a selective force, selecting for individuals that are not able to tolerate local conditions (Kraft et al. 2015). Unfavourable environmental conditions can constrain the performance and population size of non-native species by limiting the survival and reproductive success (Helms and Vinson 2001). Species that manage to survive at a location tend to share similar functional traits that enable them to persist and these phenotypic similarities indicating this persistence may be identifiable among members of the community (Kraft et al. 2015; Asefa et al. 2017). In the face of environmental filters, phenotypic plasticity allows individuals to spread and adapt faster than would be possible via natural selection alone (Chevin et al. 2010).

Spatial sorting an evolutionary mechanism driven by assortment of dispersal capacity resulting in the accumulation of highly dispersive traits at the expanding edge (Travis and Dytham 2002; Phillips et al. 2008; Shine et al. 2011). During selection for dispersal ability, spatial sorting can impact a wide range of traits including life history, morphological, physiological and behavioural traits (Chuang and Peterson 2016). A notorious example is the cane toad *Rhinella marina* invasion in Australian wetlands, where individuals at the edge of the population had longer legs which facilitated expansion (Phillips et al. 2006; Pegg et al. 2022). Density gradient arising from a rapidly expanding population can interact with spatial sorting to bring about selection of certain traits at the core or edges (Phillips et al. 2010). The high population density which characterises the invasion core tends to cause more intense intraspecific competition resulting in selection for increased competitive ability and reproduction at the expense of dispersal ability (Burton et al. 2010). On the other hand, low population density at the edge may select for higher reproduction and dispersal instead of increased investment for competitive ability (Burton et al. 2010; Phillip et al. 2010). For example, high conspecific densities of rusty crayfish *Faxonius rusticus* at the core increased the need for weapon investment (i.e. longer chelae) while the opposite was observed at the edges (Messager and Olden 2019). A combination of reduced competition and higher resource availability at the edge may also result in improved body condition (Burton et al. 2010) potentially promoting population growth (Phillips et al. 2010). However, given that these resources may differ to those in the core and/or the native range, trait plasticity can be highly valuable for novel resource utilisation (Lopez et al. 2012; Brandner et al. 2013).

The redclaw crayfish *Cherax quadricarinatus* is widely introduced in southern Africa with populations reported in several freshwater bodies (Nunes et al. 2017; Douthwaite et al. 2018; Madzivanzira et al. 2021a). Despite the widespread introductions of *C. quadricarinatus*, there is lack of information on spread dynamics and associated changes in population characteristics and structure across invasion ranges. In Zambia, *C. quadricarinatus* have been introduced to multiple locations (Douthwaite et al. 2018; Madzivanzira et al. 2020). Of particular concern in this regard are the invaded Kafue and Barotse floodplains, both biodiversity rich wetlands with high conservation value. The introduction of *C. quadricarinatus* to the Zambezi floodplains ecoregion presents an unexplored perspective on range expansion of non-native crayfish as most studies have focused on linear river systems (Hudina et al. 2012; 2017; Rebrina et al. 2015; Messager and Olden, 2019). In the Barotse, the point of introduction is known and situated in the middle of the floodplain near Mongu (Madivanzira et al. 2021a), thus upstream and downstream spread can be traced. In the present study, population dynamics of *C. quadricarinatus* on the Barotse floodplain were assessed across the invasion gradient. We test a series of hypotheses relating to population dynamics along the gradient, as well as hypotheses explaining which processes may be driving population expansion.

With regards to population dynamics, we expected that since the 2019 survey (Madzivanzira et al. 2021a), 1) crayfish will have spread extensively up and downstream across the floodplain 2) there will be a core-edge invasion gradient of declining relative abundance, and 3) sex ratios will differ between core and edge populations. To better understand the processes of population expansion, we tested for signals of: 4) environmental filtering, where morphotypes were expected to be associated to different floodplain habitats, 5) spatial sorting, where individuals pushing the leading edge of the invasion would be larger, in better body condition, with larger chelae and longer legs.

4.2 Methods

4.2.1 Study Area

The study was conducted on the Barotse floodplain of the Upper Zambezi River system located in Western Zambia in the Zambezi Floodplains Ecoregion (Abell et al. 2008). Covering an area of approximately 5500 km^2 (Turpie 1999), the floodplain is an extensive lowland area that stretches from the North at the confluence of Zambezi and Kabompo rivers in Lukulu to the South in Senanga near the Ngonye falls (Cai et al. 2017) (See Chapter 2 for the detailed description of the study area). *Cherax quadricarinatus* were illegally introduced around the central region of the Barotse floodplain at Lealui (Fig. 4.1) in the year 2012 (Douthwaite et al. 2018). Madzivanzira et al. (2021a) detected *C. quadricarinatus* around their introduction site, but they were below detection probability at the extreme upstream and downstream sites (Lukulu and Senanga, respectively), despite being anecdotally recorded. However, spread rates of 49 ± 29 km yr^{-1} downstream and 12 ± 7 km yr^{-1} upstream were estimated (Madzivanzira et al. 2021a).

4.2.2 Sampling

The study covered the entire longitudinal extent of the Barotse floodplain (upstream; S-14.343366, E-23.222265 and downstream; S-16.235489, E23.236797) (Fig. 4.1). Sampling was conducted in 2021 during both wet season/high water period (April – May) and dry season/low water period (October – November) approximately two years on from the initial Upper Zambezi survey in 2019 (Madzivanzira et al. 2021a). The main river channel, tributaries, backwaters, lagoons, canals and flooded plain were sampled. Three distributional regions along the invasion range were identified (Table 4.1, Fig. 4.1): 1) the invasion core established around central section of the floodplain (Madzivanzira et al. 2021a) covering a radius of less than 5 km from the point of introduction, 2) the intermediate range between 5 km to 18 km along the radius and 3) the invasion edge (mainly upstream and downstream area) covering a radius ranging between 18 km to 114 km from the point of introduction. A total of 48 sites were sampled from the invasion core to the invasion edge (Table 4.1, Fig. 4.1) and the coordinates for each sampling site were also recorded using the Garmin GPSMAP 78s. The sites were chosen by focusing on areas where *C. quadricarinatus* was suspected to be present based on published literature (Madzivanzira et al. 2021a) as well as anecdotal reports from fishers on the Barotse floodplain. All the sites sampled in the 2019 surveys were re-sampled.

Table 4.1 Sites sampled during the wet and dry season across the three distributional regions (core, intermediate and edge) on the Barotse floodplain.

Invasion region	Sampling radius around point of introduction (km)	Sites sampled			Total no. of sites
		Wet & Dry season	Wet season	Dry season	
Core	< 5	4	1	-	5
Intermediate	$\geq 5 < 18$	16	6	1	23
Edge	$\geq 18 < 114$	7	-	13	20

The number of sampling sites in each location ranged from 1 to 3 depending on the availability of water bodies. In localities with more than five water bodies (i.e. ponds), two or three water bodies with the surface area at least 400 m^2 were sampled. The distance between sampling sites varied between 0.3 to 1 km for sites within the same locality and 2 to 26 km for sites in different localities across the invasion range.

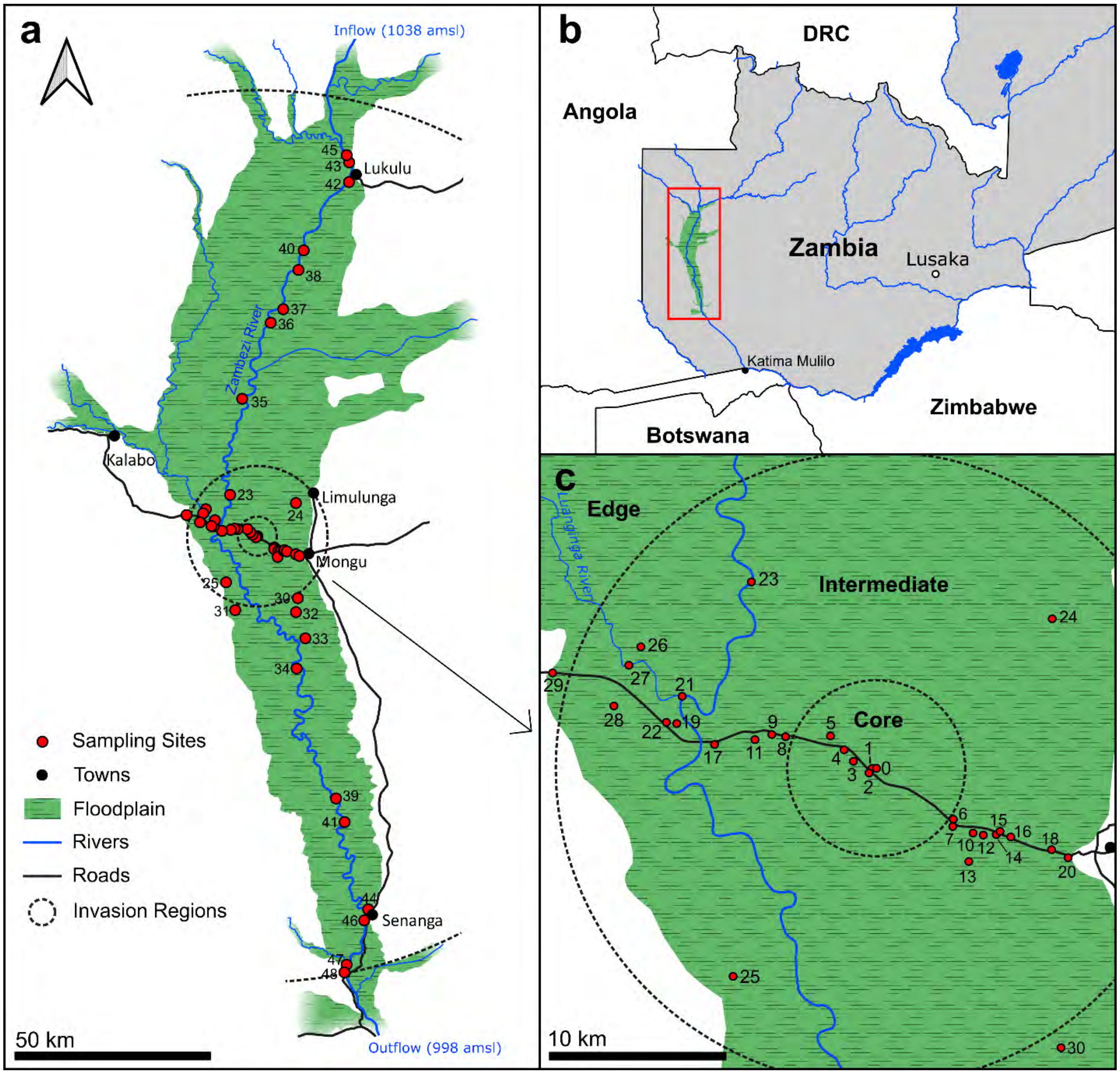

Figure 4.1 Distribution (a) of 48 sampling sites across the three invasion regions (core, intermediate and edge) on the Barotse floodplain of the (b) Upper Zambezi System in Zambia. Insert (c) shows sampling sites around the central section of the Barotse floodplain. Sites are numbered in the order of increasing distance from the point of introduction in Lealui (Site 0).

Collapsible Promar traps (610 mm x 460 mm x 200 mm: mesh size; 10mm) were used as a standard sampling tool (Madzivanzira 2021b; Nunes et al. 2017). The traps were baited with approximately 100g of dog food (Bobtail dry pellet steak flavour, RCL Foods South Africa), following Madzivanzira et al. (2021b). Between 18 to 20 traps were deployed at each site in the afternoon (17.00 - 18.00) at a distance interval of 15 – 20 metres between traps (Fig. 4.2). The traps were left overnight and retrieved the following morning (06.00- 08.00 am) in the same order as deployment, allowing for a soak time of 13 – 14 hrs. For every trapping session, crayfish caught were counted, sexed and weighed (in grams). Individuals that exhibited both male and female genitals were recorded as intersex (Madzivanzira et al. 2021b). From each specimen, five morphometric parameters; chelae length (CL), chelae width (CW), carapace length (CPL), carapace width (CPW), front leg length (FLL), and total length (TL) were measured using a digital Vernier calliper.

Figure 4.2 Collapsible Promar trap being deployed in one of the water bodies on the Barotse floodplain (Photograph: Nawa Nawa; Date: 26/11/2021).

4.3 Data analyses

All statistical analyses were conducted within the R statistical software environment (R Core Team, 2021). Mapping was done using QGIS 4.13 programme package (QGIS Development Team, 2021).

Detection probability ($P_{capture}$) expressed as a fraction of traps that caught at least one crayfish (Madzivanzira et al., 2021b) was determined for each of the three distributional regions. The obtained $P_{capture}$ across the invasion range and between invasion regions was analysed using Chi-square test of independence via 2 × 3 and 2 × 2 contingency tables respectively. The calculated detection probabilities were compared to those for the year 2019. To update the spread rate of *C. quadricarinatus*, straight line distance (km) from the 2019 invasion edges (Madzivanzira et al. 2021a) to the furthest sites where crayfish were detected (both upstream and downstream) during this study was measured using Google Earth. The distance obtained was divided by the number of years (~ 2 years) it took for crayfish to cover it.

4.3.1 Population dynamics

To determine crayfish abundance, catch per unit effort (CPUE) expressed as mean number of individuals caught per trap per night (Madzivanzira et al. 2021) was recorded. The CPUE data were zero inflated, so a delta-X transformation was applied to correct standard errors (Ellender et al. 2010). A generalised additive model (GAM) was used to model CPUE trends along the invasion gradient with respect to season. Changes in sex ratios across the invasion range were analysed using a 2 × 3 contingency table.

4.3.2 Environmental filtering

All measured traits were first corrected and standardised to account for allometry by applying Mosimann corrections, as this provides the most accurate way of identifying shape differences without losing information, as opposed to using residuals from linear regressions (Jungers et al. 1995). The correction was done by calculating the Geometric mean (GM) and dividing individual trait values by it to produce size corrected values. The GM was then used as a new trait variable to represent overall body size instead of the correlated variables of mass, TL and

CPL (Appendix 4.1). Using GM and remaining measured traits (CL. CW, CPW, FLL), a principal component analysis (PCA) was completed on the correlation matrix to determine individual overlap in morphospace with respect to habitat type and invasion region (i.e., core-edge).

4.3.3 Spatial sorting

4.3.3.1 Geometric mean

A generalised linear model with Gamma error distribution and a log link function were used to model whether Geometric mean has a relationship with distance, sex and season. In the tropical regions, dry-wet seasonal variation drive changes in physiology, morphology and behaviour of organisms (William et al. 2017).

4.3.3.2 Chelae length

A generalised linear model with Gamma error distribution and identity link function was also fitted to determine the effect of distance, sex and season on chelae length (CL). Chelae is an important weapon in competitive interaction among crayfish conspecific (Huber and Schroeder 2001). Given that competitive ability and aggression may either lead to edge dilation or exclusion from the core (Hudina et al. 2014) analysing chelae length may help establish which of the two opposing tendencies explains weapon investment along the invasion gradient.

4.3.3.3 Front leg length

A generalised linear model with an inverse Gaussian error distribution was modelled to assess relationship with distance, sex and season on front leg length (FLL). Changes in morphology (i.e leg length) at the edges is a commonly used an indicator of dispersal ability during range expansion of invasive species (Phillips et al. 2010).

All model assumptions were checked using the package DHARMa by simulating and comparing residuals. Full interaction terms were initially included, and then simplified to the most parsimonious model by removing the non-significant terms, starting with interaction terms. Variables were compared using analysis of deviance tables and Wald Chisq tests (Florian 2022). The marginal estimated means were then plotted using the package emmip (Russell 2022).

4.3.3.4 Body Condition

The body condition indices were calculated using Fulton's Condition Factor, $K = 100*(W/L^3)$ where W is wet weight (g), and L is total length (mm) (Froese 2006). Body condition gives an indication of animal health and fitness (Peig and Green 2010) and therefore a useful method when comparing crayfish population between sites (Maguire and Klobucar 2011). A generalised linear model with Gamma error distribution and a log link function was used to determine the effect of range and season on body condition. Given that body condition is sex dependent (Streissl and Hold 2002), only same sex comparisons were performed within analyses. All berried females and crayfish with missing appendages were excluded from the analyses.

4.4 Results

4.4.1 Presence/absence

Cherax quadricarinatus was detected in all the three distributional regions (core, intermediate and edge ranges) across the Barotse floodplain. Crayfish were caught in 19% of all traps set and were present at 33 of the 48 sites sampled (Appendix 4.2). Using only the sites where *C. quadricarinatus* were detected, the *P capture* across the three invasion regions was significantly different ($\chi2$= 730.87, df = 2, p < 0.01) (Appendix 4.2). Detection probability at the invasion core (*P capture* = 0.41) was significantly higher than the intermediate range core (*P capture* = 0.21: $\chi2$= 45.58, df = 2, p < 0.01) and invasion edge (*P capture* = 0.02: $\chi2$= 538.15, df = 2, p <

0.01) (Appendix 4.2). Detection probability for intermediate range was also significantly higher than the edge ($\chi 2 = 418.49$, df = 2, $p < 0.01$) (Appendix 4.2).

4.4.2 Spread rate

The furthest distance on the invasion edge where *C. quadricarinatus* was detected from the point of introduction was 113.96 km downstream in Senanga and 54.80 km upstream in Lukulu. A crayfish carcass was also observed further upstream (93.70 km) on the banks of the Zambezi River in Lukulu. Using the former invasion edges established in 2019 and live crayfish specimen captured by promar traps, the average spread rate is approximately at 53.92 km/year downstream and 27.4 km/year upstream. Recent anecdotal reports indicate that crayfish are now present and established downstream in Katima Mulilo (F Jacobs pers. obs.) approximately 142.2 km from the Okavango delta while the current upstream invasion edge is about 62.34 km from the Zambezi – Kabompo confluence.

4.4.3 Relative abundance

A total of 1310 crayfish were caught across the entire invasion range. Catch per unit effort (CPUE) of *C. quadricarinatus* changed significantly across the invasion range ($p < 0.05$), declining from the core to the front for both dry and wet season (Fig. 4.3). Seasonal comparison showed CPUE for the dry season was significantly higher ($p < 0.05$) than wet season (Fig. 4.3). The combined (wet and dry season) average CPUE at the invasion core and intermediate range was 1.471 ± 0.685 ind./trap/night and 0.695 ± 0.338 ind./trap/night respectively. Crayfish abundance at the invasion edges was relatively lower with 0.027± 0.002 ind./trap/night.

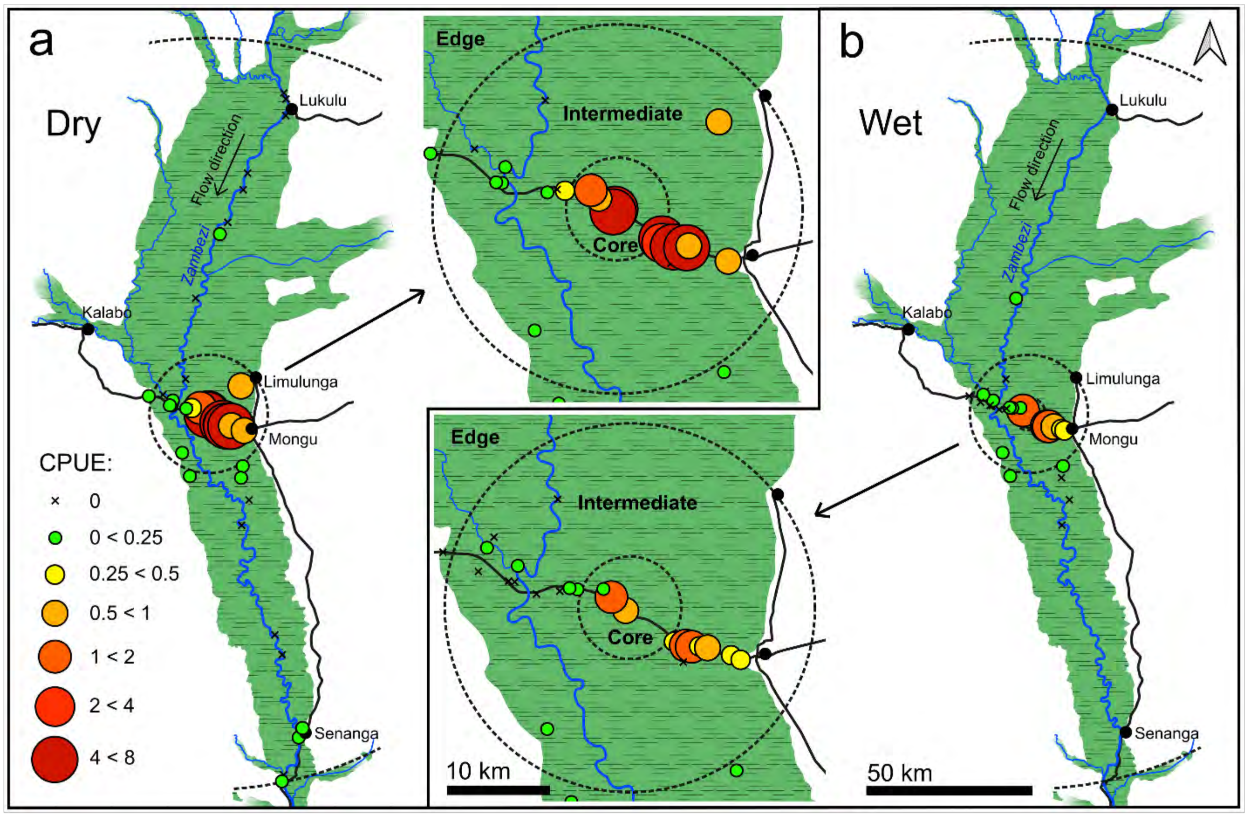

Figure 4.3 Relative abundance and spatial distribution of *C. quadricarinatus* in (a) wet and (b) dry season across the three distributional regions (core, intermediate and edge) on the Barotse floodplain. CPUE is represented by circles and absence of crayfish is indicated by **✕**.

The GAM showed that both distance and season had a significant effect on CPUE ($p < 0.05$). Both wet and dry season CPUE declined with increase in distance away from the invasion core with dry season having comparatively higher CPUE (Fig. 4.4). The average CPUE for dry season was (0.789 ± 0.518 ind./trap/night) compared to wet season (0.331 ± 0.138 ind./trap/night). A comparison of dry season CPUE of *C. quadricarinatus* between the year 2019 and 2021 showed a considerable increase in crayfish abundance at three sites sampled but comparatively similar at three other sites (Fig. 4.5).

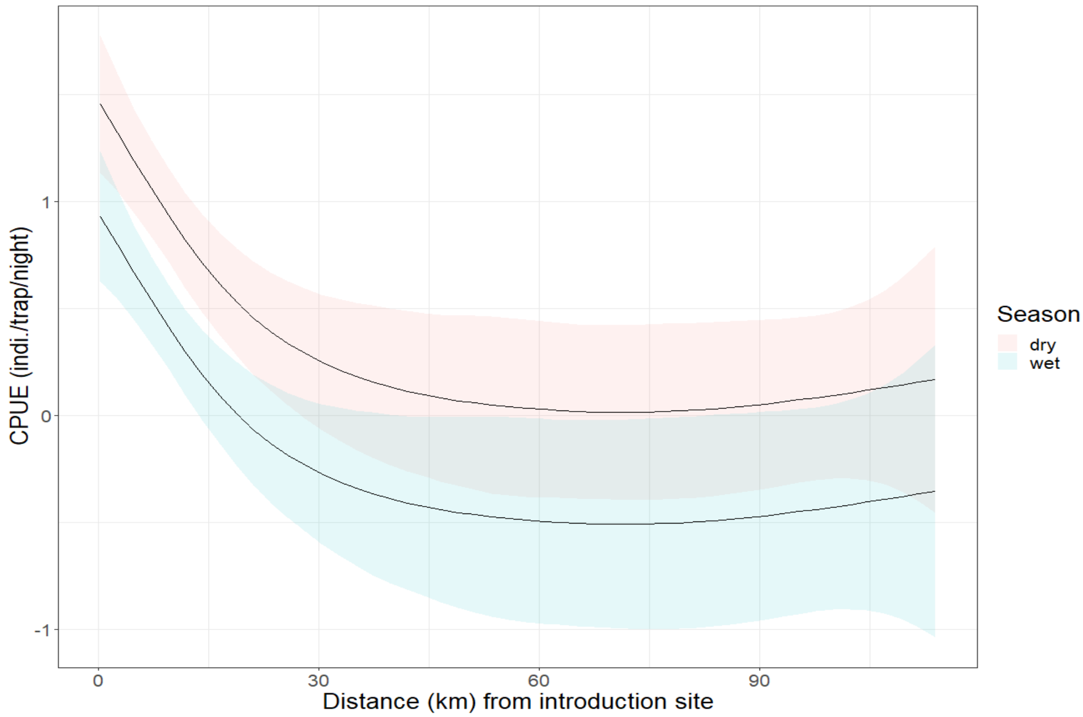

Figure 4.4 Seasonal change in catch per unit effort (CPUE) of *C. quadricarinatus* across the invasion range on the Barotse floodplain, Upper Zambezi River, Zambia. Zero (0) is the core and distance is outward from the core to the edge. Wet and dry season CPUE are comparable at the edge.

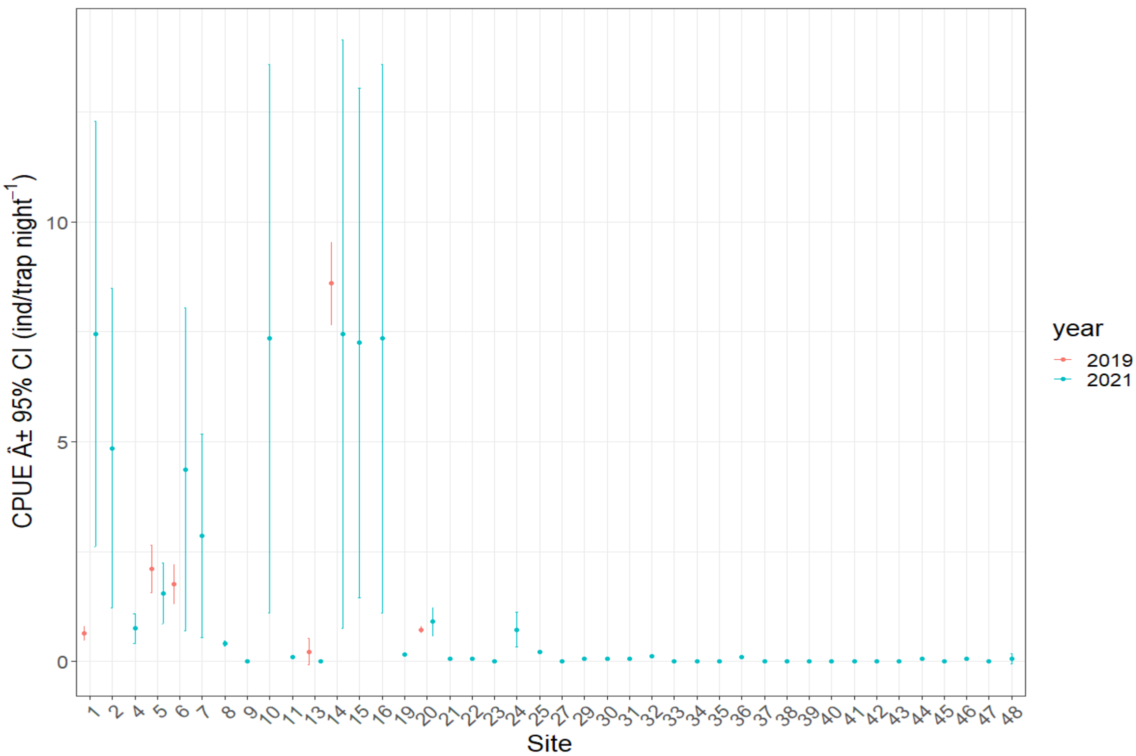

Figure 4.5 Dry season catch per unit effort (CPUE) of *C. quadricarinatus* for sites sampled in the year 2019 and 2021 on the Barotse floodplain, Upper Zambezi River, Zambia. Sites arranged in the order of increasing distance from the point of introduction. Plot of mean showing 95% confidence interval.

4.4.4 Sex ratio

Overall, male to female sex ratio did not differ significantly between the three sampled regions across the invasion range ($\chi 2 = 1.434$, df = 2, $p = 0.489$) (Appendix 4.2). Crayfish caught at the invasion core consisted of 35.1% males, 54.8% females and 10.1% intersex while the intermediate range comprised of 34.1% male, 55.5% female and 10.4% intersex (Appendix 4.2). The sex ratio at the invasion edges comprised 53.3% males and 46.7% females, with no intersex individuals sampled from this region (Appendix 4.2).

4.4.5 Environmental filtering

The principal component analysis (PCA) explained 87.4% of the variance along the first and second axes. Principal component 1 (PC 1) of the PCA accounted for 63.2% (eigenvalue = 3.17) and consisted of the variable Geometric mean while principal component 2 (PC 2) accounted for 24.2% (eigenvalue = 1.21). There was no separation along either PC1 or PC2 indicating no clear distinction in morphometric traits of *C. quadricarinatus* sampled from different habitats across the floodplain. However, individuals from the floodplain and pond habitats had broad variability in morphology (Fig. 4.6). There was also no clear difference in morphometric traits across the three invasion regions as indicated by the overlap along either PC1 or PC2. Individuals at the invasion core and intermediate range did, however, exhibit broader variability in morphometric traits than at the edge (Fig. 4.7)

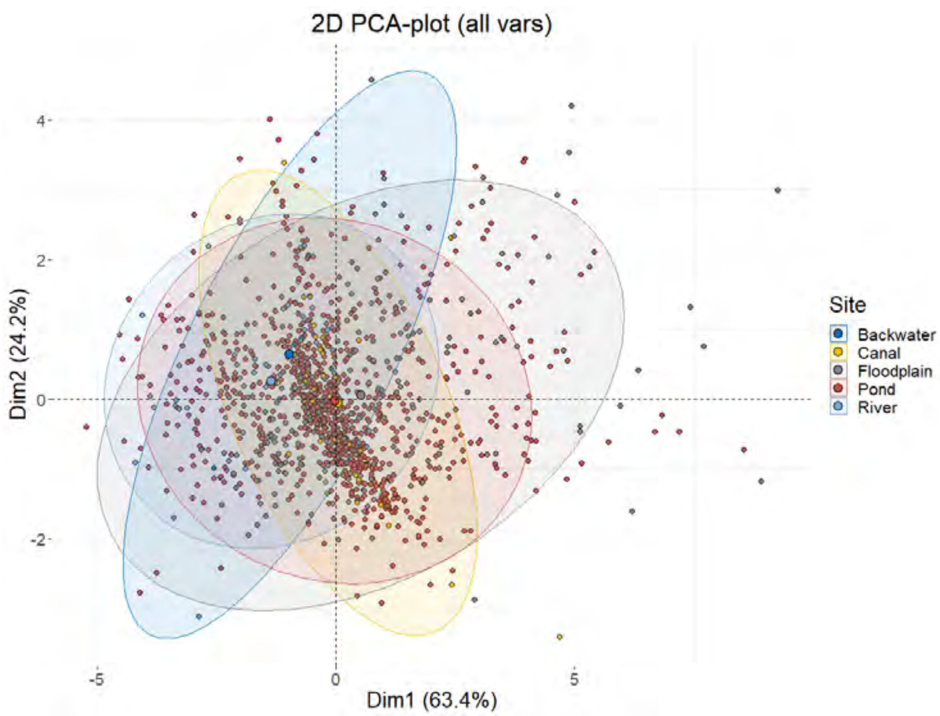

Figure 4.6 A PCA plot showing broad overlap in morphometric traits of *C. quadricarinatus* along both PC1 and PC2. Crayfish sampled from different aquatic habitats across the Barotse floodplain.

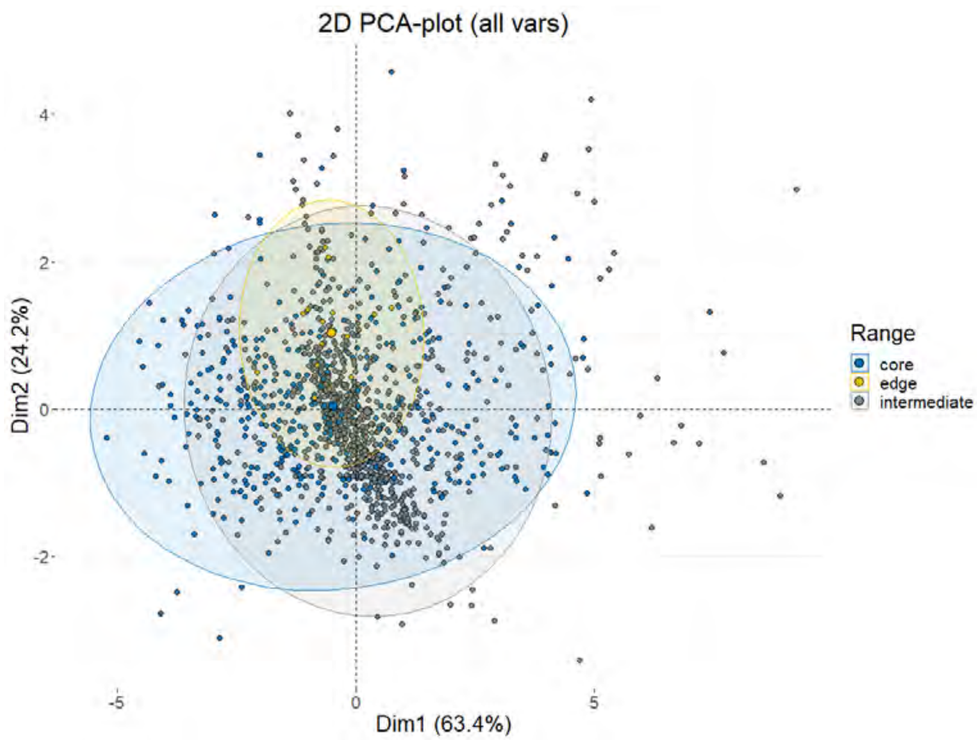

Figure 4.7 A PCA plot showing broad overlap in morphometric traits of *C. quadricarinatus* along both PC1 and PC2. Crayfish sampled from three regions across the invasion range on the Barotse floodplain.

4.4.6 Spatial sorting of traits

4.4.6.1 Geometric mean

Analyses of body size revealed significant interaction between sex and season (Table 4.2) where males and females had higher GM than intersex individuals (both, $p < 0.01$), while males had higher GM than females ($p < 0.01$). All sexes were bigger overall in the wet season compared to the dry season ($p < 0.01$) (Fig. 4.8). Distance significantly interacted with sex (Table 4.2) where males and females individuals increased GM at the invasion edge while intersex individual decreased GM (Fig. 4.8). Sex and season both had significant main effects on GM while distance did not (Table 4.2).

Table 4.2 Model terms for all factors from GLM with a gamma distribution used determine effects on Geometric mean with regards to factors "distance", "sex" and "season", using Type 3 Anova and χ^2 to report the effect size of a factor on the dependent variable.

Model term	**Chisq**	**df**	***p*-value**
Distance	69.69	1	0.062
Sex	60.48	2	< 0.001
Season	59.44	1	< 0.001
Distance * Sex	58.53	2	< 0.001
Sex * Season	57.35	2	< 0.001

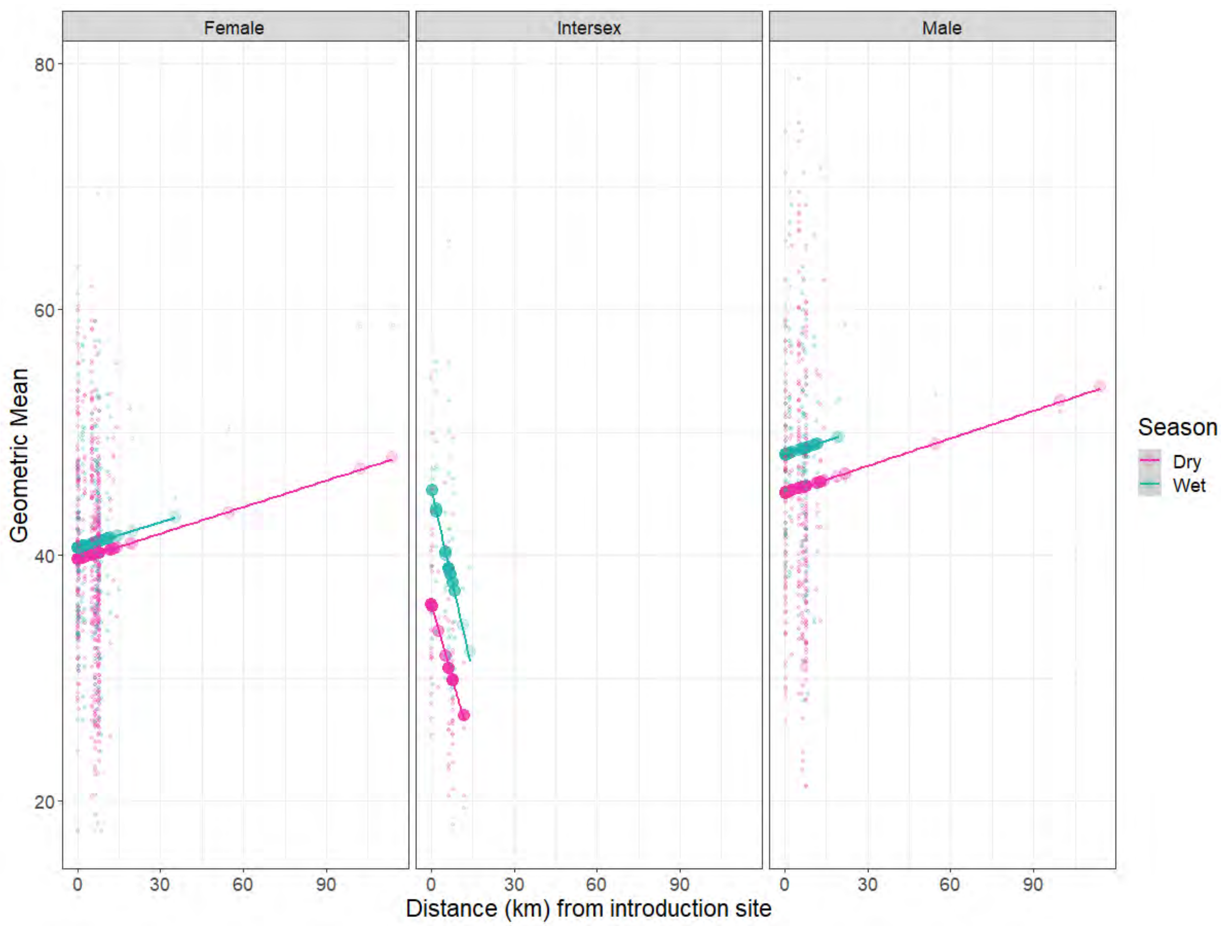

Figure 4.8 Predicted relationship of Geometric mean with distance from introduction site with respect to sex and season. Large points indicate predicted values from the GLM, and small points indicate individual data points of crayfish Geometric mean.

4.4.6.2 Chelae length

Chelae length analyses showed a significant three-way interaction between distance, sex and season (Table 4.3) where male and female chelae were longer towards the edge in wet season (Fig. 4.9). Distance significantly interacted with sex (Table 4.3) where chelae length for all sexes got longer towards the edge (Fig. 4.9). Sex significantly interacted with season (Table 4.3) where male and female chelae were longer in wet season while chelae of intersex was longer in dry season (Fig. 4.9). All the factors 'distance', 'sex' and 'season' had a significant main effect on claw length (Table 4.3).

Table 4.3 Model terms for all factors from GLM with a gamma distribution used determine effects on claw length mean with regards to factors "distance", "sex" and "season", using Type 3 Anova and χ^2 to report the effect size of a factor on the dependent variable.

Model term	**Chisq**	**df**	***p*-value**
Distance	38.82	1	< 0.001
Sex	35.58	2	< 0.001
Season	33.88	1	< 0.001
Distance * Sex	33.65	2	< 0.01
Distance * Season	33.32	1	< 0.001
Sex * Season	31.68	2	< 0.001
Distance * Sex * Season	31.40	2	<0.01

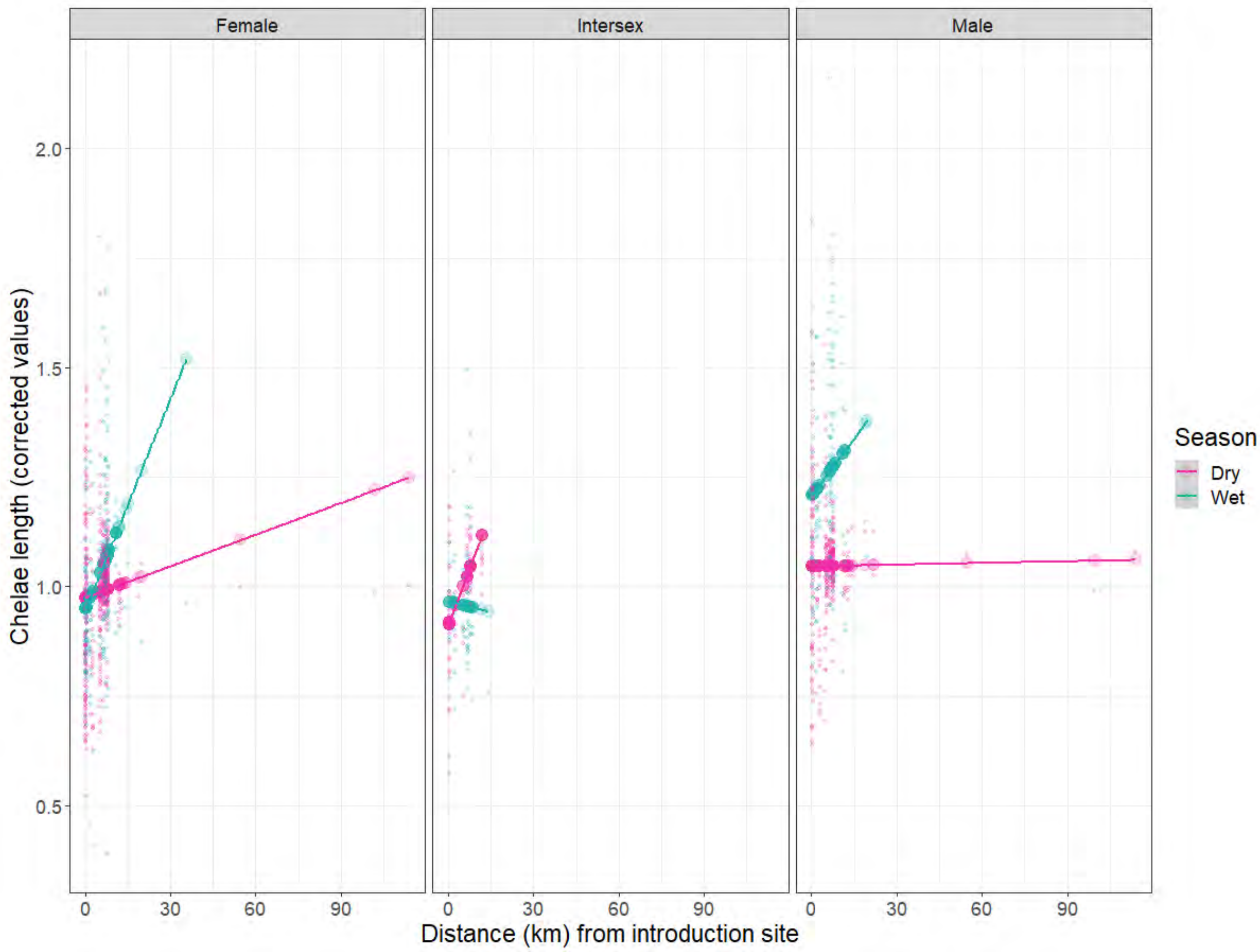

Figure 4.9 Predicted relationship of corrected chelae length with distance from introduction site with respect to sex and season. Large points indicate predicted values from the GLM, and small points indicate individual data points of crayfish chelae length.

4.4.6.3 Front leg length

Analyses of front leg length showed a significant three-way interaction between distance, sex and season (Table 4.4) where male and female front leg length were longer towards the edge in wet season (Fig. 4.10). Distance significantly interacted with sex (Table 4.4) where front leg length for all sexes got longer towards the edge (Fig. 4.10). Sex significantly interacted with season (Table 4.4) where male and female front legs were longer in wet season while chelae of intersex was longer in dry season (Fig. 4.10). Season had a significant main effect on front leg length while distance and sex did not (Table 4.4).

Table 4.4 Model terms for all factors from GLM with a gamma distribution used determine effects on front leg length with regards to factors "distance", "sex" and "season", using Type 3 Anova and χ^2 to report the effect size of a factor on the dependent variable.

Model term	**Chisq**	**df**	***p*-value**
Distance	34.49	1	0.094
Sex	34.47	2	0.729
Season	33.69	1	< 0.001
Distance * Sex	33.32	2	< 0.001
Distance * Season	33.32	1	0.085
Sex * Season	31.68	2	<0.001
Distance * Sex * Season	31.40	2	<0.05

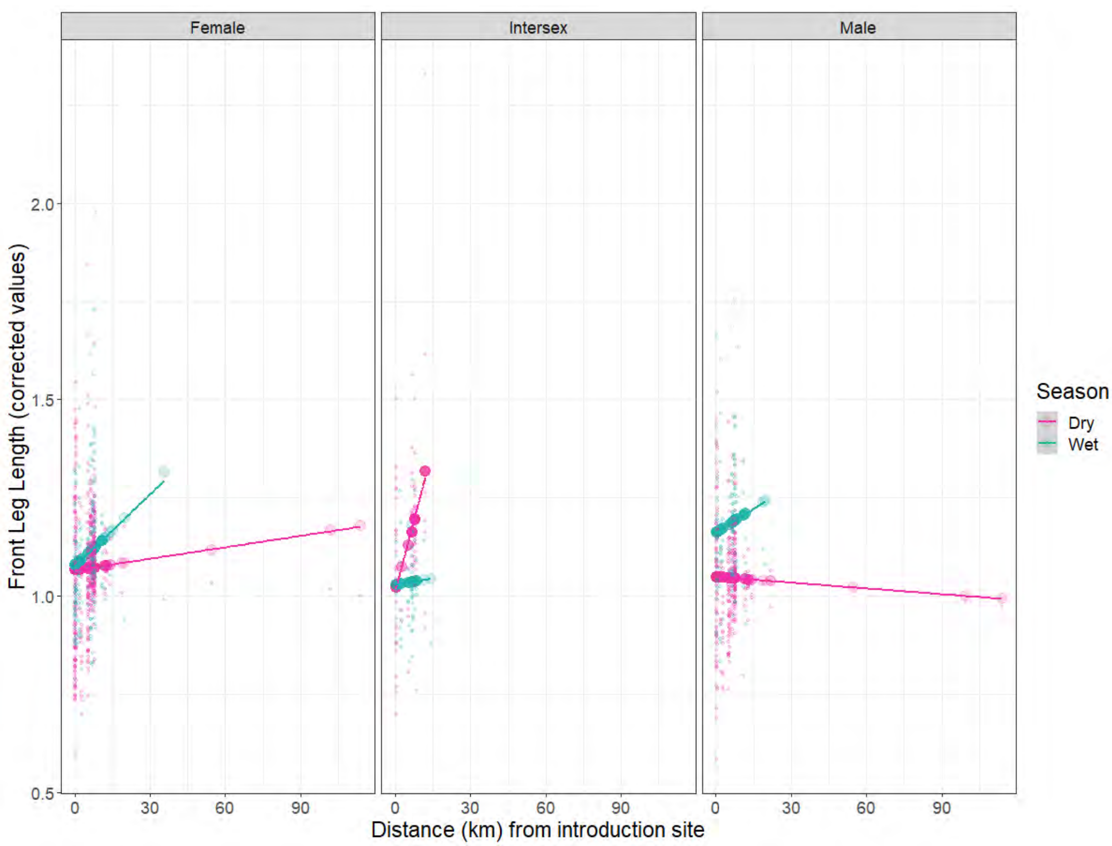

Figure 4.10 Predicted relationship of corrected front leg length with distance from introduction site with respect to sex and season. Large points indicate predicted values from the GLM, and small points indicate individual data points of crayfish chelae length.

4.4.6.4 Body Condition

Body condition analyses revealed that invasion range had a significant main effect on body condition of both male and female (Table 4.5, Model A and B respectively). The core was significantly higher than the edge (male, p = 0.02; female, p < 0.001; Fig. 4.11) but not the intermediate (male, p = 0.706; female, p = 0.846; Fig. 4.11), while intermediate was also significantly higher than the edge (male, p = 0.033; female, p < 0.001; Fig. 4.11). Season also had a significant main effect on body condition of both male and female (Table 4.5, Model A and B respectively) where body condition was higher in wet season (male, p < 0.001; female, 0.025; Fig. 4.11). Both invasion range and season did not have a significant main effect on body condition of intersex individuals (Table 4.5, Model C).

Table 4.5 Model terms for all factors from GLM with a gamma distribution used to determine effects on body condition with regards to factors "range" and "season", using Type 2 Anova and χ^2 to report the effect size of a factor on the dependent variable. Model A for male, Model B for female and Model C for intersex.

Model	**Model term**	**Chisq**	**df**	***p*-value**
A (Male)	Range	7.901	2	0.021
	Season	7.448	1	< 0.001
B (Female)	Range	11.672	2	< 0.001
	Season	11.599	1	0.024
C (intersex)	Range	2.688	1	0.059
	Season	2.688	1	0.96

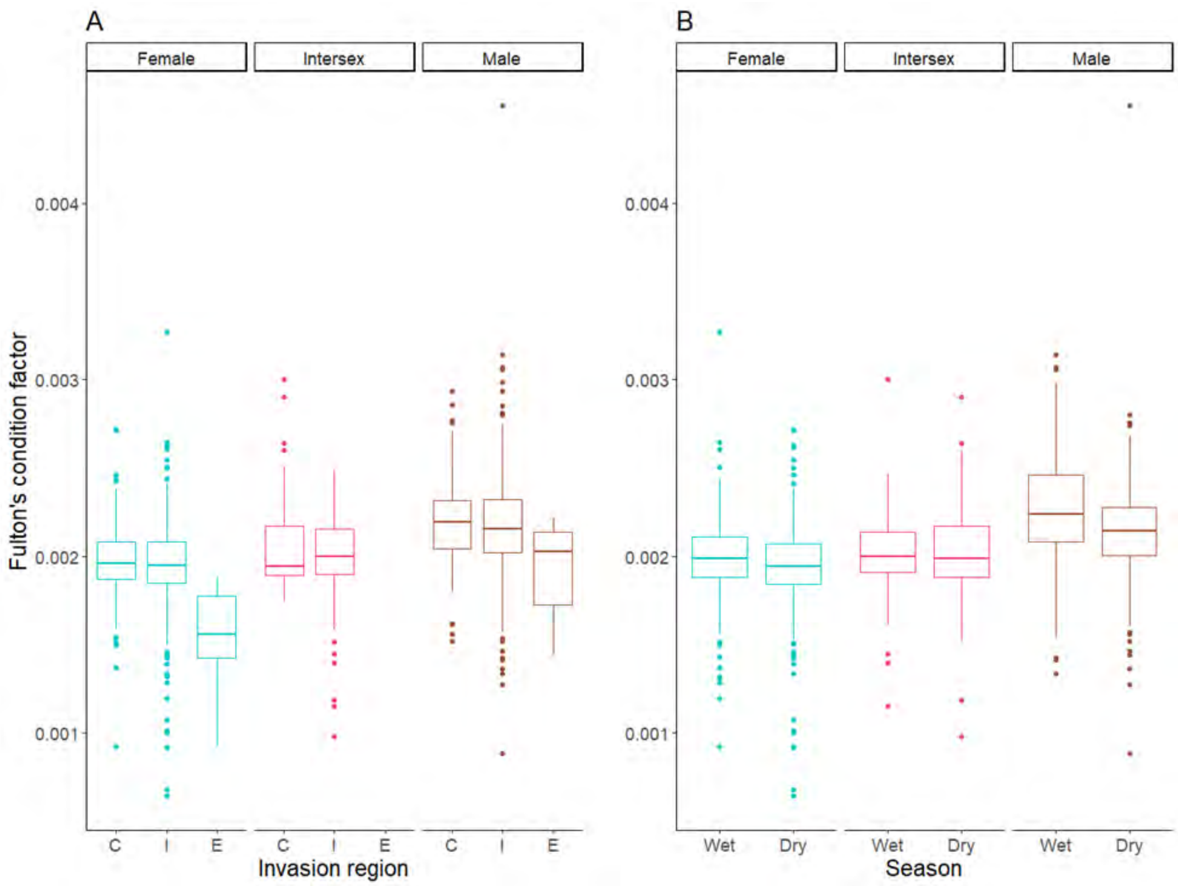

Figure 4.11 Comparison of Fulton's body condition indices of male, female and intersex *C. quadricarinatus* (A) between invasion regions (C = Core; I = Intermediate; E = Edge) and (B) seasons. Boxplots represent median and 25 – 75% interquartile range. Points are individual Fulton's condition data.

4.5 Discussion

Identifying species traits linked to high invasive capacity is critical for predicting and effectively managing the negative impacts of invasions (Kolar and Lodge 2001; van Kuijk et al. 2021). The redclaw crayfish *C. quadricarinatus* on the Barotse floodplain exhibited differences in population demographics and traits across the invasion range. As hypothesised, populations have spread across the floodplain since 2019, but further downstream than upstream. There was, however, a general gradient in population size along the core-edge gradient, with the core population being considerably larger than the edge population. Sex ratios were not different between core and edge populations indicating both male and female are dispersers. Environmental filtering effects on morphology were not evident but there were signals of spatial sorting (e.g., higher GM, CL and FLL at the edges) which elucidate some of the processes facilitating spread across the floodplain. *Cherax quadricarinatus* at the edge were larger in size than those at the core while the opposite was observed for body condition indicating density dependent processes.

This study reveals a more widespread distribution of *C. quadricarinatus* population on the Barotse floodplain than earlier reported by Madzivanzira et al. (2021a). Within a period of 2 years *C. quadricarinatus* has expanded its range approximately 107.84 km downstream and 93.70 km upstream. The high probability of capture of *C. quadricarinatus* at the invasion core and intermediate range reaffirms that there is still a well-established population in and around Mongu (Madzivanzira et al. 2021a). On the other hand, population at the edge had lower probability of detection and comparatively lower than at the former edge (Madzivanzira et al. 2021a). The low detection at the current edge is perhaps an indication of a more recent invasion (Hudina et al. 2012). The current downstream spread rate of *C. quadricarinatus* falls within the range (49 ± 29 km yr^{-1}; Madzivanzira et al. 2021a) estimated earlier while the upstream spread rate is 2 to 3 times higher than the earlier estimation (12 ± 7 km yr^{-1}; Madzivanzira et al. 2021a). Based on the current spread rate, *C. quadricarinatus* likely reach the pristine Okavango Delta downstream and Kabompo River upstream within 2 to 5 years. The spread rate also confirms the assertion that *C. quadricarinatus* is spreading much faster on the Upper Zambezi (Madzivanzira et al. 2021) compared to the Inkomati Basin (8 km $year^{-1}$, upstream and 4.7 km $year^{-1}$ downstream) in South Africa (Nunes et al. 2017). The spread rate is also relatively higher than what has been reported for other non-native crayfish species in Europe (Hudina et al. 2009; Soto et al. 2023). The flood pulse seems to contribute to the spread *C. quadricarinatus* as evidence by their occurrence on the floodplain during high water and also in isolated ponds not connected to flowing water channels. Episodic flood events have been associated with transporting non-native species like *P leniusculus* (Bubb et al. 2004) and golden mussel *Limnoperna fortunei* (de Amo et al. 2021) to isolated lakes, and climate change is expected to increase *C. quadricarinatus* spread in this manner in South Africa (van Wilgen et al. 2022). Seasonal floods may therefore be contributing to the observed non-linear dispersal pattern of crayfish on the Barotse floodplain. Given that crayfish were detected at Kalongola, the furthest sampling sites downstream, it is not surprising that reports of crayfish occurrence much further downstream at Katima Mulilo have recently emerged (F Jacobs, pers. com). However, there is need to ascertain whether the reported crayfish population is due to natural spread or a result of an additional introduction.

Cherax quadricarinatus exhibited a relatively high population abundance at the core declining towards the edge. The higher relative abundance at the core may be driving the dispersal of *C. quadricarinatus* to the edge due to increased competition for resources. Although the core has better conditions than edges, high population density in animals is expected to cause scarcity of resources such as food and shelter resulting in intense intraspecific competition (Morrell et al. 2005). The competition may in turn promote density dependent dispersal, with dispersers benefiting from optimum resource allocation and improved fitness at the edge (Einum et al. 2006; Galib et al. 2022b). Other studies have also found that under conditions of high population density intraspecific competition may push out less successful conspecifics from the core to the edge (Hudina et al. 2014). The low relative abundance of *C. quadricarinatus* at the edge could be an indication of recently established population from few initial dispersers (Hudina et al. 2012;

Rebrina et al. 2015). Additionally, the lower abundance of *C. quadricarinatus* observed during wet season across the invasion range is probably due to low detection probability as crayfish migrate on to the floodplain and become more dispersed. The migration could be a mechanism of escaping harsher conditions (i.e., poor water quality, overcrowding and predation) which characterises water bodies during dry season (Mathews and Marsh-Mathews 2003). Seasonal movement has been observed in *P. leniusculus* as a means to take advantage of high productivity, escape predation (Light 2003) or seek refuge from harsh weather conditions (Flint 1977). During dry season, the receding water level could be restricting *C. quadricarinatus* to permanent bodies hence the high detection probability observed. Similarity in relative abundance of *C. quadricarinatus* towards the core between the year 2019 and 2021 indicates a relatively stable population and perhaps a reflection of successful establishment. The observed adaption is probably due to environmental matching considering that the Barotse floodplain is similar to *C. quadricarinatus*'s native environment in Australia (McLoughlan 2014).

Sex structure of *C. quadricarinatus* showed that male to female sex ratio was not different across the three invasion regions, suggesting that both males and females are contributing towards range expansion. However, very few individuals were sampled at the edge. Crayfish studies based on linear systems, for example a study on spiny-cheek crayfish *Orconectes limosus* (Ďuriš et al. 2006) and *P. leniusculus* (Hudina et al. 2012) reported a more male biased sex ratio at the invasion front. Other studies on an invasive freshwater fish round goby *Neogobius melanostomus* reported both male biased sex ratio (Gutowsky and Fox 2011) and female biased sex ratio (Brandner et al. 2013) at the invasion edge. Dispersal of male signal crayfish from the invasion core has been associated with increased aggression arising from high conspecific density (Rebrina et al. 2015). Male crayfish tend to be more aggressive than females (Berry and

Breithaupt 2010) competing over resources such as food, shelter and mates (Fero et al. 2007). On the other hand, migration of female individuals to the invasion edge has been seen as a strategy to possibly reduce intraspecific competition for mates as well as vulnerability to predation (Gros et al. 2009).

Despite intersex individuals not being detected at the edge, their presence at the core and intermediate indicates that they could be contributing indirectly to range expansion through increased competition. In crayfish, intersex individuals can skew a population to a more female dominated population as crosses between intersex and normal female tend to produce female biased progeny (Levy et al. 2020). Intersexual individuals may be an ecologically stable strategy to enhance population fitness in highly stochastic environments (Levy et al. 2020). Female skewed populations drive rapid population growth, which in turn enhances increased competition and conspecific aggression at the core which may drive spread (Hudina et al. 2014; 2015). Intersex proportional representation across three invasion cores in Southern Africa declined with time since invasion, monitoring sex ratios may be an informative index to assess overall population status with respect to identifying boom bust dynamics along the invasion curve (Haubrock et al. 2022).

Similarity in morphometric traits exhibited by *C. quadricarinatus* across different aquatic habitats suggests that there is no environmental filtering acting on the population. This is probably due to hydrological connectivity of the population and habitats in wet season as floods exposes individuals to more similar environmental conditions (Thomaz et al. 2007; de Amo et al. 2021). Studies indicate that evidence of environmental filtering is expected to be much weaker and less prevalent when species are drawn from areas with high abiotic homogeneity (Kaft et al. 2015). Although the population of *C. quadricarinatus* becomes isolated in dry season, the separation time may not be enough for environmental filtering to act on traits. The broad variability in morphometric traits exhibited by the floodplain habitat is evidence that the flood pulse may be counteracting signals of environmental filtering. On the other hand, the wider variability in morphometric traits observed at the core and intermediate is probably due to the presence of diverse aquatic habitats (i.e. rivers, canals, ponds and backwaters). These habitats may be providing high refuge availability, reducing dispersal of organisms (Galib et al. 2022b). This could be contributing to the higher density of *C. quadricarinatus* found around the core compared to the edge. Additionally, the aquatic habitats (i.e. ponds) scattered across Barotse floodplain may also be providing refuge in dry season to dispersing individuals hence acting as source population or steppingstones for further range expansion (Johnson et al. 2008; Nunes et al. 2017).

Geometric mean of both males and females suggests that larger individuals of *C. quadricarinatus* are leading range expansion. The results are similar to the findings on round goby *N. melanostomus* invasion in Europe (Brandner et al. 2013) but contrary to its counterpart invasion in Canada (Brownscombe and Fox 2012). Given the low population density of *C. quadricarinatus* at the edges, it is expected that reduced competition would increase feeding rates and enhance energy available for growth with the opposite being true for individuals at the core (Brown et al. 2013). However, the higher body condition values at the core indicates that food resources may not be limiting but rather competition for space. Therefore, the observed pattern in body size is potentially due to a mix of adaptation to increased competition for space and molting of individuals at the core before being pushed out. The bigger sizes at edge could also be priming individuals against predation as they may be too big to be eaten. Predation on *C.*

quadricarinatus by some native fish species has been recorded on the the Kafue River system (Tyser and Douthwaite 2014).

The increase in chelae length of *C. quadricarinatus* towards the edge could be due to that the presence and pressure posed by niche competitors of genus *Potamonautes* (N Nawa, pers. obs.) resulting in selection for increased investment in competitive ability. These results are similar to findings on males of *P. leniusculus* (Hudina et al. 2012) but contrary to those of rusty crayfish *Faxonius rusticus* (Messager and Olden 2019). Relative claw size is usually associated with behavioural traits such as aggression which may be selected during dispersal (Pintor et al. 2009). Although relative claw size is important in agonistic interactions (Streissl and Hold 2002), chelae length is unreliable signaller of inter-specific agonistic interaction especially decapod species (South et al. 2020). The observed pattern of chelae length could also be driven by increased vulnerability to predation in the absence of high numbers of conspecifics. Predation risk is known to induce morphological plasticity in prey to provide fitness advantage (Kishida et al. 2010). However, the precise effect of both interspecific and predation on chelae length of *C. quadricarinatus* requires further investigation.

Increase in front leg length towards the edges is a classic spatial sorting indicating *C. quadricarinatus* are moving more often. The change in leg morphology is a dispersal selected trait (Phillips et al. 2010) and may be responsible for rapid range expansion *C. quadricarinatus* on the Barotse floodplain. Although a rarely assessed trait in range expansion studies similar finding have made for the cane toad *R. marina* in Australia (Phillip et al. 2006). Through the ‘Olympic Village Effect’, successive generations of *C. quadricarinatus* are likely to lead to rapid and further expansion (both upstream and downstream) of the population on the Upper Zambezi.

Decline in body condition of male and female individuals towards the edges suggest less fit individuals of *C. quadricarinatus* are occupying the edge. The results corroborate intense intra-specific competition as the main driver of range expansion as physiologically weaker individuals are being excluded from the densely populated core. Despite exhibiting highly competitive ability, their loss of weight due to molting may have led to a drop resource holding potential compared to conspecifics hence their dispersion to the edges. These findings however are in contrast to previous studies on linear aquatic systems which found better body condition of individuals at the edge (Lopez et al. 2012; Brandner et al. 2013; Rebrina et al. 2015).

In conclusion, this study contributes to the growing evidence of changes in population characteristics of an aquatic invasive species as it expands its range. The rapid range expansion of *C. quadricarinatus* on the Barotse floodplain is evidence of its' high invasive capacity. Since high conspecific density at the core seems to be the main driver of range expansion, management and conservation efforts for the wetland should target reducing the population size of *C. quadricarinatus* to minimise intra-specific competition and eventual spread. If the population is left uncontrolled, the increase in conspecific density has the potential to cause more adverse impact on ecosystems (Galib et al. 2022a). Although there is no evidence of environmental filtering, spatial sorting does seem to cause changes on traits of *C. quadricarinatus* across the invasion range. However, the influence of spatial sorting does not clearly manifest perhaps due to short invasion history (approx. 9 years from time field surveys were conducted) and small sample size at the edges. It is therefore imperative to continue monitoring the edge population to establish a clearer pattern of changes in traits. Implementing early monitoring through field trapping could prove useful in future (Manfrin et al. 2019). Future studies should also consider assessing the influence of interspecific competition as it has potential to cause variation in traits across the invasion range (Burton 2010). Identifying factors that promote trait changes is important for enhancing our understanding of how invasive species successfully expand their range and eventually cause ecological and socio-economic impact. The insights from this study are particularly important for management and conservation of dynamic non-linear wetland systems like river-floodplain systems.

CHAPTER 5

QUANTIFYING THE ECONOMIC IMPACT OF AUSTRALIAN REDCLAW CRAYFISH *CHERAX QUADRICARINATUS* ON THE BAROTSE FLOODPLAIN ARTISANAL FISHERY

Abstract

Biological invasions cost global economies the equivalent of billions of US dollars through corrosion of ecosystem services and incurred management costs. Available evidence suggests that the widespread introduction of *Cherax quadricarinatus* in the Zambezi basin has the potential to cause severe socio-economic impacts, however, this remains unquantified in the Upper Zambezi. In this study, creel surveys were implemented to assess the economic impact of *C. quadricarinatus* on the Barotse floodplain artisanal fishery. Fishers encountered *C. quadricarinatus* as a bycatch species in 9 types of fishing gears across the floodplain with crayfish encounter and abundance being higher in dry season and highest in invasion core (Mongu stratum). Damage to fish catch was exclusively incurred by gillnet users and was also more extensive at invasion core during dry season. Damage was evident on 15 of the 16 fish species/group harvested, with the most important fisheries species *Clarias* spp, *H. cuvieri*, *O. andersonii*, *S. macrocephalus, C. rendalli* and *Serranochromis* spp being the most frequently affected. The economic cost arising from fish damage in Mongu during dry season was estimated to be US$ 21, 587 per annum. Gear damage due to crayfish occurred in 3 types of fishing gear but was most prevalent among gillnet users, higher in the dry season and most extensive at the invasion core. The loss of fishing time was most prevalent among fishers using seine nets and more common in dry season and mostly at invasion core. The economic costs incurred are significant for those affected, but the relative spatial restriction of such to the invasion core reflects a new invasion the costs of which are likely to increase These findings highlight the threat posed by invasive species to the livelihood of African communities, and the need to prioritise management of biological invasions in the region.

Keywords

Invasive alien species, economic cost, gear damage, fish damage, time cost, livelihood, management

5.1 Introduction

Biological invasions are a serious anthropogenically facilitated threat to biodiversity and ecosystem function (Simberloff et al. 2013; Blackburn et al. 2019; Pyšek et al. 2020). Invasive alien species (IAS) can also have profound negative effects on the economy (Vilà and Hulme 2017; Bacher et al. 2018) and human wellbeing (Bradshaw et al.2016; IPBES 2023). Globally, economic costs attributed to IAS have been reported to have reached a minimum US$ 1.288 trillion in damages (Diagne et al. 2021a). On the African continent, the cost of invasion is reported to be between US$ 18.2 billion and US$ 78.9 billion for the period 1970 and 2020 (Diagne et al. 2021b). Despite such huge costs, implementation of measures to prevent and control biological invasions remains limited mostly due to undervaluing of effects associated with IAS by decision makers (Courchamp et al. 2017). Determining economic cost associated with biological invasion is therefore essential to communicate negative impacts for motivation of the development of IAS policy and further strengthening of biosecurity (Seebens et al. 2017; 2020; Cuthbert et al. 2021; Diagne et al. 2021a).

The redclaw crayfish, *Cherax quadricarinatus,* is an emerging global invader which has been introduced in several African river basins (Nunes et al. 2017; Douthwaite et al. 2018; Madzivanzira et al. 2021a; Haubrock et al. 2021a). *Cherax quadricarinatus* was first introduced to the Zambezi Basin in 2001 for aquaculture purposes and has since established feral populations in the Kafue Floodplains Ecoregion and Upper Zambezi Floodplains Ecoregion and the Middle Zambezi (Douthwaite et al. 2018; Madzivanzira et al. 2020; 2021a). Although specific impacts are unknown, fishers have reported catch spoilage, with up to a third of catch damaged on the Kafue Flats (Weyl et al. 2017). In addition, gillnet processing times and repair costs are reported to have increased (AES and WWF 2017). On the Barotse floodplain, anecdotal reports have emerged from artisanal fishers with regards to *C. quadricarinatus* spoiling their fish catch through partial consumption of fish caught on gillnets and as well as damage to the nets (N. Namasiku pers com.). Partial consumption of fish renders the catch unsuitable for trade, resulting in cascading impacts throughout the value chain (Madzivanzira et al. 2022). In the Lake Kariba invasion core, in the Middle Zambezi, US$ 512 352.92 loss is attributed to damage by crayfish (Chakandinakira et al. 2023; Madzivanzira et al. 2023). Potential of escalating economic cost is of great concern as the Barotse floodplain fishery is a fundamental source of livelihoods and food provisioning for approximately 70, 000 people across the floodplain and immediate surrounding areas (CGIAR, 2013). Given that 78.6% of the rural population are estimated to be living below the poverty line in the region (ZSA, 2023), the growing invasion may be a direct threat to human wellbeing. Understanding the effects that *C. quadricarinatus* is having on the livelihood of fishers on the Barotse floodplain is critical.

The economic impact of *C. quadricarinatus* invasion on the Barotse floodplain fishery has not been quantified in the field since its introduction in 2012. Madzivanzira et al. (2022) estimated the cost incurred by extrapolating data from laboratory experiments, however these findings require verification as they represent a maximum possible cost. Here, a systematic field-based assessment was used to provide a more accurate quantification of economic cost incurred by artisanal fishers as a result of *C. quadricarinatus*. We aimed to 1) assess crayfish encounter and abundance across season (wet/dry) and invasion gradient (core vs upper/lower edges), 2) assess the prevalence of damage to fish catch and determine if fish catch damage varies by season, invasion gradient and habitat type (lentic/lotic) and if it is species specific, and 3) estimate associated economic costs (catch damage, gear damage and loss of fishing time) across season and invasion gradient.

5.2 Materials and methods

5.2.1 Study area

The study was conducted on the Barotse floodplain of the Upper Zambezi system (Ecoregion 556, Abell et al. 2008) (Fig. 5.1). The main floodplain area covers approximately 550, 000 hectares while the total wetland extends around 1.2 million hectares (Turpie 1999). Between March and November every year, fishers use a variety of fishing methods to exploit the fishery resources. Some of the common fishing gears used include gillnets, seine nets, hook and line, traps, baskets, spears, and weirs (van Gils 1988; Turpie et al. 1999; Chapter 3). Gillnets are predominantly used on the floodplain during the flood period (Chapter 3) and continue as a dominant gear in lentic habitats (i.e., lagoons and ponds) as the floods recede between May to July after which they become more dominant in lotic habitats (i.e., river and canals) as seine nets replaces them in the lentic habitats (N. Nawa pers. obs.) (see Chapter 2 for details on the study area).

Cherax quadricarinatus were illegally introduced on the Barotse floodplain in Mongu in 2012 (Douthwaite et al., 2018) and the population has since become established (Madzivanzira et al. 2021: Chapter 4). However, the crayfish population varies across the invasion range with the invasion core (Mongu) having high relative abundance (1.471 ± 0.685 ind./trap/night) compared to the invasion edge (upstream in Lukulu and downstream in Senanga) where the abundance is still relatively low (0.027± 0.002 ind./trap/night) (Chapter 4). The population also exhibits seasonal variation with high relative abundance in dry season (0.789 ± 0.518 ind./trap/night) than wet season (0.331 ± 0.138 ind./trap/night).

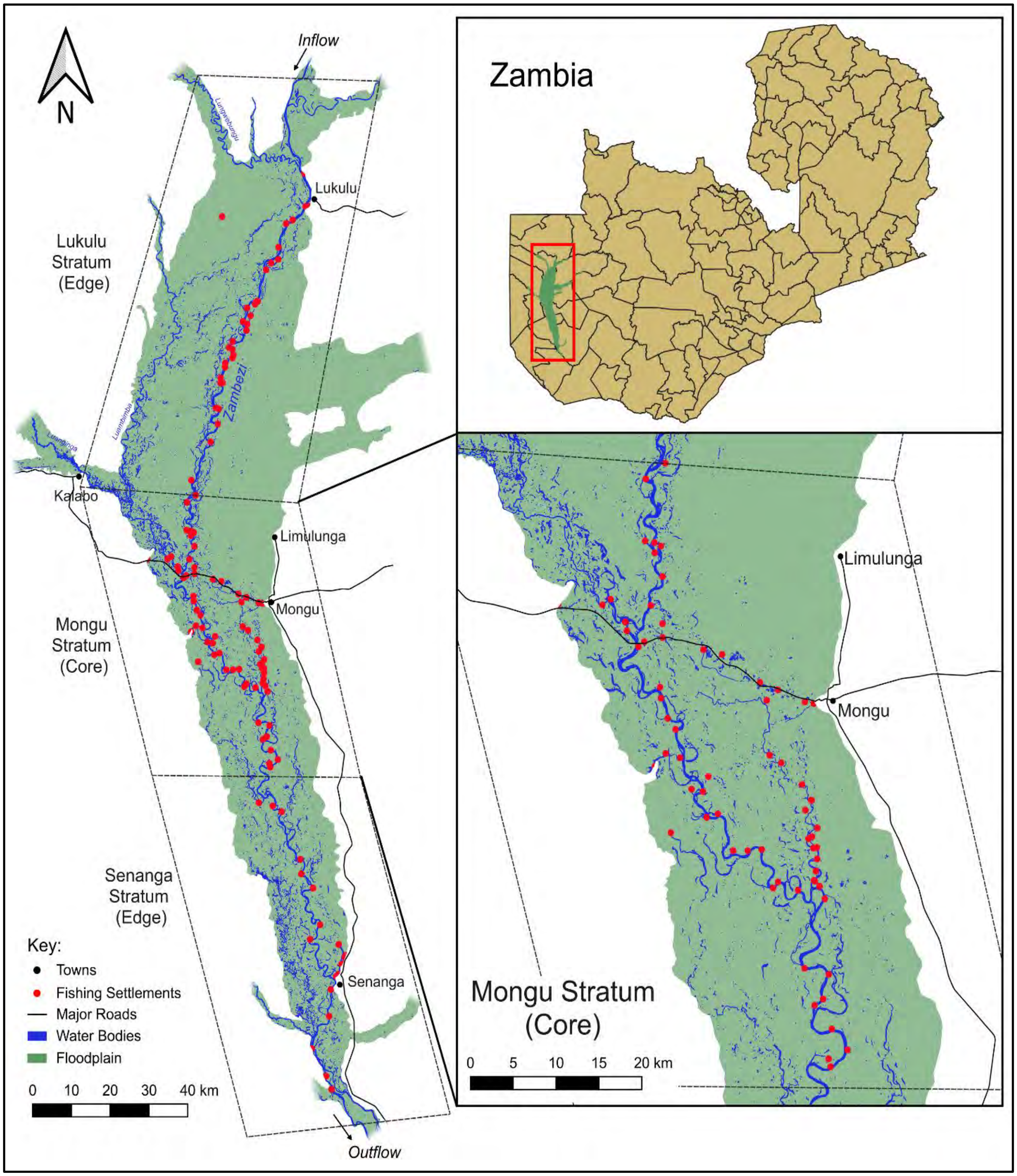

Figure 5.1 The three strata: Senanga (downstream invasion edge), Mongu (invasion core) and Lukulu (upstream invasion edge) on the Barotse floodplain where sampling was conducted.

5.2.2 Sampling

Data were collected in 2021, using a roving creel surveys method. The roving creel method is recommended for estimating catch and effort data for geographically disbursed fisheries (Pollock, et al. 1994). Two types of creel surveys were conducted: a 30 days survey and a 14 days survey. The 30-day creel surveys were conducted bi-annually focusing on both wet season (April) and dry season (October). Each survey was conducted across three strata: Senanga (downstream invasion edge), Mongu (invasion core) and Lukulu (upstream invasion edge) (Fig. 5.1). The 14-day creel surveys were conducted every month from June to September in the Mongu stratum. For data collection, an electronic based questionnaire was utilised, accessed through the ODK Collect App (version 1.30.1) installed on Lenovo tablets. The questionnaire was semi-structured, consisting of both open-ended and closed-ended questions (Appendix 5.1). Seven trained field enumerators (2 in Senanga, 3 in Mongu and 2 in Lukulu) moved randomly through their designated strata and interviewed fishers on landing sites of villages/fishing camps returning from fishing as well as those still fishing in various water bodies across the floodplain (see Chapter 3 for the detailed survey implementation process).

During each interview, fish caught were sorted into individual species or species groups based on pre-determined categories (see Chapter 3 for detailed of pre-determined categories). For each individual species or species groups fish, undamaged (whole) and (crayfish) damaged individuals were separated and the weight (kg) of each were recorded using a digital scale. Damage due to crayfish was determined by presence of slicing wounds on the fish and/ crayfish in the net. Slicing wounds are synonymous with crayfish and different from other scavenging predators, like crocodile and terrapins, which tend to cause loss of substantial parts of the fish (Chikandinakira et al. 2023). A maximum of 15 randomly selected individuals from each damaged fish category were further inspected and body parts damaged were recorded. The damaged parts were classified into the following categories, fins, mouth, eyes, stomach, skin and gills (Fig. 5.2). Additional information on fishing effort (number of days fished per week), crayfish presence, gear damage and time lost due to crayfish was also recorded during the interview.

Figure 5.2 Different type of fish species with their body parts damaged by crayfish on the Barotse floodplain (Photograph: Nawa Nawa; Date: 11/10/2021).

To make seasonal comparisons, analysis of crayfish encounters and abundance, prevalence of fish damage and gear damage and time cost were all based on the 30-day creel surveys. Detailed analysis of fish damaged (i.e., daily catch rate and species composition of spoiled fish) by crayfish as well as associated economic cost was limited to gillnets (~ 100 m net/night) as they accounted for most of the damage. This analysis only incorporated fish damages incurred in Mongu stratum during the dry season. Fish damaged in Mongu stratum (wet season) as well as that of Senanga stratum (both wet and dry season) were not available for quantification as it was considered insignificant by the fishers and discarded before the time of the interview (N Nawa, pers. obs.). Lukulu stratum on the other hand was excluded due to lack of fish damage.

In-depth analyses of fish damaged in Mongu during dry season were based on the 14-day creel surveys given the small sample size from the 30-day creel survey (i.e., October). Two monthly periods (June-July and August September) and habitat type (lentic vs lotic) were used to assess the dynamics of fish spoilage in Mongu stratum during dry season. For standardisation purposes, all analyses were based on individual fishers who had completed fishing at the time of interview implying that daily fishing effort was comparable. Monetary losses arising from gear damage were not determined due to insufficient information for cost quantification (i.e., frequency of gear replacement and/or repairs as well as associated monetary cost).

5.3 Data Analysis

5.3.1 Crayfish encounter and abundance

Crayfish encounter and abundance was expressed as a relative percentage frequency of the total number of fishers who encountered crayfish and number of crayfish caught per season within each stratum respectively. Chi-square goodness of fit test was used to analyse the prevalence of crayfish encounter and relative abundance across season and strata.

5.3.2 Fish damage

Prevalence of fish damage was expressed as a relative percentage frequency of the total number of fishers' who encountered fish damaged by crayfish per season within each stratum. To assess the prevalence of fish damage among fishers between season and across strata, a Chi-square goodness of fit test was used.

Daily catch rate was expressed as individual catch per unit effort (CPUE) and calculated for both spoiled fish and intact fish. The calculation was adapted from AES and WWF (2017) as follows:

(1) CPUE for spoiled fish ($CPUE_{spoiled}$) = $kg(spoiled).\ fisher^{-1}.\ d^{-1}$

(2) CPUE for intact fish ($CPUE_{intact}$) = $kg(intact).\ fisher^{-1}.\ d^{-1}$

To assess whether there was a difference in $CPUE_{spoiled}$ across habitat (i.e., lentic, and lotic) and months (i.e., June-July and August-September) overall fish catch was taken into account by calculating the ratio of $CPUE_{spoiled}$: total fish catch ($CPUE_{spoiled}$ + $CPUE_{intact}$). The ratio was arcsine square root transformed and then used as response variable in a Generalised Linear Model (GLM) with a log link after checking for residual distribution and overdispersion. To determine whether fish damaged was related to the crayfish caught as by-catch in gillnets, Spearman Rank Correlation test was performed on the arcsine square root transformed ratio and the number of crayfish caught. To assess species specific damage relative composition of fish species spoiled was expressed as a percentage of the total weight (kg) of catch.

5.3.3 Economic losses

5.3.3.1 Total damage cost estimation

Calculation of total monetary loss incurred by fishers through fish damage was adapted from Chakandinakira et al. (2023) and expressed as follows:

(3) Monetary loss per fisher per day = $CPUE_{spoiled}$ ($kg.\ fisher^{-1}.\ d^{-1}$) × Average price of fresh fish per kg

(4) Monetary loss per fisher per year = Monetary loss per fisher per day × Effort (days fished per year)

(5) Total Monetary loss per year = Monetary loss per fisher per year × Number of gillnet fishers incurring fish damage

Fishing effort was expressed as mean number of days fished per week during a sampling period. Effort was upscaled based on six months of dry season period (June to November) considering three months fish ban period (December to February). The proportion of gillnet usage from the 2021 CAS (Chapter 2) was used to determine the number of gillnet fishers from the total population of fishers reported in the 2019 Frame Survey (DOF, 2019).

5.3.3.2 Gear damage

Gear damage was expressed as a relative percentage frequency of the total number of fishers whose fishing gear was damaged by crayfish per season within each stratum. Chi-square goodness of fit test was used to test the difference in proportion of fishers with damaged gear across seasons and strata.

5.3.3.3 Time cost

Time cost was expressed as a relative percentage frequency of the total number of fishers who lost time due to crayfish presence per season within each stratum. The Chi-square test of independence and chi-square goodness of fit test were used to difference in proportion of fishers who lost time during fishing due to crayfish across season and strata.

5.4 Results

A total of 590 catch interviews were conducted across the three strata during the 30-day wet and dry creel surveys. Mongu stratum accounted for most of the interviews followed by Senanga and Lukulu strata (Table 5.1). The 14-day creel surveys conducted in Mongu stratum from June to September yielded a total of 422 interviews. The month of June had the highest number of interviews followed by July, August, and September (Table 5.2).

Table 5.1 Number of fishers interviewed during the 30-day creel surveys conducted in wet and dry season across three strata (Senanga, Mongu and Lukulu) on the Barotse floodplain.

Stratum	Season		Total
	Wet	Dry	
Senanga	109	79	188
Mongu	89	118	207
Lukuku	74	121	195

Table 5.2 Number of fishers interviewed during 14-day creel surveys conducted in dry season (June to September) in Mongu stratum on the Barotse floodplain.

Month	June	July	August	September	Total
Number of interviews	137	128	118	39	422

5.4.1 Crayfish encounter and abundance

Fishers encountered crayfish in 9 out of 17 fishing gear types with the most frequent encounter occurring in seine nets, gillnets, drift gillnet, hook and line and mosquito nets (Table 5.3).

Overall, 22.7 % (n = 134) of fishers caught crayfish in their fishing gear across the floodplain. The proportion of fishers who encountered crayfish was significantly different across the strata ($\chi2$= 18.22, df = 2, < 0.01). The proportion of fishers who encountered crayfish was significantly higher in Mongu (52.2%) than Senanga (29.9%) ($\chi2$= 7.44, df = 1, < 0.01) and Lukulu (17.9%) ($\chi2$= 23.94, df = 1, $p < 0.01$) while the proportion in Senanga was significantly higher than Lukulu ($\chi2$= 6.25, df = 1, $p < 0.05$). A higher proportion of fishers encountered crayfish in their gear during dry season (76.9%) than wet season (23.1%) ($\chi2$= 28.87, df = 1, $p <$ 0.01).

Table 5.3 Percentage of fishers encountering crayfish in their fishing gear in wet and dry season across three strata (Senanga, Mongu and Lukulu) on the Barotse floodplain.

Fishing gear	**Senanga**		**Mongu**		**Lukulu**		**Overall**
	Wet	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**	
Seine net	10.00	63.33	12.50	48.15		78.95	47.01
Gillnet	60.00	16.67	68.75	33.33	40.00	15.79	33.58
Drift gillnet	30.00	16.67	-	3.70	40.00	-	8.96
Hook and line	-	-	-	9.26	-	-	3.73
Mosquito seine <5m	-	3.33	6.25	3.70	-	5.26	3.73
Reed basket scoop	-	-	-	1.85	-	-	0.75
Large mesh reed trap	-	-	6.25	-	-	-	0.75
Small mesh reed trap	-	-	6.25	-	-	-	0.75
Fish weir floodplain	-	-	-	-	20.00	-	0.75
Small vertical trap	-	-	-	-	-	-	-
Cast net	-	-	-	-	-	-	-
Hand spear	-	-	-	-	-	-	-
Large hooks on poles	-	-	-	-	-	-	-
Longline	-	-	-	-	-	-	-
Vertical scoop trap	-	-	-	-	-	-	-
Scoop net	-	-	-	-	-	-	-
Bottle trap	-	-	-	-	-	-	-

A total of 1235 crayfish were caught in 9 fishing gears across the floodplain. Five fishing gears (i.e., seine nets, gillnets, drift gillnet, and mosquito net) together accounted for 98.5% of crayfish catch (Table 5.4). The proportion of crayfish caught in fishing gears was significantly different across the strata ($\chi 2= 49.33$, df = 2, < 0.01). A significantly higher proportion of crayfish was caught in Mongu (62.2%) than Senanga (32.5%) ($\chi 2= 9.97$, df = 1, < 0.01) and Lukulu (5.1%) ($\chi 2= 72.07$, df = 1, $p < 0.01$) while that of Senanga was significantly higher than Lukulu ($\chi 2= 53.06$, df = 1, $p < 0.01$). A higher proportion crayfish was caught during the dry season (90.1%) than wet season (9.9%) ($\chi 2= 64.39$, df = 1, $p < 0.01$).

Table 5.4 Percentage of crayfish caught in fishing gear during wet and dry season across three strata (Senanga, Mongu and Lukulu) on the Barotse floodplain.

Fishing gear	**Senanga**		**Mongu**		**Lukulu**		**Overall**
	Wet	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**	
Seine net	12.50	43.49	26.32	76.69	-	85.96	61.86
Gillnet	35.00	5.54	55.26	20.58	50.00	10.53	18.46
Drift gillnet	52.50	42.66	-	0.72	33.33	-	14.74
Mosquito seine <5m	-	8.31	3.95	1.01	-	3.51	3.40
Small mesh reed trap	-	-	10.53	-	-	-	0.65
Hook and line	-	-	-	0.72	-	-	0.40
Large mesh reed trap	-	-	3.95	-	-	-	0.24
Reed basket scoop	-	-	-	0.29	-	-	0.16
Fish weir floodplain	-	-	-	-	16.67	-	0.08
Small vertical trap	-	-	-	-	-	-	-
Cast net	-	-	-	-	-	-	-
Hand spear	-	-	-	-	-	-	-
Large hooks on poles	-	-	-	-	-	-	-
Longline	-	-	-	-	-	-	-
Vertical scoop trap	-	-	-	-	-	-	-
Scoop net	-	-	-	-	-	-	-
Bottle trap	-	-	-	-	-	-	-

5.4.2 Fish damage

Of fishers who encountered fish damage due to crayfish, 95.7% (n =22) were gillnets users compared to 2.7% (n=1) for small mesh reed traps. Among gillnets users, fish damage due to crayfish was only detected in Mongu and Senanga strata (Fig. 5.3). The proportion of fishers with fish damage was significantly higher in Mongu (86.4%) than Senanga (13.6%) strata ($\chi 2=$

52.89, df = 1, $p < 0.01$). Within Mongu stratum, the proportion of gillnet users who encountered damaged fish was significantly higher during dry season than wet season ($\chi 2$= 40.50), df = 1, $p < 0.01$). About 81.8% of fishers found damaged fish in dry season compared to 18.2% in wet season.

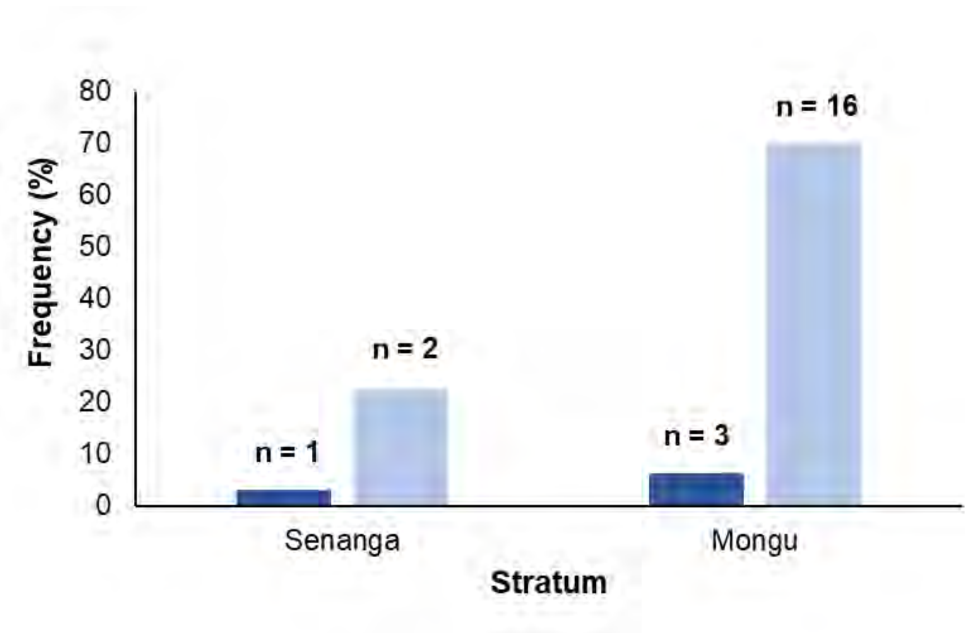

Figure 5.3 Percentage frequency of fishers with fish damaged by crayfish during wet (dark blue) and dry (light blue) seasons across Senanga and Mongu strata on the Barotse floodplain. The letter "n" represents sample size (number of fishers) per season within each stratum.

The 14-days surveys conducted in Mongu stratum during dry season (June-September) yielded a 68.2% (n=158) fish damage encounter rate among gillnet fishers. Analysis of the arcsine square root transformed ratio of $CPUE_{spoiled}$: ($CPUE_{spoiled}$ + $CPUE_{intact}$) revealed a significant interaction between habitat and months (Table 5.5) where fish damage during June-July months was higher in lentic than lotic habitat while during August-September months it was higher in lotic than lentic habitats (Fig. 5.4). Both months and habitat had no significant main effect on the CPUE spoiled (Table 5.5).

Table 5.5 Model terms for all factors from GLM with a gamma distribution used to determine effects of factors "habitat" and "season" on CPUE. Type 3 Anova and χ^2 used to report the effect size of a factor on the dependent variable.

Model term	Chisq	df	*p*-value
Habitat	5.21	1	= 0.08
Months	35.05	1	= 0.91
Habitat * Months	15.61	1	< 0.05

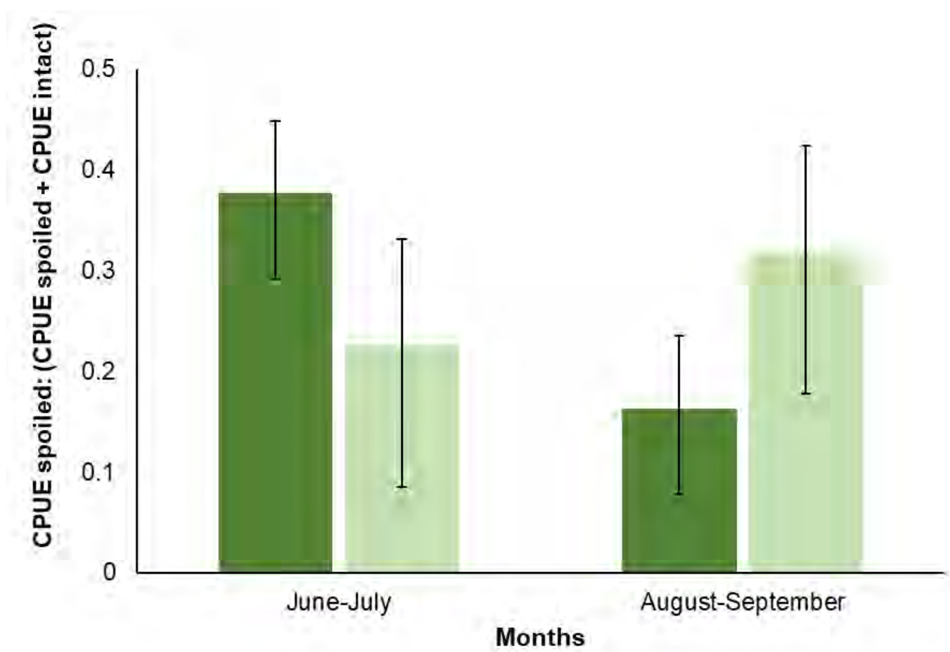

Figure 5.4 Arcsine square root transformed ratio of $CPUE_{spoiled}$: ($CPUE_{spoiled}$ + $CPUE_{intact}$) of fish catch in gillnets in lentic (dark green) and lotic (light green) habitats during the months of June-July and August-September across Mongu stratum. Error bars represent 95% confidence intervals.

There was a significant weak relationship between ratio of spoiled: intact fish CPUE and number of crayfish caught in gillnets (R^2 = 0.37, $p < 0.01$). In 12.7% of the cases, typical crayfish damage marks were recorded on different fish species caught but no crayfish were found in the nets implying crayfish are not always retained in gillnets.

Damage marks were found on 15 fish species/groups out of the 21 that were harvested in gillnets across Mongu stratum (Table 5.6). The five most damaged fish species/groups were *Clarias* spp., *S. macrocephalus*, *Sargochromis* spp., *C. rendalli,* and Small Breams (Table 5.6). Cichlids together accounted for 50.0% of the total fish damaged (Table 5.6).

Table 5.6 Percentage composition of fish species/group by total weight harvested and weight damaged by crayfish during dry season in Mongu stratum on the Barotse floodplain.

Common name/group	**Scientific name (s)**	**Total weight (%)**	**Weight Damaged (%)**
Catfishes - all types	*Clarias* spp. (*C. gariepinus, C. ngamensis,* etc.)	21.22	41.67
Purpleface Largemouth	*S. macrocephalus*	9.88	18.81
Sargos	*Sargochromis* spp.	6.79	11.63
Redbreast Tilapia	*C. rendalli*	12.44	9.34
Small Breams <10cm	Any bream < 10cm (*P. acuticeps, P. philander*)	8.80	7.41
Robbers	*M. acutidens, B. lateralis, R. maunensis*	10.03	4.92
Other Largemouths	*Serranochromis* spp	1.47	2.34
Threespot Tilapia	*O. andersonii*	2.03	0.98
Mixed Small Fish <10cm	(Cyprinidae, Mormyridae and juveniles of Cichlidae)	17.44	0.81
African Pike	*H. cuvieri*	0.09	0.55
Bulldog	*M. altisambesi*	5.15	0.49
Other Large Breams	-	0.25	0.43
Squekers	*Synodontis* spp	1.26	0.34
Silver Catfish	*S. intermedius*	0.89	0.15
Tigerfish	*H. vittatus*	0.38	0.13
Western Bottlenose	*M. lacerda*	0.32	-
Climbing Perch	*C. multispine*	0.02	-
Redeye Labeo	*L. cylindricus*	0.07	-
Nembwe	*S. jallae*	0.07	-
Small Mixed Mormyrids	*H. ansorgii, P. okavangensis, P. marianne*	1.33	-
Yellowfish	*L. codringtonii*	0.08	-

A total of 782 individual fishes from all 21 fish species/group harvested were subjected to detailed inspection for body damage. The frequently damaged parts identified were fins (81.2%), mouth (69.9%), eyes (67.1%), stomach (64.1%), skin (51.3%) and gills (42.2%). According to fishers, 54.9% of the damaged fish was to be kept for consumption, 14.1 % given to domestic animals, and 31.0% discarded.

5.4.3 Economic losses

5.4.3.1 Total cost estimation

Daily catch loss of 0.20 *kg. fisher*$^{-1}$. *d*$^{-1}$ averaged over a four-month period across Mongu stratum equates to the monetary loss of US$ 0.68 *fisher*$^{-1}$. *d*$^{-1}$ (Table 5.7). The daily monetary loss is 17.13% of the fishers' daily income (US$ 3.97). The cost assessment is based on the current average market price of US$ 3.42 per kg for fresh fish sold on the Barotse floodplain. The average weekly fishing effort over 4 months is 6.46 days per week and translates to 168.86 fishing days from June to November. Using this fishing effort, the monetary loss per fisher per year is US$ 114.83 (Table 5.7). The population of 1672 fishers in Mongu stratum (DOF, 2019) with a 16.5% gillnet usage during the dry season (Chapter 3) gives 276 as the estimated number of gillnet fishers. Based on the 68.2% fish damage encounter rate among gillnet users in Mongu stratum during dry season, the number fishers incurring fish damage is 188. Using these values, the total monetary loss per year for the Barotse floodplain landscape as represented by Mongu stratum is US$ 21, 586.76 (Table 5.7).

Table 5.7 Monetary losses incurred to fishers because of crayfish damage in Mongu stratum on the Barotse floodplain.

	Weight value (kg)	**Monetary value (US$)**
Daily catch loss/fisher/day	0.20	0.68
Annual catch loss/fisher/year	33.77	114.82
Total annual loss	6, 348.76	21, 586.16

5.4.3.2 Gear damage

Of fishers who encounter crayfish, 36.6% incurred gear damage caused by crayfish. Three types of fishing gears were damaged with gillnets being the most frequently damaged across the Barotse floodplain (Table 5.8). The proportion of fishers with damaged fishing gear was significantly different across strata ($\chi2 = 40.67$, df = 2, $p < 0.01$). The proportion of damaged fishing gear in Mongu was significantly higher than Senanga ($\chi2 = 13.22$, df = 1, $p < 0.01$) and Lukulu ($\chi2 = 51.02$, df = 1, $p < 0.01$) while that of Senanga was significantly higher than Lukulu ($\chi2 = 22.44$, df = 1, $p < 0.01$). Of all fishers with fishing gear damaged by crayfish, 61.2% were from Mongu stratum while 28.6% and 10.2% were from Senanga and Lukulu respectively. The proportion of fishers with fishing gear damaged by crayfish in dry season was significantly higher wet season ($\chi2 = 18.37$, df = 1, $p < 0.01$). About 71.4% of fishers had their fishing gear damaged by crayfish in dry season compared to 28.5% in wet season. The two major causes of gear damage identified by fishers were crayfish entangling fishing gear (41.6%) and gear getting cut through crayfish removal (29.9%).

Table 5.8 Percentage of fishers with fishing gear damaged by crayfish during wet and dry season across three strata (Senanga, Mongu and Lukulu) on the Barotse floodplain.

Fishing gear	**Senanga**		**Mongu**		**Lukulu**		**Overall**
	Wet	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**	
Gillnet	75.00	30.00	88.89	76.19	100.00	50.00	67.35
Seine net	25.00	50.00	11.11	19.05	0.00	50.00	26.53
Drift gillnet	0.00	20.00	0.00	4.76	0.00	0.00	6.12

5.4.3.3 Time cost

Overall, 91.8% fishers who caught crayfish experienced loss of time during fishing due to the presence of crayfish in their fishing gear. Loss of time was incurred by fishers in eight fishing gear types (i.e., seine nets, gillnet, drift nets, mosquito seine, hook and line, large mesh reed trap, small mesh reed trap and reed basket scoop). Seine nets accounted for 44.7% of fishers who lost fishing time while gillnets and other fishing gear combined accounted for 35.8% and 19.5% respectively. About 7.3% of fishers from both Mongu and Senanga during dry season lost over 25 minutes of fishing time (Table 5.9). The proportion of fishers who lost time was significantly different across strata ($\chi2$= 31.21, df = 2, p < 0.01). The proportion in Mongu (56.9%) was significantly higher than Senanga (31.7%) ($\chi2$= 8.09, df = 1, p < 0.01) and Lukulu (11.4%) ($\chi2$= 44.44, df = 1, p < 0.01) while that of Senanga was significantly higher than Lukulu ($\chi2$= 22.25, df = 1, p < 0.01). The proportion of fishers who lost time was significantly higher in dry season (77.2%) than wet season (22.8) ($\chi2$= 29.67, df = 1, p < 0.01).

Table 5.9 Percentage of fishers who lost fishing time due to crayfish during wet and dry season across three strata (Senanga, Mongu and Lukulu) on the Barotse floodplain.

Time lost (minutes)	Senanga		Mongu		Lukulu		Overall
	Wet	Dry	Wet	Dry	Wet	Dry	
<10min	100.00	64.91	65.22	63.11	100.00	66.67	66.18
10-24min		24.56	34.78	21.36		33.33	23.19
25-39min		10.53		10.68			8.21
40-54min				4.85			2.42

5.5 Discussion

Understanding economic cost associated with IAS has become very important as it informs resource management and policy development aimed at preventing and managing the arrival and spread of IAS species (Seebens et al. 2020). However, estimates of cost are still lacking for many taxa, impacted sectors and regions (Cuthbert et al. 2021; Diagne et al. 2021a; Kouba et al. 2022). This study provides the first in field quantification of economic cost associated with *C. quadricarinatus* invasion on the Barotse floodplain of the Upper Zambezi system. The study revealed that both crayfish encounter and abundance among fishers depends on season and invasion gradient. Fish damage due to crayfish was limited to gillnets at the invasion core during the dry season and equated to the monetary loss of ~ US$ 21,000 per annum. Although the monetary loss is limited to the invasion core, it is significant given the low social economic status of fishers on the floodplain (WorldFish Center, 2007). As the crayfish spread further and become more abundant across the floodplain the monetary loss from gillnets is likely to increase beyond US$ 50,000 per annum. In addition, gear damage and loss of time due crayfish among fishers were also dependant on season and invasion gradient.

The high encounter rate of *C. quadricarinatus* among fishers at the invasion core compared to the invasion edges is not surprising given the similar spatial pattern of crayfish abundance observed in this study. Similar observations on abundance have been made by another study using standard sampling methods (Chapter 4). The high crayfish encounter and abundance among fishers perhaps explain why significant fish damage was only detected at the invasion core. Despite *C. quadricarinatus* being caught in various fishing gears, fish damage due to crayfish was exclusively incurred in gillnets. The damage to fish caught gillnets due to crayfish scavenging has been reported in other inland fisheries in Africa (Lowery and Mendes 1977: Weyl et al. 2017; Chakandinakira et al. 2023). Susceptibility of gillnets to fish spoilage from *C. quadricarinatus* may be due to their passive usage. Given that *C. quadricarinatus* tend to be attracted to fish caught on the nets resulting in partial consumption of the fish (Madzivanzira et al. 2022; Chakandinakira et al. 2023), the long soak time associated with gillnets exacerbates the damage as crayfish has more time to feed on the fish caught. The recession of water level during dry season seems to result in higher concentrations of *C. quadricarinatus* in water bodies (Chapter 4) and subsequently causing greater damage to fish catch in gillnets.

Analysis of fish damaged in gillnets at the invasion core suggests that change in fishing methods during the dry season influences the dynamics of fish spoilage on the floodplain. The dominant usage of gillnets in lentic habitats (lagoons and ponds) during the months of July-July seems to subject a large amount of catches to scavenging activities of crayfish compared lotic habitats. Conversely, the shift of gillnet fishing to lotic habitats (rivers and canal) may be causing the fish catch to be more exposed crayfish damage than lentic habitats (N Nawa, pers. obs.). Furthermore, the high abundance of *C. quadricarinatus* in lagoons and ponds during the June-July period may also be contributing to high fish spoilage in lentic habitats during the same period (N Nawa, pers. obs.). The weak correlation between extent of fish damage and number of crayfish caught on the nets is likely due to poor retention of crayfish in gillnet re-affirming the caution against the use of such information without performing the standard sampling methods (Chakandinakira et al. 2023).

Fish that are damaged are considered unmarketable and not suitable for sale (Madzivanzira et al. 2020; Madzivanzira et al. 2022; Chakandinakira et al. 2023). In these instances, some of the damaged catch is kept for home consumption and the rest is either fed to domesticated animals or discarded. The most damaged fish species/group by *C. quadricarinatus* on the Barotse floodplain is *Clarias* spp. The high damage of *Clarias* spp is probably due to its high relative abundance as it forms 37% of the total annual weight of fish catch on the Barotse floodplain (Chapter 2). Other fish species/group highly impacted by *C. quadricarinatus* are *H. cuvieri*, *O. andersonii*, *S. macrocephalus, C. rendalli*, *Serranochromis* spp. Unlike this study, the *C. quadricarinatus* invasion on Lake Kariba mostly affects *Oreochromis niloticus* even though *Claria* spp and *C. rendalli* are also affected in small proportion (Chakandinakira et al. 2023). The large cichlids are of high commercial value on the Barotse floodplain (Tweddle et al. 2010; 2015) and their spoilage directly impacts fishers' capacity to generate income. The damage caused to low value species such as Robbers, Mixed Small Fish, *Synodontis* spp, *S. intermedius*, and Small Mixed Mormyrids is comparatively smaller. However, damage caused may have significant implications on the livelihoods of people in the regions as the low value fish species/group now form a more reliable source of protein amidst declining stock of cichlids (Tweddle et al. 2015; Chapter 3). Such smaller fish species and size-classes are also associated with important micronutrients such as vitamin A, Iron and Zinc which can leads to improved nutritional status of human populations in third world countries (Kawarazuka and Be´ne´ 2011; Islam et al. 2023)

The impact of *C. quadricarinatus* on the Barotse floodplain is a major food security concern, given the high poverty levels in the region (ZSA, 2023). The total economic cost calculated for the fishery is approximately US$ 21,586 per year with each fisher losing about US$ 114.82 annually. The damaged fish represents 1.1% of the total annual fish harvest in Mongu stratum during dry season (Chapter 3). Although overall loss seems small, taking the net household yield value of 60 to 325 US$ estimated for riparian communities on the Barotse floodplain (WorldFish Center, 2007), the annual cash loss at individual level is over 30% representing a significant detriment to human wellbeing. The economic cost to the fishery is likely to increase in future as *C. quadricarinatus* spread further and become more abundant across the landscape.

The economic cost calculated in this study, is much lower than that for Lake Kariba which approximately half a million US dollars (Chakandinakira et al. 2023). The difference in cost is likely due to the differences in fish catches with Lake Kariba recording much higher yield than the entire Upper Zambezi (DOF, 2017). In addition, crayfish invasion age and crayfish abundance may also be contributing to the difference in cost between two fisheries. The Lake Kariba invasion is a much older invasion with *C. quadricarinatus* reported to have been introduced in 2001-2002 while on the Barotse floodplain it was introduced in 2012 (Douthwaite et al. 2018). The 10 years difference in invasion age implies *C. quadricarinatus* in Lake Kariba have had more time to get establish as evidenced by mean CPUE of 4.47 ± 1.11 individuals/trap/night compared to 0.59 ± 0.44 individuals/trap/night (Madzivanzira et al. 2021a). In addition, the stable lacustrine environment of Lake Kariba characterised by slow or static water ideal for *C. quadricarinatus* (Wingfield 2002; Haubrock et al. 2021a) may have facilitated quicker establishment resulting in higher economic costs. Similarly, lacustrine conditions created by the dammed Kafue River may explain why reported crayfish damage to fishers' catch is much higher on the Kafue flats (Weyl et al. 2017) although associated cost are yet to be quantified.

The potential economic cost on the Barotse floodplain fishery may be much higher than estimated cost from fish damaged given prevalence of gear damage and loss of time. The high prevalence of gear damage and loss of time experienced by fishers at invasion core than downstream edges especially during dry season is not surprising considering the similar spatial and seasonal pattern to crayfish abundance. The susceptibility of gillnets to damage is due to the predominant use of monofilament nets (Chapter 3) mostly made off thin strands which easily get entangled and/or broken (N. Nawa pers. obs.). Monetary losses associated with gear damage although yet be quantified are likely to be significant. Complaints of crayfish entangling nets as well as associated damages have also been reported by other studies (Lowery and Mendes et al. 1977; Weyl et al. 2017; Chakandinakira et al. 2023). Loss of time is prevalent among net users partly due to the susceptibility of fishing gears to entanglement. The loss of fishing is an indirect cost as it has the potential to adversely impact fish catches. When crayfish gets entangled on the gillnet, the fishing gear losses efficacy resulting in reduced fish catches (Weyl et al. 2017; Madzivanzira et al. 2022b, Chakandinakira et al. 2023). Therefore, both economic costs from gear damage as well as loss time may be adversely impacting the livelihood of fishing communities on the Barotse floodplain.

As economic costs associated with *C. quadricarinatus* increase on the Barotse floodplain fishers may increase their fishing effort and resort to use of illegal fishing methods to make up for the lost catch (Chakandinakira et al. 2023). Considering that the use of illegal methods such as water beating, monofilament gillnets, mosquito nets and large seine nets with small mesh size is already rampant on the floodplain, sustainability of the fishery is seriously under threat (Tweddle et al. 2004; Peel et al. 2014; Chapter 3). Large commercially valuable cichlids which are already under severe fishing pressure (Peel et al. 2014; Tweddle et al. 2015; Chapter 3) risk disappearing altogether. Thus, apart to impacting the livelihood of people through economic cost, potential behavioural shift to unsustainable fishing practices as a coping strategy to *C. quadricarinatus* invasion threatens the biodiversity of fish species on the Barotse floodplain.

Biological invasion poses a serious threat to the livelihood of people, especially in the third world countries, as they lack the economic capacity to counteract invasion cost (Diagne et al. 2021b). Evidence from this study shows that artisanal fishers on the Barotse floodplain incur economic costs associated with the invasion *C. quadricarinatus*. Although the costs are limited to the invasion core, the impact on the livelihood of local people is quite significant. Expansion of this population from the core outwards could significantly increase these impacts in the future. As crayfish invasions continue to expand in range across Southern Africa, this will exacerbate the dire lack of food security and high poverty levels in the region. To attain sustainable development goals, SADC countries will have to prioritise prevention and management of IAS. Given complex socio-economic situations in most African countries, estimation of invasion cost will be very critical in aiding decision to allocate limited resource towards management of invasive species.

CHAPTER 6

FISHERS' AWARENESS, KNOWLEDGE AND PERCEPTION OF THE INVASIVE AUSTRALIAN REDCLAW CRAYFISH *CHERAX QUADRICARINATUS* ON THE BAROTSE FLOODPLAIN OF THE UPPER ZAMBEZI SYSTEM

Abstract

Invasive alien species (IAS) are a major global threat to ecosystems, economies and human well-being. Most studies have focused on the ecological and economic aspects of IAS impacts while the social dimension has received limited attention, impeding the development of effective management strategies. In this study semi-structured interviews were administered to fishers around the central Barotse floodplain (invasion core) to assess their awareness, knowledge and perception regarding *Cherax quadricarinatus* (Australian redclaw crayfish) invasion on the Barotse floodplain. All respondents were aware of *C. quadricarinatus* presence on the Barotse floodplain but most lacked knowledge about the species. The majority of the respondents perceived *C. quadricarinatus* as unbeneficial and posed more of a threat to the floodplain fishery than the environment. Most of the respondents also demonstrated a lack of awareness of management information relating to *C. quadricarinatus* and thus also reported they did not follow any management practices. However, most respondents expressed support for management measures to control *C. quadricarinatus* and reduce the spread across the floodplain. Furthermore, results showed that age, education, and residence of respondents significantly influence knowledge and perceptions of *C. quadricarinatus*. Although support for management exists, successful management of *C. quadricarinatus* on the Barotse floodplain will require enhancing local people's understanding of crayfish through education and awareness raising campaigns. This study highlights the importance of integrating public perception into planning and management of IAS especially during the early stage of an invasion.

Keywords

Invasive crayfish, social dimension, public perception, perceived benefits, perceived threats, management.

6.1 Introduction

Rapid improvement in global mobility has led to both intentional and accidental introduction of species outside their native ranges (Seebens et al. 2020). As a result, invasive alien species (IAS) have become major drivers of global environmental change through their impact on ecosystems and biodiversity (Bellard et al. 2016; Blackburn et al. 2019) economies (Bradshaw et al. 2016; Diagne et al. 2021) and human welfare (Jone 2017; Vilà and Hulme 2017). These impacts have prompted the calls for effective management of IAS (Simberloff et al. 2013; Pyšek et al. 2020). However, many IAS can also offer benefits which can bring about conflict of interest and contention surrounding their management (Crowley et al. 2017; Zengeya et al. 2017; Villatoro et al. 2019). Management of IAS therefore needs to be both comprehensive and flexible to balance ecological, economic and social impact perspectives.

The majority of biological invasion studies have been approached from the ecological and economic perspectives while the social perspective has only recently started to receive more attention (García-Llorente et al. 2008; Kannan et al. 2014; Shackleton et al. 2015; 2017). The social dimension is crucial in the effective management of IAS due to the central role that human beings play in the invasion process by facilitating establishment and spread (Meyerson and Mooney, 2007; Hulme et al. 2009; Kueffer 2017; Seebens et al. 2020) as well as possessing the capacity to act and make decision for management of species (Ricciardi et al. 2017; Pyšek et al. 2020). Effective management of IAS requires the involvement of stakeholders such as public/citizens, researchers, government departments, non-governmental organization and business entities (Novoa et al. 2018; Shackleton et al. 2019a). Stakeholder engagement is particularly important when dealing with IAS where conflict of interest exists (García-Llorente et al. 2008; van Wilgen and Richardson 2014; Shackleton et al. 2015;2019b).

Invasive alien species with both negative impacts and benefits often bring about conflicts regarding their use and management (Dickie et al. 2016; Woodford et al. 2016; Zengeya et al. 2017; Novoa et al. 2018). Conflict of interest in the management of IAS usually arises due to disagreement in stakeholder value systems which includes utilitarian values or intrinsic values. Utilitarian values are based on derived practical or economic benefits of an IAS (Zengeya et al. 2017). Conflicts centred on intrinsic values are derived from the physical or emotional appeal of an IAS and come in various forms: humanistic (i.e., species has a cultural or spiritual value) and moralistic (i.e., species evokes ethical consideration from humans, often associated with animals), aesthetic and naturalistic (i.e., species bring about human satisfaction through experience or physical appeal) (Estévez et al. 2015). For example, an invasive alien fish species rainbow trout (*Oncorhynchus mykiss*) is commonly utilized in recreational fishing industry in South Africa (Woodford et al. 2016) however it threatens native biodiversity (Cambray, 2003; Ellender and Weyl 2014). Efforts by conservation authorities to manage the trout have been strongly opposed by recreational anglers (Ellender et al. 2014; Woodford et al. 2016). Due to such conflict of interest, there has been increasing recognition of the importance of assessing public perception in IAS management (Novoa et al. 2016; Shackleton et al. 2019a).

Assessment of public knowledge and perception regarding IAS can help to mitigate conflicts by building trust and consensus resulting in the development of accepted management interventions (Verbrugge et al. 2013; Novoa et al. 2018; Shackleton et al. 2019b; Saba et al. 2021). People's perceptions of IAS are influenced by several factors which include individual characteristics, species attributes and its' effect, social-cultural, landscape, and governance factors (Shackleton et al. 2019b). Individual knowledge system is one of the key individual characteristics and reinforces beliefs about IAS based on personal observation of the species and its effect as well as through other forms of learning (e.g., formal education, media, and profession) (Shackleton et al. 2019b). Some of the strong individual beliefs about IAS involve the views on the abundance of species, effect on the environment, human health, and the economy (Shackleton et al. 2019b). Beliefs in turn do have a significant influence on public's attitudes towards management of IAS (Fischer et al. 2014). Understanding local knowledge can be helpful in gauging public perception and attitudes toward IAS providing a basis for development of shared management strategies through equitable participation in decision-making (Novoa et al. 2018). In addition, indigenous knowledge can also contribute to the enhancement of the state of knowledge on IAS management which has been historically dominated by Western knowledge systems (Nonkes et al. 2023). Despite the growing attention to the social dimension of biological invasions, studies on knowledge and perception have focused more on invasive plants than invasive animals and predominantly in terrestrial systems (Kapitza et al. 2019).

Invasive crustaceans, specifically freshwater crayfish are one of the animal groups whose social dimension remains largely unexplored (Haubrock et al. 2021, Kouba et al. 2022). Management of invasive crayfish is likely to cause conflict of interest as they present both benefits and negative impacts in their invaded range (Lodge et al. 2012; Madzivanzira et al. 2020). In the Barotse floodplain crayfish invasion context, studies on *C. quadricarinatus* to date have focused on quantifying economic cost (Madzivanzira et al. 2022; Chapter 5), with other social dimensions largely overlooked. Although cost determination is important, the social aspect of *C. quadricarinatus* invasion needs to be considered to inform management interventions. A better understanding of the social dimensions of the invasion will provide valuable insights into the development of shared management goals between natural resource managers and the local community. This is particularly important given the current absence of a comprehensive national strategy concerning the management of *C. quadricarinatus*. Although the Environmental Management Act of 2011 prohibits the introduction of IAS in the Zambia, there is lack of biosecurity-specific guidelines to prevent their spread. The Fisheries Act of 2011 on the other hand only focuses on the regulation of non-native fish species while other invasive species taxa including *C. quadricarinatus* are excluded. Additionally, there is a general lack of guidelines for implementing these regulations.

This study provides the first assessment of fishers' awareness, knowledge and perception regarding *C. quadricarinatus* invasions on the Barotse floodplain. Fishers have been identified as key stakeholders in the management of IAS in freshwater systems (Novoa et al. 2018). The main objectives are to; 1) assess the level of awareness and knowledge regarding *C. quadricarinatus*, 2) examine perceived benefits and threats of *C. quadricarinatus*, 3) assess management awareness, practice, and support with regards to *C. quadricarinatus*, 4) analyse the relationship between knowledge and perception variables/items and examine the effect of socio-demographic factors on them.

6.2 Methods

6.2.1 Study area

The study was conducted around the central section (Mongu stratum) of the Barotse floodplain, located on the upper Zambezi River system, which is the invasion core for *C. quadricarinatus* (Fig. 6.1). Local people on the floodplain utilise a mixed livelihood strategy consisting of crop farming, livestock keeping, fishing, and exploitation of other natural resources (IUCN, 2003). The floodplain fishery is an important economic activity providing food, income and employment to ~ 70, 000 people (CGIAR, 2013). The Barotse floodplain fishery is managed as a common property resource through a dual governance system consisting of the Barotse Royal

Establishment and the Zambian government through the Department of Fisheries (Madzudzo et al. 2013; Turpie 2008). (See Chapter 2 for the detailed description of the study area).

Cherax quadricarinatus were introduced around the central section of the Barotse floodplain in 2012 (Douthwaite et al. 2018) following their escape from an informal aquaculture pond by road construction workers (Madzivanzira et al. 2020). Since their introduction, the crayfish population has become established (Madzivanzira et al. 2021: Chapter 4) with higher relative abundance at the invasion core (Mongu stratum) compared to the invasion edge (upstream in Lukulu stratum and downstream in Senanga stratum) (Chapter 4). About 23% of the fishers on the floodplain encounter *C. quadricarinatus* as by-catch species in their fishing gear, with the encounters being higher at invasion core (52%) (Chapter 5).

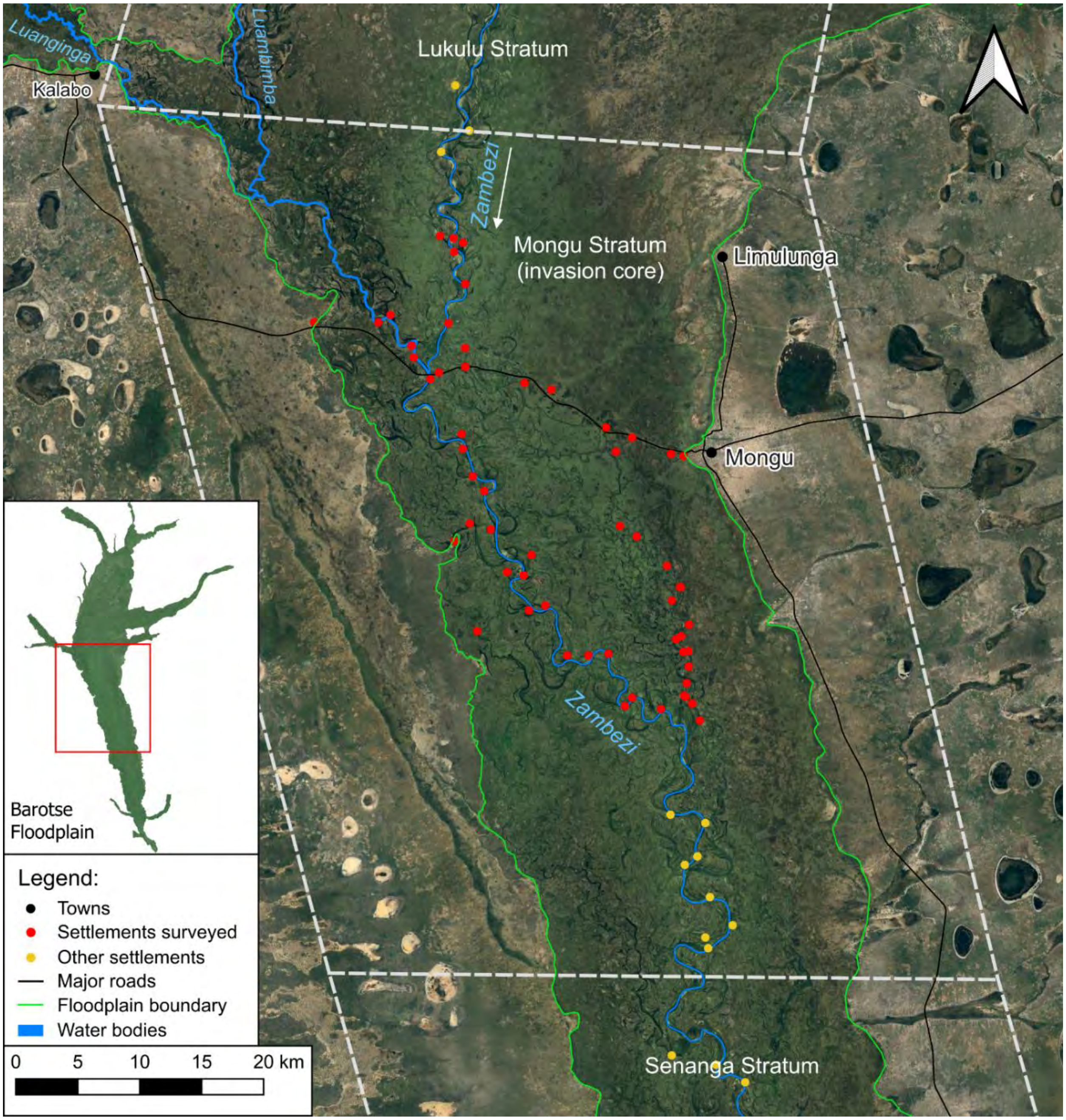

Figure 6.1 The central region (invasion core/Mongu stratum) of the Barotse floodplain showing fishing settlements where the respondents were surveyed.

6.2.2 Questionnaire development

The questionnaire was semi-structured comprising open-ended, close-ended, and five points Likert scale type questions relating to eight main sections as follows: A) socio-demographics characteristics, B) awareness and knowledge, C) perception (benefits, threats and management), D) effect on gear operation, E) change in crayfish by-catch and fish catch, F) effect on fish catch, G) other impacts and, H) uses of crayfish (Appendix 6.1). The questionnaire was reviewed and granted ethical clearance by the Rhodes University Human Ethics Committee (Reference no: 2020-1473-4635). Prior to data collection, the questionnaire was tested in a pilot structured survey with a total of 30 interviews completed and feedback used to enhance the instrument's validity and reliability.

6.2.3 Data collection

Data were collected by three enumerators through in-person interviews conducted during a 30-day survey between November and December 2020. The questionnaire was administered to fishers in fishing villages/camps around the central region (invasion core/ Mongu stratum) of the Barotse floodplain (Fig. 6.1). The upstream and downstream regions were not included in the survey as the crayfish population numbers were very low in these areas (Chapter 4). The questionnaire was administered electronically via the ODK Collect App (version 1.30.1) installed on Lenovo tablets. The respondent was screened before the beginning of the interview to ensure that the questionnaire was not administered more than once to the same individual. The respondent was also informed about the purpose of the study and that the survey was anonymous. The interviews were conducted in local language (Silozi) to limit misunderstanding questions. The duration of each interview was approximately 40 minutes. Completed questionnaires were then uploaded to the Worldwide Fund for Nature (WWF-Zambia)'s Upper Zambezi Programme database.

6.3 Data analysis

The focus of this study was awareness, knowledge and perception of *C. quadricarinatus* therefore only three sections (part of section A and the whole of sections B and C) of the questionnaire were used here. Descriptive statistics were used to analyses questions/items relating to, socio-demographic characteristics, awareness, knowledge and perception (i.e., benefits, threats and management). To explore relationships, Likert items were grouped together to form a Likert scale (i.e., perceived benefits, perceived threats to the fishery, perceived threat to the environment, management awareness, management practices, and management support). Internal consistency and reliability of the Likert scales were assessed using Cronbach's alpha and values above 0.7 were considered reliable (Saba et al. 2021). Likert items under knowledge level and information level variables did not satisfy the grouping criteria (i.e., minimum of 3 Likert items) and hence were treated as ordinal scale based on one Likert item represented by question 22 and 24 respectively. Spearman's rank correlation was used to identify relationships between variables or constructs. To assess the influence of socio-demographic factors, four variables were considered: gender, age, education level, and residence. Mann-Whitney U-test was used to determine differences for each Likert scale within gender and residence. Differences across age and education level were analysed using Kruskal-Wallis test with a Dunn test post-hoc and *p*-values adjusted for multiple comparisons using Holm-Bonferroni corrections. Analysis was carried out using Microsoft Office Excel MSO 365 (Version 2310 Build 16.0.16924.20054) and Statistical Package for Social Sciences (SPSS) (Version 20; Armonk, NY).

6.4 Results

6.4.1 Socio-demographic characteristics

Overall, a total of 687 respondents were interviewed during the survey. The majority of respondents were male (94.5%), and the majority were between the age of 18 and 45 years (82.2%) (Table 6.1). Low education level was observed among the respondents; about two-thirds of the respondents received no formal education or had primary education (8.6% and 63.0%, respectively) while 24.4% of respondents received secondary education or above (Table 6.1). The majority (94.9%) of respondents were local residents (Table 6.1).

Table 6.1 Socio-demographic characteristics of the respondents on the central Barotse floodplain around Mongu.

Socio-demographic variables		Percentage
Gender	Male	94.47
	Female	5.53
Age (years)	< 18	1.16
	18 – 45	82.24
	> 45	16.59
Education level	None	8.59
	Primary	63.03
	Secondary	28.09
	Tertiary	0.29
Residence classification	Local	94.91
	Migrant	5.09

6.4.2 Awareness and knowledge

All the respondents reported that they were aware of *C. quadricarinatus* presence on the Barotse floodplain. Respondents observed crayfish in different types of floodplain habitats with the highest observation occurring in lagoons, followed by rivers, canals, and flooded grassland (82.5%, 75.7%, 44.3% and 2.9% respectively; Figure 6.2). When asked specifically about their first sighting of *C. quadricarinatus*, 78.8% of the respondents reported that they first saw the crayfish 3 to 5 years ago, 8.9% more than 6 years ago, and 12.4% less than 3 years ago.

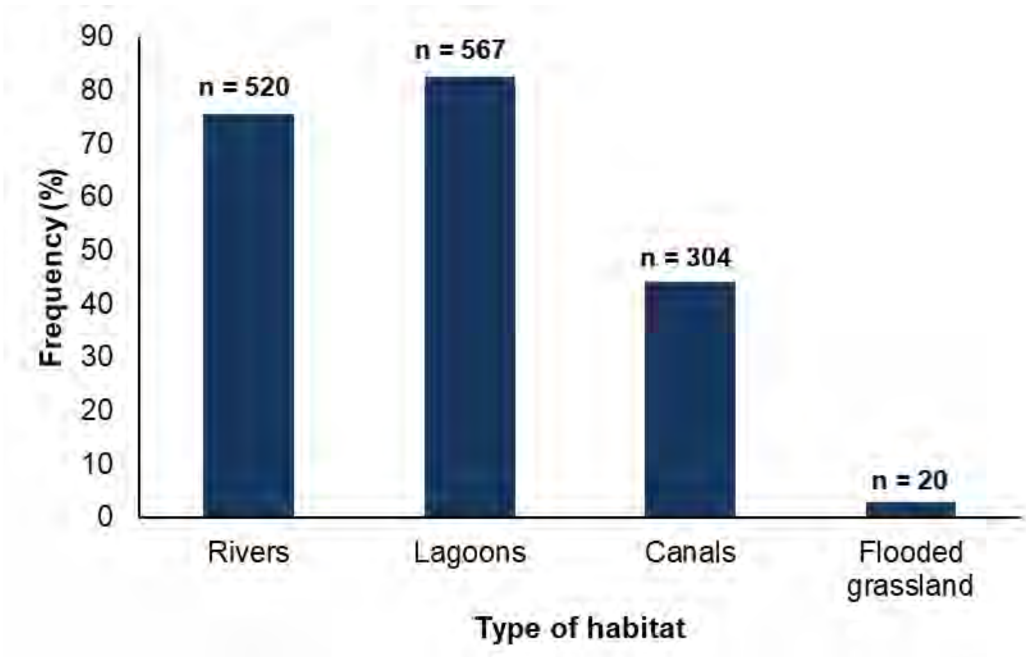

Figure 6.2 Percentage frequency of respondents sighting *C. quadricarinatus* in different types of aquatic habitats on the central Barotse floodplain.

Despite all respondents being aware of the presence of *C. quadricarinatus*, none of them reported knowing the common or scientific name of the crayfish introduced on the floodplain. The majority of respondents (97.2%) believed *C. quadricarinatus* was a non-native species while the remaining 2.8% thought it was a native species to the area. Of those who said the crayfish was a non-native species, 85.6% believed it originated from China while 14.4% did not know its origin. When asked how *C. quadricarinatus* was introduced, 59.0% of the respondents correctly said that crayfish escaped from the breeding pond on the floodplain. Of the remaining 41% who were incorrect, 12.7% believed the crayfish escaped from a nearby farm, 28.8% believed it was deliberately put in water bodies and 58.5% did not know. With regards to being knowledgeable about *C. quadricarinatus* as non-native 88.4% reported they did not know anything and 11.6% reporting knowing little. Most respondents (98.8%) reported they were not knowledgeable about non-native in general (Table 6.2). Most respondents also felt they were not well informed about *C. quadricarinatus* with > 98% indicating that they had not been taught or read anything relating to the crayfish (Table 6.2).

Table 6.2 Respondents' reported knowledge and information level relating to *C. quadricarinatus* on the Barotse floodplain. Median score represents numerical coding of the five-point Likert: nothing (1), little (2), some (3), much (4), extensive (5).

Variable and survey questions	Median score	Five-point Likert scale (%)				
		Nothing	Little	Some	Much	Extensive
Knowledge level						
• How much do know about the redclaw crayfish as a non-native species?	1	88.36	11.64	0.00	0.00	0.00
• How much do you know about non-native species in general?	1	98.84	0.73	0.29	0.15	0.00
Information level						
• How much have you been taught about the redclaw crayfish?	1	98.84	1.16	0.00	0.00	0.00
• How much have you read about the redclaw crayfish?	1	99.13	0.87	0.00	0.00	0.00

6.4.3 Perceived benefits and threats

Overall, the majority (82.5%) of the respondents perceived *C. quadricarinatus* to be non-beneficial. About 95% of the respondents disagreed or strongly disagreed that *C. quadricarinatus* was a source of food and 88.7% disagreed or strongly disagreed with the crayfish being a source of income (Table 6.3). When asked if *C. quadricarinatus* was a source of food for domesticated animals there was more variation between respondents as 63.7% disagreed or strongly disagreed while 30.0% agreed or strongly agreed (Table 6.3). Generally, the majority of the respondents perceived *C. quadricarinatus* to be a threat to the fishery (95.3%). A total of 97.4% of the respondents agreed or strongly agreed that *C. quadricarinatus* caused damage or spoilage to the fish catch (Table 6.3). Furthermore, 96.9% of the respondents agreed or strongly agreed that *C. quadricarinatus* caused damage to fishing gears and 91.7% of the respondents indicated that *C.*

quadricarinatus was a nuisance costing them fishing time (Table 6.3). However, in relation to *C. quadricarinatus* posing a threat to the environment, 64.2% of the respondents felt it was not a threat and 29.6% were unsure. About 70.4% of respondents disagreed or strongly disagreed that *C. quadricarinatus* affected the water in floodplain waterbodies (Table 6.3). Around two-thirds of respondents disagreed or strongly disagreed that *C. quadricarinatus* affected aquatic animals (61.6%) or aquatic plants (64.2%) (Table 6.3).

Table 6.3 Respondents' level of agreement to statements relating to perceived benefits and threats of *C. quadricarinatus* on the Barotse floodplain. Median score represents numerical coding of the five-point Likert: strongly disagree (1), disagree (2), not sure (3), agree (4), and strongly agree (5).

Variable constructs and survey statements (questions)	Median score	Five-point Likert scale (%)				
		Strongly disagree	Disagree	Not sure	Agree	Strongly agree
Perceived benefits						
• Crayfish are a source of food to people.	1	90.83	4.22	2.91	1.02	1.02
• Crayfish are a source of income.	1	84.43	4.22	5.53	3.35	2.47
• Domesticated animals (i.e., pigs, chicken) benefit by eating crayfish.	1	56.33	7.42	6.26	29.11	0.87
Perceived threat to the fishery						
• Crayfish spoil fish catch.	5	1.16	0.15	1.31	4.22	93.16
• Crayfish damage fishing gears.	5	1.46	0.73	0.87	5.82	91.12
• Crayfish delay fishing activities.	5	2.91	3.78	1.60	28.53	63.17
Perceived threat to the environment						
• Crayfish negatively affects the water in floodplain waterbodies.	1	51.82	18.63	25.91	2.91	0.73
• Crayfish negatively affects aquatic animals.	2	49.34	12.23	28.38	6.70	3.35
• Crayfish negatively affects aquatic plants.	2	47.45	13.25	34.35	3.35	1.60

6.4.4 Management awareness, practices, and support

Most of the respondents were not aware of any management intervention relating to the *C. quadricarinatus* invasion of the floodplain (86.8%). Most of the respondents (85.7%) disagreed or strongly disagreed that information on management of IAS in freshwater bodies was available

(Table 6.4). When asked if they were aware that the law regulates the use, storage, transportation and disposal of *C. quadricarinatus*, 92.4% of the respondents disagreed or strongly disagreed (Table 6.4). In addition, 82.1% disagreed or strongly disagreed that the government disseminated information on the control of *C. quadricarinatus* (Table 6.4). With regards to management practices, the majority (93.6%) of the respondents did not adhere to any IAS laws or regulations. About 93.1% of the respondents disagreed or strongly disagreed that they handle and transport *C. quadricarinatus* according to the regulation (Table 6.4). When the respondents were asked if they disposed of *C. quadricarinatus* according to the regulation, 94.1% disagreed or strongly disagreed (Table 6.4). The majority (93.7%) of the respondents also disagreed or strongly disagreed that they advised others to handle, transport, and dispose of *C. quadricarinatus* according to the regulation (Table 6.4). Despite lack of reports on management undertaken by respondents, overall, most of the respondents expressed support for management *C. quadricarinatus* on the floodplain (97.8%). Most of the respondents (97.4%) agreed or strongly agreed that there was a need to manage the population of *C. quadricarinatus* in the water bodies (Table 6.4). Almost all respondents (98.5%) agreed or strongly agreed that they would like to learn how to control the population of *C. quadricarinatus* (Table 6.4). Similarly, 97.4% agreed or strongly agreed to participate in interventions aimed at controlling the population of *C. quadricarinatus* (Table 6.4).

Table 6.4 Respondents' level of agreement to statements relating to management awareness, practice and support regarding *C. quadricarinatus* invasion on the Barotse floodplain. Median score represents numerical coding of the five-point Likert: strongly disagree (1), disagree (2), not sure (3), agree (4), and strongly agree (5).

Variable constructs and survey statements (questions)	Median score	Five-point Likert scale (%)				
		Strongly disagree	Disagree	Not sure	Agree	Strongly agree
Management awareness						
• There is available information regarding management IAS in freshwater bodies.	1	76.13	9.61	12.52	0.87	0.87
• The law regulates the use, storage, transportation and disposal of crayfish.	1	81.95	10.48	6.99	0.29	0.29
• Government disseminates information regarding control of crayfish.	1	72.93	9.17	16.45	0.87	0.58
Management practices						
• You handle and transport crayfish according to the regulation.	1	91.99	6.26	1.16	0.29	0.29
• You dispose of crayfish according to the regulation.	1	93.01	5.68	0.87	0.29	0.15
• You advise others to handle, transport, and dispose of crayfish according to the regulation.	1	92.58	5.97	0.73	0.44	0.29
Management support						
• There is a need to control the population of crayfish in the water bodies.	5	1.02	0.29	1.31	4.08	93.30
• You are willing to learn how to control the population of crayfish.	5	0.87	0.44	0.15	4.66	93.89
• You are willing to actively participate in controlling the population of crayfish.	5	1.16	1.16	0.29	5.53	91.85

6.4.5 *Correlational comparisons*

The relationships between knowledge and perception variables were generally weak however some significant correlations were observed (Table 6.5). The respondents' knowledge of *C. quadricarinatus* invasion was significantly positively correlated with information level ($p < 0.05$) and management practices ($p < 0.01$) but negatively correlated with perceived threat to the fishery ($p < 0.05$). The respondents' level of information regarding *C. quadricarinatus* was significantly positively correlated with management awareness ($p < 0.01$). Respondents' perceived benefit of *C. quadricarinatus* was significantly positively correlated with perceived threat to the environment ($p < 0.01$) and management awareness ($p < 0.01$) and significantly negatively correlated with perceived threat to the fishery ($p < 0.01$). The perceived threat to the fishery significantly negatively correlated with the perceived threat to the environment ($p < 0.01$), management practices ($p < 0.01$) and significantly positively correlated with support for management ($p < 0.01$). The perceived threat to the environment was significantly positively correlated with management awareness ($p < 0.01$), and management practice ($p < 0.01$) and significantly inversely correlated with management support ($p < 0.01$). Respondent's management awareness significantly positively correlated with management practices ($p < 0.01$) and significantly negatively management support ($p < 0.01$) and whilst management practices significantly inversely correlated with management support ($p < 0.01$).

Table 6.5 Spearman rank correlation matrix showing strength of relationship between respondent's knowledge and perception variables regarding *C. quadricarinatus* on the Barotse floodplain. * = statistical significant at $p < 0.05$; ** = statistical significant at $p < 0.01$.

Variables	Knowledge level	Information level	Perceived benefits	Perceived threat to fishery	Perceived threat to the environment	Management awareness	Management practices	Management support
Knowledge level	1							
Information level	0.10*	1						
Perceived benefits	0.05	-0.03	1					
Perceived threat to the fishery	-0.09*	0.01	-0.24**	1				
Perceived threat to the environment	0.07	0.06	0.23**	-0.16**	1			
Management awareness	0.05	0.12**	0.17**	0.02	0.51**	1		
Management practices	0.12**	0.06	0.07	-0.17**	0.10**	0.14**	1	
Management support	0.01	0.02	-0.05	0.24**	-0.17**	-0.08*	-0.15**	1

6.4.6 Socio-demographic effect

A summary of the comparison of respondents' knowledge, perception, and attitudes regarding *C. quadricarinatus* based on socio-demographic variables (gender, age, education level and residence classification) is presented in Table 6.6. Gender has no significant influence on the item or variable constructs. (Table 6.6). Age had a significant effect on respondents' perceived threat to the environment, management practices, and management support (Table 6.6). Respondents aged between 18 and 45 showed a higher level of disagreement regarding perceived threat to the environment, management awareness, and management practices than respondents aged 46 and above (all $p < 0.05$). Education level significantly influenced respondents' knowledge, perceived threat to the environment, management awareness, and management support (Table 6.6). Respondents who received secondary education were less disagreeable to knowing about *C. quadricarinatus* than those with primary education ($p < 0.05$). Respondents with secondary education also exhibited a lower level of disagreement with regard to perceived threat of *C. quadricarinatus* to the environment than those with primary education and those without formal education (both $p < 0.05$). With regards to management awareness, respondents who received secondary education had a lower level of disagreement than those who received primary education and those who were not educated (both $p < 0.05$) while those with primary education had a lower level of disagreement than the uneducated one ($p < 0.05$). In addition, respondents with secondary education showed higher levels of agreement with regard to management support ($p < 0.05$). Residence classification had a significant influence on respondents' perceived benefits, perceived threat to the fishery, and management support (Table 6.6). Local fishers had higher levels of disagreement about perceived benefits than migrant fishers. But exhibited higher levels of agreement with regard to perceived threat to the fishery and management support (all $p < 0.05$)

Table 6.6 Effect of socio-demographic variables on respondents' knowledge, perception, and attitudes towards *C. quadricarinatus* on the Barotse floodplain.

Variables	Gender	Age	Education level	Residence classification
Knowledge level	0.096	0.902	$p < 0.05$	0.586
Information_level	0.419	0.735	0.125	0.836
Perceived benefits	0.239	0.056	0.572	$p < 0.05$
Perceived threat to the fishery	0.994	0.408	0.160	$p < 0.05$
Perceived threat to the environment	0.556	$p < 0.05$	0.052	0.091
Management awareness	0.434	0.168	$p < 0.05$	$p < 0.05$
Management practices	0.308	$p < 0.05$	$p < 0.05$	0.411
Management support	0.050	$p < 0.05$	$p < 0.01$	0.282

6.5 Discussion

Consideration of the public's perception can enhance the acceptance of IAS management strategies resulting in their successful implementation (Crowley et al. 2017; Cordeiro et al. 2020; Shackleton et al. 2019a). This study provides valuable insight into local fishers' knowledge and perception regarding *C. quadricarinatus* invasion on the Barotse floodplain. Results revealed that although respondents were aware of *C. quadricarinatus* presence, they were not knowledgeable about the crayfish. Respondents perceived *C. quadricarinatus* as unbeneficial implying that effort to manage the crayfish is unlikely to face opposition from the community. Respondents' support for management of *C. quadricarinatus* was driven by the perceived of *C. quadricarinatus* threat to the fishery. Despite the existing support, successful management of *C. quadricarinatus* on the Barotse floodplain will require increasing local people's knowledge of crayfish through education, training and raising awareness activities.

6.5.1 Awareness and knowledge

All the respondents were aware of *C. quadricarinatus* presence on the Barotse floodplain with the crayfish reportedly observed in various types of waterbodies. The high level of awareness among respondents is not surprising given the high encounter rate of *C. quadricarinatus* as a by-catch species among fishers in and around the central Barotse floodplain (Chapter 5). These findings are similar to other studies that have reported great awareness of IAS presence among local people especially in rural areas (Shackleton et al. 2015; Yapi et al. 2023) as they get to have first-hand experience of invasions (Shackleton et al. 2015). Most first sightings of *C. quadricarinatus* by fishers have occurred less than 5 years ago which indicates the spreading and growing crayfish population on the floodplain (Chapter 4).

Although most of the respondents knew that *C. quadricarinatus* is a non-native species they were not knowledgeable on the species, its introduction or indeed its origin. The lack of knowledge among people regarding IAS in their own community is not unusual; for example, in South Africa local people have been found to have poor knowledge about IAS in their surroundings (Shackleton and Shackleton 2016; Jubase et al. 2021). When the public is not knowledgeable, they care less about IAS (Juabse et al. 2021) which perhaps explains why the introduction of *C. quadricarinatus* on the Barotse floodplain did not face resistance from the local people. This lack of concern can also lead to risky behaviours which facilitate further spread of IAS (Gates et al. 2009). As such, increasing the public's knowledges about IAS can help to prevent their introduction and spread as well as facilitate their control through active participation in management action and support for management strategies (Ford-Thompson et al. 2015; Nanayakkara et al. 2018)

The low knowledge level observed in this study is associated with the lack of available information about *C. quadricarinatus*. The information deficit is probably due one or a combination of the following reasons: a lack of public awareness-raising activities, poor dissemination of information, funding limitations, lack of information on the target species or simply a lack of interest in the information disseminated (Jubase et al. 2021; Shackleton and Shackleton 2016). Public knowledge or understanding of IAS can therefore be increased through active public engagement activities (i.e., workshops, media, outreach activities, training programs and education activities) aimed at educating people about crayfish impacts and control methods (Ford-Thompson et al. 2012; Novoa et al 2017). Raising public awareness using tools such as brochures, field guides, websites, publication of science articles etc., can also be an effective approach especially when funds are limited (Marchante et al. 2010)

6.5.2 Perceived benefits and threats

The majority of the respondents perceived *C. quadricarinatus* to be of no economic value as they reported not regarding the crayfish as a source of food and income. However, few respondents reported that *C. quadricarinatus* is a source of food for domesticated animals such as pigs and chickens. Contrary to these results, other studies have shown some IAS can be very beneficial to the public, offering significant provisioning (i.e., food and income) and cultural services (i.e., aesthetics) (Potgieter et al. 2019; Wood et al. 2021; Kumar et al. 2023). In rural areas where livelihood options are limited, IAS provisioning services can quickly be realised by communities as an alternative source of livelihood (Yapi et al. 2023) positively influencing their perception (Potgieter et al. 2019). For example, in older invasions *C. quadricarinatus* such as that of the Kafue River and Lake Kariba, local fishers have begun to derive income by harvesting and selling the crayfish (Eilitta et al. 2023). Since the invasion of *C. quadricarinatus* on the Barotse floodplain is relatively recent, there is a chance the same may happen over time but whether that would result in a change of most fishers' perception regarding crayfish benefits remains to be seen.

Most of the respondents perceived *C. quadricarinatus* as a threat to the fishery corroborating findings from the other study (Chapter 5) that fishers at the invasion core are incurring significant economic costs due crayfish through damage to fish catch and fishing gear as well as costs them valuable fishing time. Negative perceptions of IAS arising from economic costs have also been reported by other studies (Ngorima and Shackleton 2019; Yapi et al. 2023). However, most the respondents reported that *C. quadricarinatus* did not pose a threat to the environment, as they did not agree that the crayfish species adversely impacts water, aquatic flora and fauna. On the contrary, other studies have reported negative perceptions towards IAS due to their environmental impacts except this was associated with communities that are well-informed and knowledgeable about environmental issues (Cordeiro et al. 2020; Saba et al. 2021). The lack of knowledge about *C. quadricarinatus* in this study perhaps explains why respondents were less concerned about the crayfish's potential threat to the environment. Besides, the ecological impacts of *C. quadricarinatus* has yet to be comprehensively quantified with empirical evidence (Haubrock et al. 2021). In addition, unlike provisioning services ecosystem regulating or supporting services are difficult to quantify and attach monetary value hence IAS impacts on such services are unlikely to be directly felt to cause more negative perceptions (Potgieter et al. 2019).

6.5.3 Management awareness, practices and support

Most of the respondents were unaware of management information relating to the control and biosecurity of *C. quadricarinatus* on the Barotse floodplain. This lack of management awareness was linked to the lack of information about *C. quadricarinatus* reflecting a much broader information deficit. Limited awareness may negatively affect management implementation as the public engage less in IAS control and biosecurity activities (Höbart et al. 2020; Jubase et al. 2021). The lack of management awareness is probably the reason why most respondents on the Barotse floodplain did not follow any management practices with regard to *C. quadricarinatus* invasion. These findings are in line with a study conducted in South Africa that found that not only were lay people uninformed about the nature of IAS they were also unaware of IAS policy and regulation which in turn hindered the implementation of management practises (Jubase et al. 2021). The absence of clear guidelines regarding the management of *C. quadricarinatus* is of great concern and may also be contributing to the lack of management practices among respondents. Studies have shown that when IAS management guidelines are put in place, they can encourage management practices among members of the public (Shackleton et al. 2015; 2017). However, this is not always the case for IAS that presents both benefits and negative impact due to conflict of interest (Woodford et al. 2016; Zengeya et al. 2017)

Despite the lack of management awareness and practice, most of the respondents were in support of management measures to control *C. quadricarinatus* and prevent the further spread on the floodplain. The support for management was primarily associated with perceived threats to fishery-based livelihoods. These results are consistent with studies that reported support for the management of IAS due to increased invasion costs and negative impacts on people's livelihoods (Shackleton et al. 2015; 2017). Other studies, however, have attributed public support for the management of IAS to the perceived harmful impacts on the environment in general (Cordeiro et al. 2020; Wood et al. 2021). Although respondents in this study are already supportive of IAS management, the support could be further enhanced by raising awareness and increasing knowledge about *C. quadricarinatus* (Novoa et al. 2017). The absence of conflict of interest indicates that an attempt to manage *C. quadricarinatus* is likely to face little resistance from the local community. However, for management to be successful more explicit control and biosecurity guidelines will need to be put in place to complement the two legislations (i.e., Environmental Management Act of 2011 and Fisheries Act of 2011). In addition, the low capacity to enforce the law by the Department of Fisheries which seems to be a recurring challenge in the fishery (Tweddle et al. 2015; Chapter 2) will need to be addressed.

6.5.4 Socio-demographic effects

Age had a notable effect on respondents' perception with individuals aged between 18 and 45 being more unaware of management information and lacking management practices relating to *C. quadricarinatus*. This perhaps suggests that older fishers (> 45 years) may have been exposed to impacts of other IAS and therefore be more concerned about IAS and positive for management. These results align with previous studies that found that increase in age was associated with higher levels of IAS awareness (Nanayakkara et al. 2023) and support for management (Bremner and Park 2007). The positive effect of age on environmental awareness has been attributed to cumulative exposure to environmental information (Otto and Kaiser 2014). However, given the lack of information on *C. quadricarinatus* on the Barotse floodplain, it is not clear what other IAS is driving the influence of age.

Results showed that secondary education had a more positive effect on respondents' knowledge and perceived environmental threat relating to *C. quadricarinatus* than primary education. This is consistent with research that found that more educated individuals were more environmentally aware and hence more likely to perceive the negative impacts of IAS (Potgieter et al. 2019). Furthermore, secondary educated individuals in this study were less uninformed about management and more supportive of the management of *C. quadricarinatus* than their primary educated counterparts. Similarly, other studies have found that more educated individuals to are more supportive of the management of IAS (Walizek et al. 2017; Saba et al. 2020). Given the low level of education the impact of *C. quadricarinatus* is likely to be higher due to lack of knowledge. Therefore, as a long-term management measure, improving the education of resident communities will be key in reducing the threats posed by *C. quadricarinatus* on the Barotse floodplain and other RAMSAR wetlands.

Resident classification significantly influenced perception, with local fishers expressing a higher perceived threat to the fishery and greater support for the management of *C. quadricarinatus* than migrant fishers. This is expected as the local fishers are likely to be more exposed to the damage caused by *C. quadricarinatus* (Chapter 5). Similarly, a study conducted in South African also found that the impact of IAS on livelihood were more obvious to rural residents than urban residents (Shackleton and Shackleton 2016). Another study by Zeng et al. (2021) also found that people's perceived threats of IAS may differ according to locality. The influence of residence underscores the importance of considering the perspectives of indigenous people in IAS management, a factor often overlooked.

In conclusion, this study shows that fishers on the Barotse floodplain were aware of the presence but lack knowledge of *C. quadricarinatus*. The limited knowledge is likely due to the lack of available information relating to *C. quadricarinatus*. Fishers perceived *C. quadricarinatus* to be unbeneficial and were more concerned about the threat it posed to the fishery than the environment. Despite fishers' lack of management awareness and practices, they were in support of the management of *C. quadricarinatus* due to its negative impact on fishery-based livelihood. Furthermore, the knowledge and perception of fishers were influenced by age, education, and resident status. Although the high level of support for the management of *C. quadricarinatus* on the Barotse floodplain is reassuring, successful management will require collaboration between public and other stakeholders (i.e., local authorities, researchers and NGO etc.) in co-designing management interventions. The interventions should be aimed increasing public knowledge of IAS through engagement activities such workshops, media, education and outreach activities, and training programs. The focus of these engagements should be what crayfish are, where they are from, what their impacts are, control and biosecurity measures as well as reporting of illegal behaviour (Novoa et al. 2017). Targeted awareness-raising initiatives using printed documents such as brochures and field guides should also be utilised (Marchante et al. 2010). In addition, crayfish-specific management guidelines will need to be formulated whilst strengthening the enforcement of environmental and fisheries laws and regulations. This study highlights the importance of integrating social dimensions into planning and management of IAS especially at the early stage of an invasion as it builds trusts and reduces conflict of interest.

CHAPTER 7

SYNTHESIS AND CONCLUSION

Cherax quadricarinatus, the second most cultured and harvested crayfish species worldwide, has been translocated and established in freshwater ecosystems globally (Haubrock et al. 2021a). Populations of *C. quadricarinatus* have established in South Africa, Eswatini, Zimbabwe and Zambia (Madzivanzira et al. 2020) as a result of escapes from aquaculture facilities, pet trade and unauthorized releases by recreational fishers (Lodge et al. 2012; Madzivanzira et al. 2020). Given the lack of indigenous freshwater crayfish on the mainland Africa, crayfish invasions may be particularly problematic on continent given limited co-evolved biotic resistance potential (Madzivanzira et al. 2020). Given the prevalence of *C. quadricarinatus* on the Barotse floodplain, their role in contributing to shifts in ecological and socioeconomic fisheries dynamics required assessment. In this thesis, extensive field-based surveys provide a better understanding of the current status of the Barotse floodplain fishery and implication of the introduced *C. quadricarinatus* on the fishery and communities reliant thereon. The findings in this thesis highlights the importance of fisheries assessment and taking a holistic approach (i.e., incorporating ecological, economic and social dimensions) to the understanding of biological invasion in ensuring sustainable fisheries and conservation of biodiversity.

The assessment of the Barotse floodplain fishery revealed multi-gear multi-species fishery. The fishery had an average catch rates of 5.83 kg per fisher per day and estimated annual harvest of 3123 tonnes per annum. The average catch rate was lower than previously estimated which partly explains the observed decline in annual fish yield when compared to historic yields (Chapter 3). Despite the decline, the high fishing effort and participation indicates fishing is a primary activity and serves as a backstop during harsh economic times. Results also showed that a wide range of fish species were harvested but the species composition reflected a shift in species dominance from previous large cichlids (Peel et al. 2014) to smaller prolific adult fishes and juveniles of large cichlids (Chapter 3). The presence of a non-native fish species *O. niloticus* in the catch also represents the first time the species has been officially reported on the Barotse floodplain (Chapter 3). Its occurrence in the fishery is of ecological concern due its ability to hybridise with native *Oreochromis* spp. (Deines et al. 2014). Size structure analysis revealed that the majority of large fish species were being harvested before they reach maturity signifying overfishing in the fishery. The overfishing is likely responsible for the decline in large cichlids species and the change in species composition. The problem of overfishing has been observed in the fishery since the early 2000s now and has been attributed to high fishing pressure plus the use of unstainable fishing methods (Tweddle et al. 2004). A wide range of fishing gear were recorded with gillnets, hook and line, seine net, large hooks on poles and mosquito nets being the most common (Chapter 3). The use of a wide range of fishing gears has been a prominent feature of the fishery for the past forty year (Bell-Cross 1974; Tweddle et al. 2004; Peel et al. 2014) and explains the diverse fish species/group harvested. The result also revealed a predominant use of illegal fishing gears, the small mesh size (< 3 inches) gillnets and monofilament gillnets in both wet and dry season across the floodplain (Chapter 3). The high prevalence of small mesh size can both be symptom of overexploitation and cause of the observed decline in large valuable species. The continuous use of monofilament gillnets and small-meshed gillnets together with the use of active fishing methods such as water beating (*mindili* or *kutumpula)*, mosquito nets, and large seine nets is likely to cause further decline in CPUE and potential collapse of remaining economically valuable species. Of central importance to the larger investigation, results indicated that the invasive *C. quadricarinatus* was the most dominant by-catch species.

Crayfish by-catch was more prevalent in dry season and mostly at the invasion core. The presence of *C. quadricarinatus* represents a significant change in the fishery considering that no crayfish by-catch was recorded in the previous survey conducted in 2014 (DOF 2014).

The prevalence of *C. quadricarinatus* as a by-catch species prompted a more comprehensive assessment to understand the crayfish population distribution and factors driving its range expansion on the Barotse floodplain (Chapter 4). Results from the study revealed that the *C. quadricarinatus* population on the Barotse floodplain had spread up and down-stream from the former invasion edges detected in 2019 by Madzivanzira (2021a). The flood pulse seems to be contributing to the spread of *C. quadricarinatus* as evidenced by their occurrence on the floodplain during high water and also in isolated lagoons or ponds not connected to flowing water channels. The study also showed that *C. quadricarinatus* exhibited higher relative abundance at the invasion core (Chapter 4) suggesting a well-established population in and around Mongu compared to fewer dispersers at the edges. The lower abundance of *C. quadricarinatus* observed during wet season across the invasion range could be attributed to the low detection probability as crayfish migrate on to the floodplain and become more dispersed. The spatial and seasonal pattern with regards to crayfish abundance aligns with prevalence of crayfish by-catch among fishers observed in Chapter 3. Increased competition at the core due to higher relative abundance there seems to be driving the dispersal of *C. quadricarinatus* by pushing weaker individuals to edge. The results further revealed that sex ratios were not different between core and edge populations indicating both male and female are dispersers. Effects of environmental filtering on morphology *C. quadricarinatus* were not evident, perhaps due to the high connectivity of fragmented dry season refugia during the flood period. However, there were signals of spatial sorting (e.g., body size, longer claw length and front leg length at the edges) which appear to have strong influence of spread of *C. quadricarinatus* across the floodplain. The finding confirms the high invasive potential of *C. quadricarinatus* and the risk of it invading and establishing in other pristine wetlands in Southern Africa is a matter of great concern.

Determination of economic costs associated with *C. quadricarinatus* invasion provided insights into how the crayfish invasion is likely to impact the livelihood of fishers as the invasion spreads across Barotse floodplain (Chapter 5). Results revealed fishers encountered *C. quadricarinatus* bycatch in various fishing gears, with the highest encounter rate occurring at the core during the dry season reflecting the high crayfish abundance as observed in Chapter 4. The high encounter rate explains the extensive fish damage exclusively incurred in gillnets at the core. The most impacted species included *Clarias* spp, *H. cuvieri*, *O. andersonii*, *S. macrocephalus, C. rendalli*, and *Serranochromis* spp. The fish damage in gillnets equated to the monetary loss of ~ US$ 21,000 per annum. Although the total monetary loss seems small, the annual cash loss at individual level represents a significant impact to human livelihood. Additionally, there was a higher occurrence of gear damage and time loss among fishers in the invasion core compared to the edges, particularly during the dry season aligning with crayfish abundance patterns. Gillnets were the most frequently damaged fishing gear due to their susceptibility to entanglement. The findings concur with observations of fish and gillnet damage due to crayfish reported by other studies elsewhere (Lowery and Mendes et al. 1977; Weyl et al. 2017; Chakandinakira et al. 2023). The recent shift to more active gears (i.e., seine nets, kutumpula/mindili) driven by decline in catch rates (Tweedle et al. 2015) implies very little passive gears are sets where crayfish can have the largest impact. Therefore, overfishing is potentially mitigating impact of *C. quadricarinatus* on the fishery.

Crayfish are now well established and having significant impact on the Barotse Floodplain fishery. There is therefore the need to consider interventions that mitigate their impacts through limiting spread and invasion elsewhere or formulation of specific control measures. Taking into consideration the public's view regarding IAS can help in the development of accepted management strategies. The findings from Chapter 6, where fishers at the invasion core (central floodplain) were assessed about their knowledge and perception regarding *C. quadricarinatus* revealed that all respondents were aware of the crayfish presence on the Barotse floodplain but most lacked knowledge of it. Results showed that the lack of knowledge was associated with inadequate information about *C. quadricarinatus* which is consistent with the finding of Jubase et al. (2021) and Shackleton and Shackleton (2016) in South Africa. Result also revealed that majority of the respondents perceived *C. quadricarinatus* as unbeneficial and that it posed more of a threat to the floodplain fishery than the environment. The substantial economic cost determined in Chapter 5 re-affirms this perception. The study further revealed that despite respondents' lack of management awareness and practise, they expressed support for management of *C. quadricarinatus* on the floodplain. The support for management seems to be driven by the perception of *C. quadricarinatus* threat to the fishery. Similar findings have also been reported by other studies (Shackleton et al. 2015; 2017). The influence of age, education, and residence of respondents' knowledge and perceptions of *C. quadricarinatus* highlights the importance of incorporating socio-demographic factors when engaging the public regarding IAS.

Conclusion and recommendations

The findings presented in this thesis contribute greatly to understanding the current status of the Barotse floodplain fishery and the impact of the relatively recent *C. quadricarinatus* invasion. This information significantly advances the knowledge on invasive impacts and has consequences for biological invasion elsewhere in Africa. Of great concern is the overexploitation of fishery resources, evidenced by key fishery indicators which included decline in catch rates, reduced mean sizes, shift in species composition and prevalent use of illegal fishing gear. The occurrence of non-native species *O. niloticus* and *C. quadricarinatus* in the fishery threatens biodiversity of Barotse floodplain and raises questions around the integrity of Zambia biosecurity. The rapid spread of *C. quadricarinatus* on the floodplain implies the risk of it is reaching pristine ecosystems such as the Okavango Delta and the Kabompo River is imminent. The economic costs incurred by fishers due *C. quadricarinatus* although mostly confined to invasion core, are significant and will likely escalate as the crayfish spreads and population increases. The lack of knowledge among fishers regarding *C. quadricarinatus* and its management may to lead to further introductions and spread of the crayfish exacerbating it's impacts on human livelihood and freshwater ecosystems. There is need therefore to address the problem of overexploitation and invasive species on the Barotse floodplain to ensure sustainability of the fishery and conservation of biodiversity.

Clearly, the Department of Fisheries faces many challenges given the level of overexploitation and burgeoning cases of non-native species introduction in the fishery. The persistent use of illegal fishing gears despite them being prohibited is indicative of weakness in the enforcement of fisheries law by the Department of Fisheries (DOF). The problem of poor enforcement is a recurring challenge in the fishery and has been attributed to the lack of financial and human resources in the Department of Fisheries (M Maliko pers. obs.). Increased financial investment in the Department of Fisheries would help bolster its enforcement capacity through recruitment and training of additional personnel, procurement of necessary equipment and implementation of robust monitoring and surveillance systems. The other problem that is hindering enforcement in the fishery is the lack of cooperation between the Department of Fisheries and the traditional authority, Barotse Royal Establishment (BRE). The bylaws formulated by traditional leadership to govern fisheries resources contradicts the national fisheries law resulting in reduced adherence to fishery regulation. To address this challenge, there is need to promote co-management to minimise misunderstanding and the encourage local community compliance in the implementation of sustainable fishing methods as well as enforcement of fishing nets and licensing requirements.

The other big challenge facing the Barotse floodplain fishery is the lack of regular monitoring of fisheries resources as evidenced by the fishery going for seven years without any catch assessment being conducted prior to this study (Chapter 3). The inconsistencies in the assessment of fisheries seems to be a common problem for most fisheries in Zambia and is likely linked to be the issue of inadequate funding. Therefore, increased funding is also required for regular monitoring of the fisheries through catch assessment surveys, frame surveys and socio-economic or household-based surveys. Monitoring of the fishery should also include fish biology studies, a component which has been lacking in the fishery. Information on the fish biology of the Barotse floodplain is limited to a few species conducted over three decades ago (Tweddle et al. 2015). Conducting research on fish biology is important to understand how the fish stock is responding to increased fishing pressures and other anthropogenic activities. Improved monitoring will therefore enable better fishery management as decisions will be based on empirical evidence.

With regards to management of *C. quadricarinatus* on the Barotse floodplain, several methods can be utilised. Considering how well-established and how far the population of *C. quadricarinatus* has spread, attempts to eradicate the population are unlikely to succeed. Effective management of invasive crayfish is very difficult to achieve due to the interconnectedness of aquatic systems. Since the high density of *C. quadricarinatus* at the invasion core is driving its range expansion on the Barotse floodplain, methods aimed at suppressing crayfish population at the invasion core could prove helpful to slow down the spread. However, it must be noted that population suppression techniques are more effective in smaller contained dams and reservoirs than larger open systems. Traditional survey methods such as the use of promar traps (see Chapter 4) should continue to be used to monitor the invasion edges both upstream and downstream, especially the pristine areas such as the Okavango Delta and Kabompo River. Modern techniques such as environmental DNA (*e*DNA) can also be incorporated into crayfish monitoring, as they are an effective tool in the early detection of crayfish invasion (Madzivanzira et al. 2020). Monitoring of *C. quadricarinatus* is important to inform environmental managers which areas to prioritise for management.

To mitigate economic cost incurred by fishers due *C. quadricarinatus* on the Barotse floodplain fishery, an adaptive strategy which makes use of misdirection traps can be effective in suppressing the crayfish population and reducing damage to fish catch (Madzivanzira et al. 2023). The other alternative is to encourage more people to harvest *C. quadricarinatus* since the crayfish makes up a significant portion of the fishery's by-catch species (Chapter 3). This may be a viable option as they are already reports of few local fishers harvesting *C. quadricarinatus* for sale to foreign nationals (N Namasiku per. com.), presumably for food. But these crayfish could potentially also be harvested, for example, to supplement protein feed for domesticated and farmed animals. Harvesting of fish has the potential to offset losses incurred by fishers as well as indirectly minimise damages by reducing the population of *C. quadricarinatus* (Chakandinakira et al. 2023). Advocating for people to harvest *C. quadricarinatus* for animal husbandry or sale should, however, be treated with caution because it may generate perverse incentives to expand the crayfish population resulting in further introductions (Quintana et al. 2023). Realisation of benefits may cause the local people to become unsupportive of crayfish management strategies leading to conflicts with the Department of Fisheries and other natural resources management agencies.

Natural resources management agencies should take advantage of fishers' current support for management of *C. quadricarinatus* to work with community to manage the crayfish. There is need to promote citizen science by raising awareness and educating the community about the impacts of aquatic invasive species (both *O. niloticus* and *C. quadricarinatus*) and what to do to prevent further introductions and spread. The local community should be sensitised about what the Zambian fisheries law stipulates regarding introductions of non-native species prior to the enforcement of the law. Furthermore, there is need to find out what the Department of Fisheries is currently doing and what challenges it is facing with regards to management of AIS on the Barotse floodplain. Understanding the challenges faced by Department of Fisheries will be key to the successful management of *C. quadricarinatus* and other AIS on the floodplain.

Once AIS become established it is difficult to eradicate them and any management effort after that usually comes at a huge cost. Therefore, the first line of action against AIS is to prevent their introduction. The ease with which *C. quadricarinatus* in particular was introduced on the Barotse floodplain and indeed several other locations across the country is a symptom of weakness in the enforcement of the Zambian regulations governing AIS. Other than the Environmental Management Act of 2011 and Fisheries Act of 2011, which stipulates the management of non-native species in the Zambia there are no detailed and specific biosecurity guidelines which indicate how each AIS should be managed once introduced in the country. Based on the latest (2020) annual report from the Zambia Environmental Management Agency (ZEMA), guidelines and strategies for the managing IAS in the country were still being formulated (ZEMA 2020). In the absence of clear biosecurity guidelines, it will be difficult to effectively manage AIS on the Barotse floodplain or indeed anywhere else in the country. In addition, the government of Zambia should implement more strict biosecurity measures at all entry points into the country to prevent future introduction of AIS. Regional biosecurity measures aimed at governing shared aquatic systems, such as the SADC Protocol on Fisheries, which restricts the introduction of non-native species into aquatic environments without the consent of all riparian states, should be strengthened (SADC 2001).

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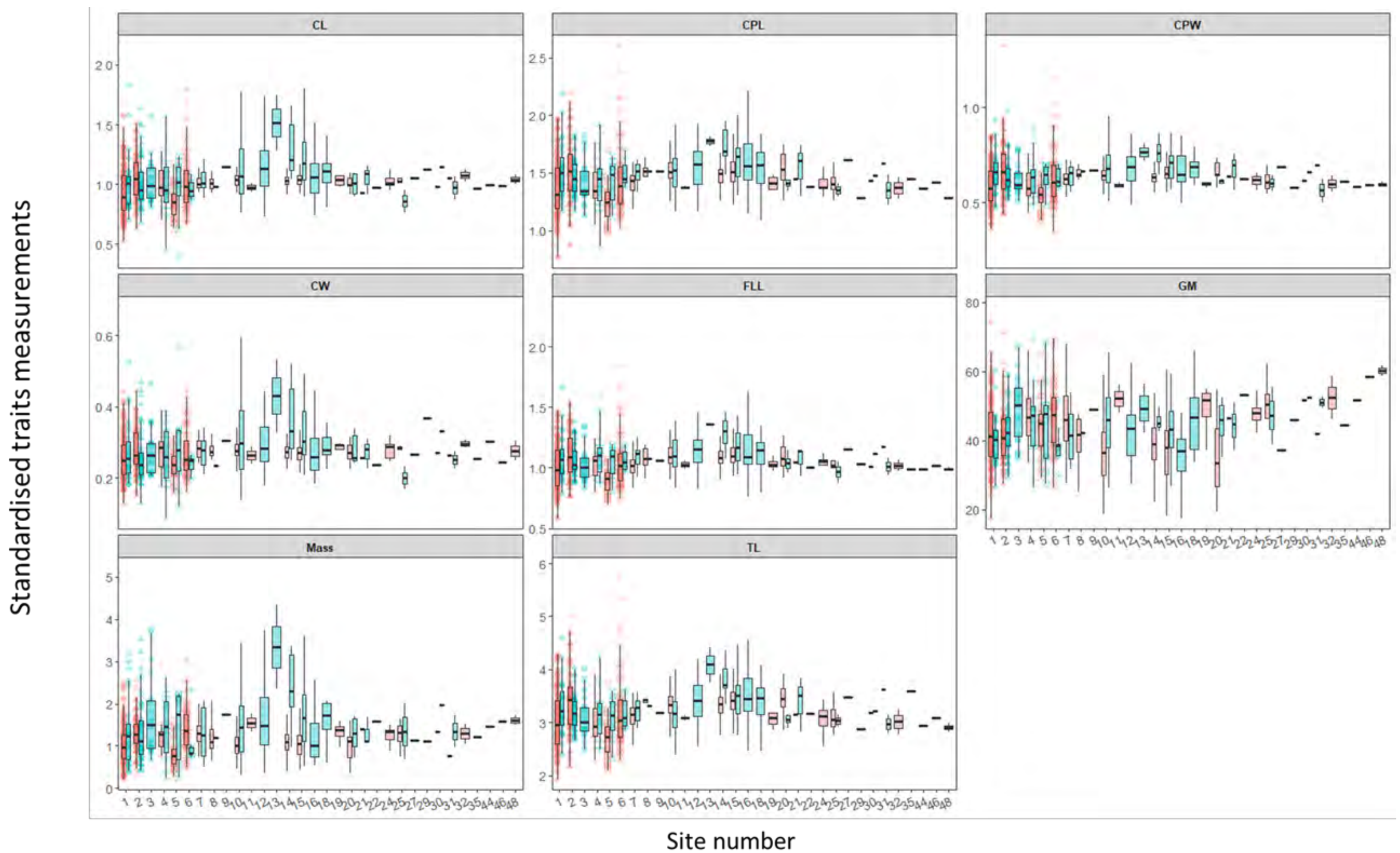
APPENDICES

Appendix 3.1 Creel survey questionnaire used to assess the Barotse floodplain fishery of the Upper Zambezi system.

1. INTERVIEW DETAILS
1.1 Name of interviewer
1.2 Which stratum are you working in? A) Senanga [ ] B) Mongu [ ] C) Lukulu [ ]
1.3 Is the interview being conducted on the river / pool where fishing is being undertaken or in the village after fishing has been completed? A) River or Pool [ ] B) Village [ ]
1.4 What type of habitat are you conducting the interview at? A) River or flowing canal [ ] B) Floodplain pool or still/stagnant water [ ]
2. FISHING HISTORY AND EFFORT
2.1 Did you fish yesterday? A) Yes [ ] B) No [ ]
2.2 Did you fish the day before yesterday? A) Yes [ ] B) No [ ]
2.3 How many days have you fished in the last 7 days?
2.4 How many fishers (total) participated today? Including the fisher
2.5. How much of today's fishing has been completed by the fisher? A) Less than half [ ] B) Half [ ] C) More than Half D) Complete [ ]
3. FISHING VESSEL
3.1 Did you use a boat (vessel) for any type of fishing activity today? A) Yes [ ] B) No [ ]
3.2 Do you own the boat (vessel)? A) Yes [ ] B) No [ ]
3.3 What type of boat (vessel) did you use? A) Dugout- Mukolo [ ] B) Tree Bark [ ] C) Plank-Sisepe [ ] D) Fibre-Banana [ ] Other [ ]
3.4 Does the boat have an outboard motor? A) Yes [ ] B) No [ ]
3.5 What horsepower (size) is the outboard motor?
4. FISHING EQUIPMENT
4.1 Select the type of fishing equipment used today to catch the fish present: A) Gillnet [ ], B) Drift gillnet [ ], C) Seine net [ ], D) Cast net [ ], E) Scoop net [ ], F) Mosquito seine SMALL <5m [ ], G) Hook and line [ ], H) Longline [ ], I) Large hooks on poles [ ], J) Hand spear [ ], K) Reed basket scoop [ ], L) Vertical scoop trap [ ], M) Large mesh reed fish trap [ ], N) Small mesh reed fish trap [ ], P) Small vertical trap [ ], Bottle trap [ ], Q) Fish weir Floodplain [ ]
4.2 What is the seine net made from? A) Silon / Monofilament [ ], B) Cotton / Tanzania / Multifilament (Kwazi) [ ], C) Mixed types [ ], D) Shade cloth [ ], E) Mosquito mesh [ ]
4.2 What is the size of the mesh of gillnets? ½ inch [ ], 1 inch [ ], 1¼ inch [ ], 1½ inch [ ], 1¾ inch [ ], 2 inch [ ], 2¼ inch [ ], 2½ inch [ ], 2¾ inch [ ], 3 inch [ ], 3¼ inch [ ], 3½ inch [ ], 3¾ inch [ ], 4 inch [ ], 4¼ inch [ ], 4½ inch [ ], 4¾ inch [ ], 5 inch [ ], 5¼ inch [ ], 5½ inch [ ], 5¾ inch [ ], 6 inch [ ], 6¼ inch [ ], 6½ inch [ ], 6¾ inch [ ], 7 inch [ ], Mosquito mesh [ ]
4.2 What size hooks did you use?
4.3 What type of string is the net made from? A) Silon / Monofilament (small cotton) [ ], B) Thin multifilament [ ], C) Cotton / Thick multifilament (Kwazi) [ ], D) Glass / Ghost cotton / Satanic [ ]

4.3 How many hooks per longline?
4.4 What is the length (in meters) of the fishing gear?
4.5 How many of did you use to catch the fish (observed during the interview) today?
4.6 How many of this fishing gear did you set in total?
4.2 How many basket traps did you use in total to catch the fish today?
4.7 If other type of gear is used provide a description.
4.8 Did you use 'beating' (Mindili)? A) Yes [ ] B) No [ ]
5. FISH CATCH
5.1 Have any fish been caught? A) Yes [ ] B) No [ ]
5.2 Select the type of fish caught: Catfish (all types) [ ], African Pike [ ], Tigerfish [ ], Red Breast Tilapia[ ], Threespot Tilapia[ ], Nembwe [ ], Purpleface Largemouth[ ], Niloticus [ ], Other Largemouths [ ], Sargos [ ], Other Large Breams [ ], Small Breams <10cm [ ], Bulldog [ ], Yellowfish [ ], Silver Catfish [ ], Small Mixed Mormyrids [ ], Marcusenius [ ], Bottle nose [ ], Squeakers [ ], Climbing Perch [ ], Western Bottlenose [ ], Mixed Small Fish all types <10cm [ ], Robbers [ ], Other Species[ ]
5.2 If others species what is the name?
5.3 What is the total weight in kg of all fish (selected fish species/group)?
5.4 Did you take a sample of because there are too many to count? A) Yes [ ] B) No [ ]
5.5 What is the weight of the sub-sample?
6. CATCH LENGTH
6.1 Measure the length of selected fish in the sub-sample or catch (maximum of 20 individuals)
7. FISH EATEN OR SOLD
7.1 Were any fish eaten before the interview? A) Yes [ ] B) No [ ]
7.2 How many were eaten? (i.e., individuals or buckets)
7.3 Were any fish sold before the interview? A) Yes [ ] B) No [ ]
7.4 How many were sold? (i.e., individuals or buckets)
7.5 How much were the fish sold for?
8. BY-CATCH SPECIES
8.1 Where any by-catch species caught today? Yes [ ] B) No [ ]
8.2 Which of the following non-fish species were caught today? A) Terrapin [ ], B) Bird [ ], C) Crocodile [ ], D) Crayfish [ ], E) Crabs [ ], F) Otter [ ], G) Other species [ ]

Appendix 4.1 Mosimann corrected trait measurement of *C. quadricarinatus* sampled from 33 sites across the invasion range on the Barotse floodplain. Traits are represented as; CL= claw length; CW = claw width; CPL = carapace length; CPW = caparace width; FLL = front leg length; TL = Total length and mass. New trait variable is represented as GM = Geometric mean



Appendix 4.2 Attributes of 48 sampling sites on the Barotse floodplain sampled for *C. quadricarinatus*. Invasion region site name, site number, coordinates, distance to point of introduction (km), habitat type, season, catch per unit effort (CPUE, as crayfish individuals and biomass), average mass (g), average carapace length (CL, in mm) and number of males (M), females (F) and Intersex (I) caught at each sampling site. SE stands for standard error, LZ for Little Zambezi River, Z for Zambezi River, L for Lwanginga River and M for Mota River.

Invasion Region	Site Name	Site no.	Coordinates	Distance to intro. site (km)	Habitat	Season	Traps (N)	CPUE ind./trap/night (mean ±SE)	CPUE (g/trap/night) (mean ±SE)	Mass (mean ±SE)	CL (mean ±SE)	M	F	I
Core	Lealui	1	S-15.227739, E23.016011	0.25	Pond	Wet	20	0.25 ±0.28	22.13 ±25.91	88.51 ±32.59	64.27 ±9.68	2	3	0
						Dry	20	7.45 ±2.61	334.23 ±105.40	44.86 ±2.08	57.19 ±0.94	52	82	15
					Floodplain	Wet	20	1.10 ±0.42	54.59 ±26.44	49.63 ±6.72	60.08 ±2.33	4	18	0
		2	S-15.230092, E23.014479	0.50	Pond	Wet	20	0.70 ±0.30	59.04 ±31.12	84.35 ±12.11	69.81 ±3.52	4	9	1
						Dry	20	4.85 ±1.57	262.82 ±84.04	54.19 ±1.88	61.82 ±0.77	32	55	10
					Floodplain	Wet	19	2.00 ±1.62	103.15 ±82.69	51.58 ±6.08	59.54 ±1.87	14	15	5
	Liyala	3	S-15.224144, E23.006270	1.35	Pond	Wet	20	0.20 ±0.30	14.17 ±24.72	70.84 ±30.92	57.76 ±12.95	2	2	0
					Floodplain	Wet	19	0.45 ±0.33	45.22 ±40.55	68.62 ±6.90	66.16 ±2.66	5	3	1
		4	S-15.218324, E23.001399	2.08	Pond	Wet	20	1.25 ±0.79	85.77 ±61.76	68.62 ±6.90	66.16 ±2.66	8	12	5
						Dry	20	0.75 ±0.56	46.26 ±23.36	61.68 ±9.78	64.39 ±2.03	8	7	0
					Floodplain	Wet	20	0.20 ±0.30	14.17 ±24.72	70.84 ±30.92	57.76 ±12.95	2	2	0
		5	S-15.211238, E22.994137	3.16	River (LZ)	Wet	20	0.10 ±0.22	4.19 ±11.37	41.94 ±29.52	51.28 ±9.89	0	2	0
						Dry	20	1.55 ±1.14	58.83 ±24.90	37.96 ±3.66	54.27 ±1.73	12	16	3
					Floodplain	Wet	20	0.40 ±0.44	32.61 ±39.23	81.54 ±18.74	67.30 ±6.65	4	4	0
Intermediate	Nalusa	6	S-15.253463, E23.058766	5.20	Pond	Wet	20	0.05 ±0.22	1.72 ±7.69	34.38	55.54	0	0	1
						Dry	19	4.37 ±0.97	284.77 ±61.06	65.19 ±2.93	65.77 ±0.99	28	51	4
					Floodplain	Wet	19	0.42 ±1.83	18.18 ±79.24	43.18 ±11.24	58.30 ±3.83	0	3	5
		7	S-15.257160, E23.058496	5.42	Pond	Wet	20	0.35 ±0.33	26.27 ±26.31	75.05 ±29.48	62.22 ±6.34	2	3	2
						Dry	21	2.86 ±0.82	189.09 ±49.65	65.77 ±4.23	65.20 ±1.35	34	26	0
					Floodplain	Wet	19	0.05 ±0.23	3.87 ±16.88	73.56	69.02	1	0	0
	Mabuto	8	S-15.211842, E22.970701	5.39	Pond	Wet	20	0.05 ±0.22	2.54 ±11.35	50.74	64.09	0	1	0
						Dry	20	0.40 ±0.57	23.19 ±38.93	57.97 ±15.31	62.89 ±5.04	2	6	0
					Floodplain	Wet	20	0.00	0.00	-	-	0	0	0
	Lyeneno	9	S-15.210761, E22.963527	6.17	Pond	Wet	20	0.05 ±0.22	4.26 ±19.06	85.26	74.29	1	0	0
						Dry	20	0.00	0.00	-	-	0	0	0
					Floodplain	Wet	20	0.00	0.00	-	-	0	0	0
	Matongo	10	S-15.260411, E23.069190	6.56	Pond	Wet	20	1.65 ±0.46	126.70 ±33.29	76.79 ±9.69	67.75 ±2.54	12	11	10
						Dry	20	7.35 ±1.56	298.23 ±67.49	40.58 ±1.72	55.18 ±0.85	41	95	11
					Floodplain	Wet	19	1.16 ±0.79	97.14 ±65.16	83.90 ±14.54	71.63 ±3.94	8	8	6
	Indoo	11	S-15.213504,	7.00	Pond	Wet	19	0.00	0.00	-	-	0	0	0

			E22.954705			Dry	19	0.11 ±0.22	8.60 ±18.69	81.69 ±17.81	71.38 ±4.83	1	1	0
					Floodplain	Wet	20	0.00	0.00	-	-	0	0	0
	Matongo	12	S-15.261432,	7.12	Pond	Wet	20	1.40 ±0.37	101.82 ±32.09	76.79 ±9.69	66.55 ±3.13	10	12	6
			E23.074536		Floodplain	Wet	19	1.32 ±0.73	92.24 ±3.32	70.10 ±6.90	66.30 ±2.35	5	19	1
		13	S-15.275068,	7.42	River	Wet	20	0.00	0.00	-	-	0	0	0
			E23.067098		(LZ)	Dry	20	0.00	0.00	-	-	0	0	0
					Floodplain	Wet	19	0.11 ±0.46	18.11 ±78.92	172.00 ±73.00	87.19 ±10.80	2	0	0
	Imbowa	14	S-15.261064,	7.72	Pond	Wet	20	0.35 ±0.24	41.99 ±30.50	119.97 ±16.90	77.31 ±4.71	4	2	1
			E23.081305			Dry	20	7.45 ±1.09	299.08 ±80.01	40.15 ±1.72	55.32 ±0.79	44	84	21
					Floodplain	Wet	19	0.21 ±-0.28	18.59 ±45.02	88.28 ±7.90	74.79 ±1.53	0	4	0
			S-15.259446,	7.82	Pond	Wet	20	0.85 ±0.50	66.41 ±39.01	78.13 ±13.46	67.30 ±3.93	9	7	1
		15	E23.083234			Dry	20	7.25 ±2.36	333.70 ±48.76	46.03 ±1.81	57.57 ±0.71	49	92	4
					Floodplain	Wet	19	1.21 ±0.64	101.05 ±88.22	83.48 ±9.69	71.28 ±2.50	9	10	4
		16	S-15.262259,	8.54	Pond	Wet	20	0.65 ±0.39	27.45 ±21.77	60.99 ±13.45	64.10 ±4.69	2	4	3
			E23.088955		Floodplain	Wet	20	0.70 ±0.45	25.40 ±15.93	36.29 ±4.35	53.89 ±2.36	3	9	2
	Lyatolo	17	S-15.216161,	9.18	Pond	Wet	20	0.00	0.00	-	-	0	0	0
			E22.933587		Floodplain	Wet	20	0.00	0.00	-	-	0	0	0
	Nandimba	18	S-15.268584,	10.88	Pond	Wet	20	0.50 ±0.34	71.96 ±41.95	98.74±14.64	72.56±3.74	6	5	0
			E23.110286		Floodplain	Wet	20	0.20 ±0.30	10.94 ±17.41	54.70 ±17.80	62.32 ±7.18	0	4	0
	Likundu	19	S-15.205557,	11.49	Pond	Wet	21	0.00	0.00	-	-	0	0	0
			E22.913785			Dry	19	0.16 ±0.21	11.98 ±17.80	75.86 ±20.69	71.16 ±8.69	3	0	0
					Floodplain	Wet	19	0.00	0.00	-	-	0	0	0
		20	S-15.272560,	11.91	Canal	Wet	20	0.30 ±0.26	21.27 ±19.63	70.90 ±19.22	64.84 ±4.95	4	2	0
	Harbour		E23.118967			Dry	20	0.90 ±0.62	33.65 ±28.86	37.39 ±5.04	53.35 ±2.51	5	6	7
					Floodplain	Wet	20	0.00	0.00	-	-	0	0	0
	Liyoyelo	21	S-15.191542,	11.64	River (Z)	Wet	20	0.15 ±0.67		58.03 ±9.80	67.73 ±5.27	1	1	1
			E22.916457			Dry	20	0.05 ±0.22	3.24 ±14.47	64.72	67.14	0	1	0
		22	S-15.204996,	12.07	Pond	Wet	19	0.00	0.00	-	-	0	0	0
	Likundu		E22.908333			Dry	20	0.05 ±0.22	4.21 ±19.33	84.27	73.30	0	1	0
					Floodplain	Wet	21	0.00	0.00	-	-	0	0	0
	Makono	23	S-15.132491,	12.68	River	Wet	19	0.00	0.00	-	-	0	0	0
			E22.952128		(Z)	Dry	19	0.00	0.00	-	-	0	0	0
	Limulunga	24	S-15.150034, E23.109432	13.02	Canal	Dry	18	0.72 ±0.22	47.80 ±16.11	66.18 ±7.48	66.82 ±2.03	8	5	0
	Kaama	25	S-15.335165,	14.31	Backwater	Wet	19	0.11 ±0.22	7.27 ±18.40	69.05 ±42.79	64.30 ±13.80	0	1	1
			E22.944392		(Z)	Dry	19	0.21 ±0.21	13.76 ±15.12	65.38 ±15.70	68.93 ±4.85	2	2	0
	Sifuriti	26	S-15.166364, E22.894664	14.85	Backwater (Z)	Wet	20	0.00	0.00	-	-	0	0	0
		27	S-15.175808,	15.08		Wet	20	0.05 ±0.22	2.09 ±2.09	41.80	59.72	0	1	0
	Shungwe		E22.888452		River (L)	Dry	20	0.00	0.00	-	-	0	0	0
		28	S-15.175808,	15.23	Pond	Wet	19	0.00	0.00	-	-	0	0	0
			E22.888452		Floodplain	Wet	19	0.00	0.00	-	-	0	0	0
Edge		29	S-15.180083,	18.96	Pond	Wet	20	0.00	0.00	-	-	0	0	0
	Tapo		E22.848645			Dry	20	0.05 ±0.22	2.55 ±11.41	51.01	58.90	1	0	0
					Floodplain	Wet	19	0.00	0.00	-	-	0	0	0
		30	S-15.370210,	18.97		Wet	20	0.05 ±0.22	5.18 ±23.19	103.69	77.43	1	0	0
	Butoya		E23.116250		River (LZ)	Dry	19	0.05 ±0.23	3.63 ±3.63	69.01	74.23	0	1	0
	Ndao	31	S-15.399355,	19.79	River (M)	Wet	20	0.10 ±0.32	6.91 ±30.89	69.08 ±21.51	69.25 ±8.98	1	1	0

		E22.966853			Dry	20	0.05 ±0.22	1.62 ±7.25	32.42	66.61	0	1	0
Siko-buliba	32	S-15.402645, E23.112087	21.85	Backwater (LZ)	Wet	20	0.00	0.00	-	-	0	0	0
					Dry	18	0.11 ±0.47	7.68 ±32.59	69.12 ±20.42	71.14 ±3.68	2	0	0
Mukakani	33	S-15.463094, E23.135053	28.92	Canal	Wet	20	0.00	0.00	-	-	0	0	0
					Dry	18	0.00	0.00	-	-	0	0	0
Nalolo	34	S-15.533179, E23.115015	35.37	River (Z)	Wet	20	0.00	0.00	-	-	0	0	0
					Dry	20	0.00	0.00	-	-	0	0	0
Libonda	35	S-14.909869, E22.978925	35.52	Backwater (Z)	Wet	20	0.05 ±0.22	2.69 ±12.03	53.82	64.51	0	1	0
					Dry	19	0.00	0.00	-	-	0	0	0
Silonga	36	S-14.733030, E23.045375	54.80	Backwater (Z)	Dry	19	0.11 ±0.22	7.46 ±15.81	70.90 ±0.23	72.67 ±0.37	1	1	0
Ngulwana	37	S-14.343366, E23.222265	58.53	River (Z)	Dry	18	0.00	0.00	-	-	0	0	0
Mulembe	38	S-14.610362, E23.110148	69.02	Backwater (Z)	Dry	18	0.00	0.00	-	-	0	0	0
Nambindi	39	S-15.833130, E23.212343	70.13	River (Z)	Dry	18	0.00	0.00	-	-	0	0	0
Kambai	40	S-14.564828, E23.122243	74.18	Backwater (Z)	Dry	18	0.00	0.00	-	-	0	0	0
Matula	41	S-15.887538, E23.233562	76.58	River (Z)	Dry	18	0.00	0.00	-	-	0	0	0
Mbowe	42	S-14.405788, E23.228290	93.70	River (Z)	Dry	18	0.00	0.00	-	-	0	0	0
Katongo	43	S-14.360101, E23.228374	98.61	River (Z)	Dry	18	0.00	0.00	-	-	0	0	0
Wayama	44	S-16.089156, E23.292304	99.67	River (Z)	Dry	17	0.06 ±0.24	4.16 ±17.66	74.93	70.36	1	0	0
Namayula	45	S-14.343366, E23.222265	100.27	River (Z)	Dry	18	0.00	0.00	-	-	0	0	0
Imatanda	46	S-16.114609, E23.283135	102.17	River (Z)	Dry	17	0.06 ±0.24	5.14 ±5.29	92.50	83.11	0	1	0
Kalongola	47	S-16.217697, E23.241841	112.16	Backwater (Z)	Dry	18	0.00	0.00	-	-	0	0	0
	48	S-16.235489, E23.236797	113.96	River (Z)	Dry	17	0.11 ±0.47	10.73 ±32.19	96.56±4.37	77.39 ±1.66	1	1	0

Appendix 5.1 Creel survey questionnaire used to assess economic impact *Cherax quadricarinatus* on the Barotse floodplain artisanal fishery.

<table>
<tr><td colspan="4">9. Effect on gear operation</td></tr>
<tr><td colspan="4">1. Did your fishing gear catch crayfish or was there any damage to your fish catch due to crayfish?</td></tr>
<tr><td colspan="4">2. What gear did you catch the crayfish in?</td></tr>
<tr><td colspan="4">3. Has crayfish damaged your fishing gear?</td></tr>
<tr><td colspan="4">4. How has crayfish caused damage to your fishing gear?</td></tr>
<tr><td colspan="4">5. Did the crayfish get entangled in your fishing gear?</td></tr>
<tr><td colspan="4">6. How much time did you spend removing the crayfish from the net today?</td></tr>
<tr><td colspan="4">10. Effect on fish catch</td></tr>
<tr><td colspan="4">7. How many crayfish have you caught in your fishing gear?</td></tr>
<tr><td colspan="4">8. What is the total weight (kg) of crayfish caught in your fishing gear?</td></tr>
<tr><td colspan="4">9. How would you classify your crayfish catch, is Intentional or By-catch?</td></tr>
<tr><td colspan="4">10. Has crayfish damaged your fish catch?</td></tr>
<tr><td colspan="4">11. What is the total weight of fish catch damaged by crayfish?</td></tr>
<tr><td colspan="4">12. For each type of fish damaged please answer the following questions</td></tr>
<tr><td colspan="4">a) What type of fish has been damaged by crayfish?</td></tr>
<tr><td rowspan="2">Name of fish species</td><td colspan="3">Part and Proportion Damaged</td></tr>
<tr><td>Head (%)</td><td>Trunk (%)</td><td>Tail ((%)</td></tr>
<tr><td></td><td></td><td></td><td></td></tr>
<tr><td colspan="4">b) What are you going to do with damaged fish?</td></tr>
<tr><td colspan="4">c) What would be the value of fish if they were not damaged?</td></tr>
<tr><td colspan="4">d) What is the value of fish now that they are damaged?</td></tr>
<tr><td colspan="4">11. Uses of crayfish</td></tr>
<tr><td colspan="4">13. What are you going to do with the crayfish you have caught?</td></tr>
<tr><td colspan="4">14. If it is discarding, how are you going to do it?</td></tr>
<tr><td colspan="4">15. If it is for sale, how much are you going to sell the crayfish?</td></tr>
</table>

Appendix 6.1 Survey questionnaire used to assess fishers' awareness, knowledge, and perception regarding *Cherax quadricarinatus* on the Barotse floodplain of the Upper Zambezi system.

A. **Socio-demographic information**

1. Gender: Male [ ] Female [ ]
2. Age: ……… years
3. Name of Town: ……………………………….
4. Name of Area: ………………………………..
5. Are you a permanent resident of this area/town: Yes [ ] No [ ]
6. If not, where do you live? …………………………………….
7. How long have you been staying in this area/town? ………………………………
8. Education level: A. Primary [ ] B. Secondary [ ] C. Tertiary [ ]
9. Fishing category: A. Fisher [ ] B. Fisher's helper [ ]
10. How long have you been a fisher: ………………………………………
11. How would you classify fishing occupation? Primary [ ] Secondary [ ]
12. How many people make up your household including yourself? ………………
13. What position are you in the household:

    A. Head of house [ ] B. Spouse [ ] C. Child [ ] D. Others dependants[ ]

B. **Awareness and knowledge**

14. Have you seen the redclaw crayfish here on the floodplain? (**show picture**)

    A. Yes [ ] B. No [ ] **If No, end interview**.

15. Where exactly have you seen the redclaw crayfish on the floodplain? ***please select all appropriate***

A. River [ ] B. Pool/Lake [ ] C. Canal [ ] D. Other specify…………………….................

16. When did you first notice crayfish on the floodplain or water bodies?

    A. less than 1 year ago [ ] B. 1-2 years ago [ ] C. 3-5 years ago [ ] D. 5-10 years ago [ ]

    E. More 10 years ago [ ]

17. Do you know the name of crayfish you have seen? A. Yes [ ] B. No [ ]

18. If Yes, what is the name ………………………………….

19. Do you think the redclaw crayfish is native to the area? A. Yes [ ] B. No [ ]

20. If No to **Q17**, what is the native area for the redclaw crayfish? …………………………...

21. How was the redclaw crayfish introduced on the floodplain? ……………………………..

22. How much do know about the redclaw crayfish as a non-native species?

    A. Nothing [ ] B. Little [ ] C. Some [ ] D. Much [ ] E. Extensive [ ]

23. How much do you know about non-native species in general?

    A. Nothing [ ] B. Little [ ] C. Some [ ] D. Much [ ] E. Extensive [ ]

24. How much have you been taught about the redclaw crayfish?

    A. Nothing [ ] B. Little [ ] C. Some [ ] D. Much [ ] E. Extensive [ ]

25. How much have you read about the redclaw crayfish?

    A. Nothing [ ] B. Little [ ] C. Some [ ] D. Much [ ] E. Extensive [ ]

C. Perception (benefits, threats, and management)

26. State how much you agree or disagree with the following statement.

Potential Benefits	Strongly disagree	Disagree	Neither agree nor disagree	Agree	Strongly agree
Crayfish are a source of food to people					
Crayfish are a source of income					
Domesticated animals benefit from eating crayfish					
Threats to fisheries	Strongly	Disagree	Neither agree	Agree	Strongly

	disagree		nor disagree		agree
Crayfish spoil fish catch					
Crayfish damage fishing gears					
Crayfish delay fishing activities					
Threats to the environment	Strongly disagree	Disagree	Neither agree nor disagree	Agree	Strongly agree
Crayfish negatively affects the water in floodplain waterbodies.					
Crayfish negatively affects aquatic animals					
Crayfish negatively affects aquatic plants					
Management awareness	Strongly disagree	Disagree	Neither agree nor disagree	Agree	Strongly agree
There is available information regarding management of IAS in freshwater bodies					
The law regulates the use, storage, transportation and disposal of crayfish					
Government disseminates information regarding control of crayfish					
Management practices	Strongly disagree	Disagree	Neither agree nor disagree	Agree	Strongly agree
You handle and transport crayfish according to the regulation					
You dispose of crayfish according to the regulation					
You advice others to handle, transport and dispose crayfish according to the regulation					
Management support	Strongly disagree	Disagree	Neither agree nor disagree	Agree	Strongly agree
There is need to control the population crayfish in the water bodies					
You are willing to learn how to control the population of crayfish					
You are willing to actively participate in controlling the population of crayfish					

D. Effect on gear operation

27. How often do you go for fishing in a month?

A. Once [ ] B. Twice [ ] C. Once a week [ ] D. 2-4 times a week [ ] E. 5-7 times a week

28. Do you catch crayfish in your fishing gears? A. Yes [ ] B. No [ ] **If No end interview**

29. How often do you get crayfish in your fishing gear?

A. Once [ ] B. Twice [ ] C. Once a week [ ] D. 2-4 times a week [ ] E. 5-7 times a week

30. What fishing gear(s) catches crayfish? ***please select all appropriate*** (**Use CAS options**)

31. How would you classify crayfish catch? A. Intentional [ ] B. By catch [ ]

32. Does crayfish damage your fishing gear? Yes [ ] No [ ] If No (**go to Q39**)

33. How does crayfish cause damage to fishing gear (s)? ……………………………………..

……………………………………………………………………………………………

34. Which fishing gear is more susceptible to damage? ……………………………………....

Explain why ……………………………………………………………………………….

35. At these three time points, how would you say damage to fishing gear(s) has changed?

	Significantly decreased	**Decreased**	**No change**	**Increased**	**Significantly increased**	**N/A**
1 year since crayfish appearance						
5 years since crayfish appearance						
10 years since crayfish appearance						

36. How often do you repair your fishing gear when it is get damaged by crayfish?

A. Never [ ] B. Once a month [ ] B. 1-2 times a week [ ] C. 3-4 times a week [ ] D. Everyday [ ]

37. How much does it cost you on average to repair the damages each time? ………………...

38. How often do you replace your fishing gear?

A. Once 2-3 years [ ] Once a year [ ] B. 2-5 times a year [ ] C. 6-9 times a year [ ] D. Every month [ ]

39. How much on average do you spend on a new fishing gear each time? …………………..

40. At these three time points, how has replacement of fishing gear(s) changed?

	Significantly decreased	Decreased	No change	Increased	Significantly increased	N/A
1 year since crayfish appearance						
5 years since crayfish appearance						
10 years since crayfish appearance						

E. Change in crayfish by-catch and fish catch

41. At these three time points, how would you say the crayfish catch has changed?

	Significantly decreased	Decreased	No change	Increased	Significantly increased	N/A
1 year since crayfish appearance						
5 years since crayfish appearance						
10 years since crayfish appearance						

42. At these three time points, how would you say the fish catch has changed?

	Significantly decreased	Decreased	No change	Increased	Significantly increased	N/A
1 year since crayfish appearance						
5 years since crayfish appearance						
10 years since crayfish appearance						

F. Effect on fish catch

43. Does crayfish damage the fish caught in fishing gears? Yes [ ] No [ ] **If No (go to Q46**)

44. How much of your fish catch gets damaged by crayfish? …………………………

A. 1- 25% [ ] B. 26- 50% [ ] C. 51- 75% [ ] D. 76- 100% [ ]

45. What do you do with damaged fish? ***please select all appropriate***

A. Eaten [ ] B. Sold [ ] C. Given away [ ] D. other uses specify ………………………

46. Which fishing gear has a high fish damage due to crayfish? …………………………….

Give reasons ……………………………………………………………………………..

47. At these three time points, how would you say the amount of fish damage has changed?

	Significantly decreased	**Decreased**	**No change**	**Increased**	**Significantly increased**	**N/A**
1 year since crayfish first seen						
5 years since crayfish first seen						
10 years since crayfish first seen						

G. Other impacts

48. Apart from damaging fish and fishing gear, is there any other way crayfish negatively affect your fishing activity?

………………………………………………………………………………

49. Have you changed the way you fish due to crayfish presence?

Yes [ ] No [ ]

50. What fishing strategies have you adopted since the appearance of crayfish? ……………..

……………………………………………………………………………………………

H. Uses of crayfish

51. Do you eat crayfish caught in your fishing gear? Yes [ ] No [ ] **If No, go to Q51**

52. How often do you eat crayfish?

A. Once a month [ ] B. 1-2 times a week [ ] C. 3-4 times a week [ ] D. Everyday [ ]

53. Do you give away crayfish caught in your fishing gear to other people to eat?

A. Yes [ ] B. No [ ]

54. Do you sell crayfish caught in your fishing gear? A. Yes [ ] B. No [ ] **If No, go to Q65**

55. How is crayfish sold? A. Alive [ ] B. Dead [ ] C. Both Alive and dead [ ]

56. How often do you sell crayfish?

B. Once a month [ ] B. 1-2 times a week [ ] C. 3-4 times a week [ ] D. Everyday [ ]

57. How much do you sell them for? ………………………………………………………...

58. Do you sell crayfish to Zambian citizens?

A. Yes [ ] B. No [ ] **If No, go to Q60**

59. Where do Zambian customers come from? ***Select both if applicable***

A. Within district [ ] B. Other districts [ ] C. I don't know [ ] **If answer is not (B) go to Q59**

60. If they are coming from other districts mention some of them? ………………………..

61. Why do you think Zambians buy crayfish?

A. Consumption [ ] B. Sale [ ] C. I don't know [ ] D. other uses specify ……………….

62. Do you sell crayfish to foreign nationals?

A. Yes [ ] B. No. [ ] **If No, go to Q63**

63. How would you categorise the foreign nationals?

A. Tourists [ ] B. Constructors [ ] C. Traders [ ] D. I don't know E. Others specify …...

64. Why do you think foreign nationals buy crayfish? ***please select all appropriate***

A. Consumption [ ] B. Sale [ ] C. I don't know [ ] D. other uses specify ……………

65. Do you sell crayfish to business enterprises?

A. Yes [ ] B. No. [ ] **If No, go to Q65**

66. What kind of business enterprises buys your crayfish? ……………………………………

67. Apart from eating or selling, what is the other use of crayfish caught in your fishing gear?

……………………………………………………………………………………………..

68. Do you discard crayfish caught in your fishing gear?

A. Yes [ ] B. No [ ] **If No, end interview**

69. How do you do you discard the crayfish? A. Alive [ ] B. Dead [ ]

70. Where exactly do you discard the crayfish?

A. In water where caught [ ] B. In water elsewhere [ ] C. On land [ ]

D. Other specify ………………………………………………