# Understanding a West African recreational fishery as a complex social-ecological system – a case study of the fishery for giant African threadfin *Polydactylus quadrifilis* (Cuvier, 1829) in the Kwanza Estuary, Angola

A thesis submitted in the fulfilment of the requirement for the degree of

DOCTOR OF PHILOSOPHY

*in*

ICHTHYOLOGY AND FISHERIES SCIENCE

*of*

RHODES UNIVERSITY

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December 2019

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# ABSTRACT

Despite increasing global recognition of the importance of recreational fisheries, their management largely remains poor. This is because they exhibit unique human-nature relationships and are nested within complex social-ecological systems (SESs). Recreational fisheries in the developing world have large potential for socio-economic development, but are generally underappreciated, in terms of their value and their impact, and are poorly governed. This is particularly concerning as they are highly complex and often compete for resources with dependent artisanal and subsistence fisheries. Developing world recreational fishery SESs are not well understood and present an important research gap for improved governance. The general aim of this thesis was to explore the recreational fishery targeting *Polydactylus quadrifilis* on the Kwanza Estuary, Angola, and provide context for how managers should approach recreational fisheries in the developing world and in Africa. To do this, the recreational fishery SES was explored using a combination of methodologies including those characteristic of traditional fisheries science, and new methods involving biology, sociology, and economics. The thesis contains an introductory chapter, a chapter describing the background, study area and study species, five data chapters and a discussion chapter.

Chapter 3 aimed to investigate the reproductive style of *P. quadrifilis*. Results identified the species as a protandrous hermaphrodite. Evidence to suggest this included degenerating testicular tissue and the presence of early developing ovarian tissues in transitional individuals. Early-stage oocytes were commonly found in the outer area of male regions and residual late-stage spermatids and spermatozoa were found in the luminal space of ovarian regions, suggesting a process of sex change from the outside inwards. Owing to the species' reliance on large highly fecund females for reproduction, it is likely that *P. quadrifilis* will be sensitive

to fisheries that target larger individuals, such as trophy recreational fisheries and line fisheries within other sectors.

Chapter 4 aimed to investigate alternative methods for adequately describing the growth of *P. quadrifilis* individuals belonging to either one of two distinct hypothetical life-history pathways: pathway I ('changers') – initial maturation as a primary male followed by a sex change to female; pathway II ('non-changers') – initial maturation as a male fish with no subsequent sex change, using von Bertalanffy Growth Functions (VBGFs). Other specific objectives included determining the size- and age-at-maturity and size- and age-at-sex-change for *P. quadrifilis*. Otolith aging revealed rapid growth and early maturation ($L_{50}$ = 399.2 mm FL, $A_{50}$ = 1.50 years) and sex change occurred over a wide size (790–1125 mm FL) and age (3–8 years) range. There was strong evidence for partial protandry in *P. quadrifilis* with several extremely old male fish (up to 22 years) observed in the population. When compared to the conventional model produced for the entire population, there were significant differences in the models for the 'non-changers' (LRT, $p < 0.01$) and their parameters $L\infty$ (full model = 130.8, 'non-changers' = 113.3, $p < 0.01$), k (0.32, 0.44, $p < 0.01$) and t0 (0.23, 0.43, $p = 0.03$) in the first approach and the models (LRT, $p < 0.01$) and their $L\infty$ ('changers' = 113.7, $p < 0.01$) values in the second approach. This suggests that utilising conventional modelling techniques may be inappropriate for the stock assessment and management of *P. quadrifilis* and, potentially, other sequentially hermaphroditic fishery species.

Chapter 5 aimed to assess the sensitivity of *P. quadrifilis* to recreational C&R within the foreign recreational fishery using a rapid assessment approach. To do this, a number of C&R variables including fight time, air exposure, hook placement, hooking injury, total time of the stress event, river depth and angling method were measured and related to two indicators of fish health and survival – the physiological stress indicators blood glucose and blood lactate concentration and reflex action mortality predictors (RAMPs). Air exposure was identified as a major contributor to motor impairment (Cumulative Link Model: $p < 0.01$) and fight time was an important contributor to motor impairment via its interaction with air exposure (Cumulative Link Model: $p = 0.02$). Handling practices appear to be particularly important for larger individuals as fish size was positively correlated with air exposure (Pearson's *r* coefficient = 0.41, $p < 0.01$) and fight times (0.88, $p < 0.01$). The findings suggest that recreational C&R may result in mortalities directly, via C&R, and indirectly, via predation, and several recommendations were made for best practice.

Chapter 6 aimed to assess the direct economic contribution of the recreational fishery for *Polydactylus quadrifilis* on the Kwanza Estuary. Results indicated that the recreational fishery for contributed significantly to the economy of an area that would otherwise likely receive little external input ($282 054 per four-month fishing season). However, high rates of economic leakage from the study area were identified (58.7%–92.9% of locally spent revenue) and were attributed to the sourcing of lodge supplies, services and staff outside of the local area and the repatriation of profit by foreign business owners. Capacity building within the local community is likely required to develop 'linkages' between the local community and the recreational fishery. Greater community involvement in the fishery is suggested to incentivise the protection of recreationally important fishery species and their associated ecosystems.

Chapter 7 aimed to investigate the resource user groups involved within the SES. Results illustrated that artisanal and domestic recreational anglers are well-established and are characterised by long histories of participation. The artisanal fishery was highly valued as a source of livelihoods for the local community. Artisanal fishers were eager for involvement in the recreational sector, through the chartering of their vessels, due to the attractiveness of extra earnings. Both recreational and artisanal fishers reported recent decreases in *P. quadrifilis* catch and anticipated further declines. Domestic recreational anglers appeared to be highly consumptive in their use of the fishery and C&R angling was uncommon. User conflict may be problematic for future management as recreational anglers perceived the artisanal gill-net fishery to be a threat towards *P. quadrifilis* stocks.

In conclusion, the open-access nature of the fishery was identified as the most pertinent threat to its sustainability and likely needs to be addressed. Potential solutions involve offering users the opportunity to purchase access rights (e.g. day permits), thus initiating the concept that users must pay for their use of public resources. Management should aim to protect large female fish due to their increased reproductive value and worth as trophy fish. Thus, C&R angling is likely to be an important interaction between users and the resource. However, angler behaviour will need to be manipulated to promote C&R and minimise C&R-related mortalities. Solutions include angler educational drives and interventions and the implementation of competitive C&R-only angling. Foreign recreational fisheries, although touted as potential ecotourism ventures, will only succeed in improving the lives of local people if they fully integrate the community into the operation of the fishery.

## ACKNOWLEDGMENTS

The completion of this thesis would not be possible without the help and support I received from numerous individuals along the way. First and foremost, I would like to thank my two supervisors, Prof. Warren Potts and Dr Amber-Robyn Childs, for the unbelievable amount of time and effort that they have provided me over the past four years. Not only have they provided me with immeasurable amounts of help and support, but also trusted in me and allowed me the opportunity to work, fish and live in Angola for 12 months. I can conservatively say that those were the best times of my life thus far and my time spent at the Kwanza taught me about more than just fish and how to catch them. Last, but certainly not least, thank you for welcoming me into your home and family. As a result, I feel like I have gained a home away from home here in the Eastern Cape where I know I will have friends for life.

On that note, to the self-proclaimed (rightly-so) barbudo expert, Professor Manuel (Manny) Milner, my time spent in Angola would not have been possible, or nearly as enjoyable, without you. Firstly, thank you for taking an interest in giant African threadfin. Without your initial intrigue and subsequent passion for my study species, I doubt that I would have had a PhD topic in the first place. Secondly, I can't thank you enough for all of the life-lessons, advice, love and support you gave me during my time in Angola, from holding the torch and scribing during late-night dissections, and being eaten alive by mosquitoes, to having an absolute jol (party) and meeting countless new and interesting people along the way.

To our collaborator Prof. Andrea Saayman, thank you so much for the time and effort you put in to helping me get to grips with the unfamiliar world of tourism economics. I wouldn't have been able to complete my thesis without your help.

I would like the thank Mr Rico Sakko for allowing me to use the lodge facilities and boats to carry out my research and for allowing me your trust to work and live at the lodge, a place I will forever cherish. Thanks goes to George and Vega Diamondis for all of their help and support in my last three months at the lodge, I truly appreciate it and hope to be back soon! To my friends at the lodge - Maibe, Baptista, Adriano, Viera, Malaik, Mingito, Ze, Agostinho, Bata Pisa, Bota, Cachito and all of the other amazing people I crossed paths with along the way, thank you so much for all of the help, the laughs, and the invaluable Portuguese lessons. Muito obrigado para tudos amigos.

To Dr Iain Nicolson, thank you for the help and advice you have given me during my time at the Kwanza and subsequently over the phone. I have really valued your input during my studies and would have found it difficult to achieve what I have had it not been for your help, so thank you.

I'd like to thank all of the artisanal and recreational fishermen that shared their insights with me during my surveys, I truly value your contributions and your involvement in my study is highly appreciated.

To Matthew Farthing and Bianca Hannweg, thanks for all of the help fishing, scribing, dissecting fish, extracting fish blood and (this one is important) drinking beers. It was amazing having familiar faces around to help with my research from time to time and, I'm sure we can agree, we shared some pretty amazing times. To Binks, I can't thank you enough for the unconditional love and care you gave me during my PhD, especially during long stints away from home, and for always being there for me when I needed it most. To Judge Inglis, Nick van Vyk, my brother, JD Dunn, and my mom, Linda Butler, thank you for coming to the Kwanza and visiting me, it was unbelievable sharing that experience with you.

Lastly, to my friends and family, thank you for the love and support you've shown me over the past couple years, I wouldn't be here without you. To my house mates, spanning four houses over the past four years, thanks for all the help, the laughs and the good times. You certainly gave me some respite from tedious thesis work. I can recall countless late-night fishy conversations over a quart or two which certainly shaped aspects of my thesis and hopefully my future career. Lastly, to my siblings, my mom and my late father, thanks for always encouraging me to follow my passion for fish. Not many people are allowed the opportunity to be a student for as long as I have and I’ve certainly been extremely fortunate to attend this amazing institution for 8 years, a privilege that many aren’t afforded, particularly in the country that we live in, so thank you.

## Publications arising from this thesis

A number of the chapters within this thesis were prepared for submission to peer-reviewed journals. One has been published in the journal *Environmental Biology of Fishes* and another has been submitted to the journal *Fisheries Research* and is currently under review. The remaining chapters are in preparation and will be submitted in the near future. As a result, there is a certain degree of repetition between the introduction and discussion sections of certain chapters. Although a number of collaborators contributed to each publication, in all cases, I was involved with the study design and methodology, I collected all data and analysed it, and I wrote the manuscript. Below is a list of the publications completed during my candidature.

Butler, E. C., Childs, A.-R., Winkler, A. C., Milner, M. V., and Potts, W. M. (2018) Evidence for protandry in *Polydactylus quadrifilis* in the Kwanza Estuary, Angola, and its implications for local fisheries. *Environmental Biology of Fishes*, **101**: 301–313.

Butler, E. C., Childs, A.-R., Milner, M. V., Farthing, M.W., Duncan, M., Winkler, A. C., and Potts, W. M. (2020) Do contemporary age-growth models overlook life-history complexities in protandrous fishes? A case study on the large protandrous polynemid, the giant African threadfin *Polydactylus quadrifilis*. Fisheries Research. (in review).

## Associated publications during candidature

Arkert, N., Childs, A.-R., Parkinson, M., Winkler, A., Butler, E., Mannheim, S., and Potts, W. (2018) Evaluating the effects of catch-and-release angling on Cape stumpnose *Rhabdosargus holubi* in a South African estuary. *African Journal of Marine Science*, **40**: 235–244.

Mannheim, S. L., Childs, A.-R., Butler, E. C., Winkler, A. C., Parkinson, M. C., Farthing, M. W., Zweig, T., et al. (2018) Working with, not against recreational anglers: Evaluating a pro-environmental behavioural strategy for improving catch-and-release behaviour. *Fisheries Research*, **206**: 44–56.

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# Chapter 1

## General introduction

### 1.1 The development of social-ecological science and its principles

Social and ecological sciences have developed separately over time and thus the study of culture and nature has largely taken place independently of one another (Berkes et al. 2003) and therefore they do not combine well (Ostrom, 2009). Only recently have scientists from both disciplines begun to acknowledge that there is a need to understand social-ecological systems (SESs) as "linked systems of people and nature, emphasising that humans must be seen as a part of, and not apart from, nature" (Berkes & Folke, 1998). The first major combination of the two disciplines took place through the development of integrative areas of science that encompassed both disciplines and included environmental ethics, political ecology, environmental history, ecological economics, traditional ecological knowledge and common property (Berkes et al. 2003). All of these areas are now encompassed within SES science, although it would seem that the majority of work is driven through the issues of common property and the "tragedy of the commons".

Since then much work has gone into developing SES science, which has largely focused in the economically important areas of agriculture, commercial fisheries and forestry and has been driven by Elinor Ostrom and her team following her initial landmark papers (Ostrom, 2007, 2009) and subsequently via numerous developmental publications (Ostrom & Cox, 2010; McGinnis & Ostrom, 2014). Due to increasing overexploitation of our natural resources and the acknowledgement of systems of natural resource use as being highly complex; complexity theory and adaptive SES science is now receiving attention as a more holistic approach towards natural resource management (Ostrom, 2009; Ostrom & Cox, 2010). Additionally, there is a realisation that previous approaches tended to analyse these systems with oversimplified theoretical models that did not take all aspects into account (Ostrom, 2007; Ostrom & Cox, 2010).

Ostrom (2007, 2009) developed a framework for dealing with SESs so as to 'harness' their complexity, 'rather than eliminate it'. The framework was developed with the intention of creating a 'common language' that could be used by researchers working in entirely different fields and allow them to test theories and models that predict which outcomes, interactions, drivers and influences are particularly relevant under specific settings (McGinnis & Ostrom, 2014). The general framework is widely accepted (Arlinghaus, 2017) but is constantly being manipulated and changed as different researchers apply it to new fields of science (McGinnis & Ostrom, 2014). The general framework involves four first level core subsystems; resource systems (e.g. a particular river), resource units (e.g. fish or fishing areas), governance systems (government, law or other regulations) and users (people using the resource system in diverse ways) (Figure 1.1). Each of these subsystems is comprised of numerous second level subsystems (for example – socio-economic attributes of the users) which are comprised of further third level subsystems (for example – catch orientation (see Arlinghaus, 2006)) and so on. The relationship between the four core subsystems affect (and are affected by) each other as well as other SESs (for example – the broader ecosystem in which they are nested) and social, economic and political settings (Figure 1.1) (Ostrom, 2009). Interactions between these subsystems lead to particular outcomes which then feed back into the system (Figure 1.1).

### 1.2 SES science in fisheries and the need for its application in recreational fisheries

Although Ostrom's modern SES framework has been increasingly applied to some fisheries sectors (Basurto et al., 2013; Kittinger et al., 2013), it has not strongly featured in recreational

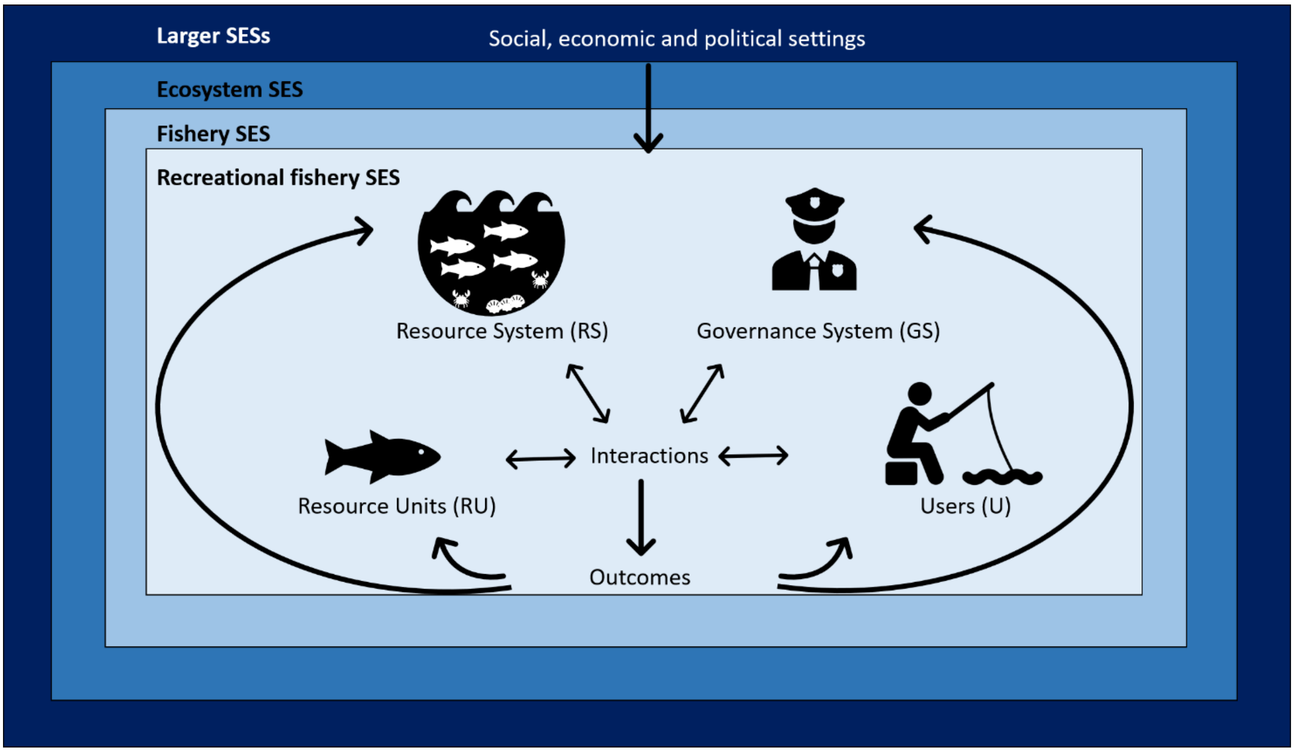


**Figure 1.1:** Elinor Ostrom's (2009) core subsystems for assessing social-ecological systems. All SESs involves four core multi-level subsystems including resource units (for example – a particular fish), the resource system (for example – a particular river), governance systems (for example – the government) and the users (for example – fishers). Each core subsystem contains numerous second level subsystems (for example – socio-economic attributes of the users) which are comprised of further third level subsystems (for example – user behaviours) and so on. Interactions between the core subsystems result in outcomes which feed back into the system. Additionally, the SES is influenced and impacted by external social, economic and political settings and via linkages to larger SESs in which they are nested.

fisheries, despite being highly applicable. In an in-depth review of developing SES science in freshwater recreational fisheries, Arlinghaus et al. (2017) made a call for the further development of the subject. They felt that recreational fisheries science thus far has focused predominantly in the biological sciences with little focus on social aspects and almost no focus on the combination of the two using Ostrom's applied framework. Additionally, other researchers have recently also made direct calls for its development and application in the developing world (Wood et al., 2013; Bower, 2017). The application of SES science in recreational fisheries is thought to have value both towards the assessment and sustainable management of recreational fisheries and towards a better understanding of the relationships between people and nature (Arlinghaus, 2017). Furthermore, Potts et al. (2019) reviewed the state of global recreational fisheries governance and found that it lags behind that of commercial and small-scale fisheries. In addition, despite its potential for economic benefit in poor areas, the governance of recreational fisheries in developing countries was rated to be particularly poor. Therefore, the application of SES science to recreational fisheries is not only novel, but it can make real contributions towards bridging the realms of the biological and social sciences and contribute to the improvement of recreational fisheries management in general.

Recreational fisheries are being increasingly acknowledged for their large economic, socio-cultural and ecological value and they are rapidly growing in line with increased individual wealth and a growing middle-class (Arlinghaus et al., 2013; Herfaut et al., 2013; Arlinghaus, 2017). Additionally, recreational fisheries have the potential to make large contributions to overall fisheries mortalities and can be highly destructive (Holtzhausen et al., 2001; Coleman et al., 2004). Therefore, the appropriate management of recreational fisheries is necessary in order to maintain positive feedbacks between people and the environment and also to sustain fish species that are important to other larger SESs (e.g. food source for subsistence fishermen; source of ecosystem services). However, management is often complicated by the fact recreational fisheries incorporate a self-subsidising, widely dispersed and highly mobile user group (Post et al., 2002). By applying an SES approach to the investigation of recreational fisheries, it may be possible to develop more holistic and effective management approaches. Through the appropriate acknowledgement of the value of recreational fisheries, it may be possible to create economic incentives to protect recreationally important species. This also has the potential to create knock-on effects through the overall protection of the ecosystem and can result in benefits such as the indirect management of other fish species which may have high value as a food source in the subsistence or small-scale sectors (Wood et al., 2013).

Several aspects of recreational fisheries are unique and provide the opportunity for valuable additions towards the study of SESs in general. For example, recreational fisheries can involve purposefully capturing specific wild animals, such as trophy fish, to simply release them again (willingly). This is very much unlike the behaviour associated with other fishing sectors. Furthermore, recreational fishing, unlike other fisheries sectors, is not entirely centred around catching fish and other motivations such as the appeal of 'a day out', 'getting out of the city', or 'being surrounded by nature' may also drive participation (Post et al., 2002; Post, 2013). Certain aspects of recreational fishing have only recently been questioned for the first time, such as the effects of recreational catch-and-release on the survival of fish that were previously assumed to be healthy and survive following their release (Cooke & Cowx, 2004; Arlinghaus et al., 2007; Butler et al., 2017). Furthermore, recreational fisheries fit into larger SESs and may therefore be influenced, and have the potential to influence, the greater community.

The social and cultural aspects of recreational fisheries are also highly complex due to the high variety of user groups and their potential motives for fishing recreationally. For example, let us assume that two fisheries exist and have identical biological and ecological traits including the same target species. The first fishery is located in a remote area where the majority of users are middle- to upper-class sport fishermen who travel to the area to target 'trophy fish' that are released and therefore very few fish are killed and harvested. The other system is located in a highly populated area and consists of a variety of user groups with a range of economic and social backgrounds. Here the crowding and cost of recreational fishing is offset by 'keeping some fish for the pan'. Although the biological traits of these fisheries are identical, the social structures and value systems of the user groups are different and therefore trying to manage these two fisheries with the same blanket regulations would likely fail (Ostrom & Cox, 2010). In many recreational fisheries, there are also highly complex management systems in place with different layers of governance at international, national and regional levels and through organisations (e.g. angling clubs) and even individuals (through self-governance) (Arlinghaus, 2017). Understanding the impact of these complexities and the potential steps required to maintain a state of self-governance has obvious advantages towards the promotion of sustainability and the building of resilience in recreational fisheries.

### 1.3 Recreational fisheries in the developing world and in Africa

Recreational fishing is increasingly acknowledged as a critical component of global fisheries due to its numerous socio-economic and cultural benefits to humans as well as its potential for environmental impacts (FAO, 2012; Cooke et al., 2018; Arlinghaus et al., 2019). As such, there has been a largescale push for policymakers and managers to acknowledge and appreciate recreational fisheries globally (FAO, 2012; Potts et al., 2019). This has largely been driven through the importance of recreational angling in the developed world where it occupies the main use of freshwater fish stocks and is a highly important use of coastal marine resources in many countries (FAO, 2012; Potts et al., 2019). However, the recreational fisheries of the developing world are still largely unknown, unacknowledged in many cases and generally underappreciated in the scientific literature from both a social and environmental standpoint (Belhabib et al., 2016; Bower, 2017; Arlinghaus et al., 2019; Brownscombe et al., 2019).

Fisheries research in the developing world has traditionally been driven through the agendas of commercial fisheries and has focussed on the collection of catch and effort data, basic biological research and the economic value of a few important species (Wood et al., 2013; Belhabib et al., 2016; Bower, 2017). Additionally, there has often been large focus on the importance and value of small-scale sectors, which include artisanal and subsistence fisheries, due to their importance as a source of livelihoods and food security (Andrew et al., 2007; Béné et al., 2010; Belhabib et al., 2015). As a result, recreational fisheries in the developing world have traditionally received relatively less research attention and are largely understudied. Thus, there are numerous ‘knowledge gaps’ that need to be addressed, ranging from beginning baseline data collection to applying complex SES science (FAO, 2012; Wood et al., 2013; Bower, 2017).

Developing world recreational fisheries, when compared to those of the developed world, are unique and are influenced by a highly different set of socio-economic, cultural and political settings (FAO, 2012). Therefore, it is critical that they are studied and understood in order to facilitate their appropriate management. It is important that managers do not attempt to simply apply western fisheries science in the developing world without an appropriate understanding of the human and environmental characteristics of the systems in which recreational fisheries exist (Berkes and Folke, 1998). For example, in certain cases, precolonial local culture, value systems, local knowledge and potential management systems have been overlooked by modern science as ‘newly discovered’ developing world fisheries have been managed and evaluated with a disregard for pre-existing local systems (Berkes and Folke, 1998), often leading to a failure to achieve management objectives (Johannes et al., 2008).

The characteristics of recreational fisheries user groups are more diverse in developing countries and in Africa due to higher levels of poverty and large wealth inequality (FAO, 2012). Here, users within domestic sectors often exhibit a wide variety of motives for fishing and this affects their behaviour. For example, domestic recreational anglers have been shown to demonstrate high rates of consumptive angling, driven by motives for fishing such as subsistence (Belhabib et al., 2016; Bower, 2017). Therefore, anglers are often more reliant on fish, gathered from recreational fishing, as a food source, compared to anglers in the developed world (Cooke et al., 2018). As a result, anglers may have different perceptions about the appropriate use of recreationally angled fish (i.e. as a source of food rather than sport) and pro-environmental actions, such as voluntary catch-and-release (C&R) angling, may be uncommon, potentially resulting in a reduced conservation ethic amongst anglers. This may be further compounded by the often open-access nature of many recreational fisheries, as developing nations often have limited experience with their management (FAO, 2012; Potts et al., 2019). As a result, domestic recreational fisheries have the potential to contribute significantly to fisheries mortalities (e.g. Holtzhausen et al., 2001) and negatively impact other sectors.

Foreign angling tourism is growing rapidly in the developing world and in Africa, where it is highly valuable and has the potential to contribute towards the development of rural areas (FAO, 2012; Belhabib et al., 2016; Arlinghaus, 2017). Users within this sector of the fishery may display a highly different set of preferences and behaviours largely driven by their motivation to fish for sport rather than food (Kyle et al., 2007). Furthermore, the behaviour of anglers in foreign tourism sectors is often governed by the institutions and people that facilitate their fishing, such as fishing camps, lodges and guides. Therefore, certain behaviours, such as C&R angling for example, may become more prevalent within fisheries that contain angling tourism (see Dellacasa & Braccini, 2016). Additionally, foreign angling tourisms operators have the ability to control other aspects of the angling experience and can enforce strict fish-handling protocols, limit the type of equipment used by clients and generally control angler behaviour, in order to ensure high rates of fish survival following C&R.

The resource systems in which both domestic and foreign recreational fisheries exist in the developing world are often highly important to other resource users, such as artisanal and subsistence fishermen (FAO, 2012; Bower et al., 2014). As a result, research focussing on the development of recreational fisheries in the developing world often has to appreciate the potential impacts it may have on other more dependant resource users (Wood et al., 2013). This complexity obscures management decisions and the allocation of user rights should acknowledge issues such as equity and food-security (FAO, 2012). Ordinarily, in developed countries, allocation is based on maximising the welfare of resource use to society in general. However, in developing countries, this approach may not be appropriate as it may favour the allocation of resources to recreational fisheries, thereby jeopardizing the livelihoods of dependant users (FAO, 2012). Therefore, it has been suggested that allocation should be based on economic impact adjusted by objectives that prioritise equity and food-security (FAO, 2012).

Foreign angling tourism may, however, be able to provide an economic incentive for the allocation of fisheries resources to recreational sectors, via the provision of livelihoods and food-security to locals (Potts et al., 2009; Wood et al., 2013; Barnett et al., 2016; Belhabib et al., 2016). In particular, foreign tourism fisheries have the potential to raise the value of catch due to the high 'willingness to pay' for recreational fishing (Wood et al., 2013). This, in combination with the fact that many recreational fisheries practice C&R angling, has prompted certain authors to suggest that recreational fisheries may act as forms of ecotourism (Zwirn et al., 2005; Barnett et al., 2016), providing a socio-economic incentive for their development. However, it is important that foreign tourism sectors are developed with caution as numerous ecotourism ventures have been prone to failure in the short- to medium-term (Garrod, 2003; Wood et al., 2013). Therefore, appropriate allocations of fish resources can only be made to foreign recreational sectors if there are tangible socio-economic benefits for local fishing communities and local food-security is not constrained (FAO, 2012). To ensure this, it is critical that feasibility studies that predict the local economic benefit are conducted.

### 1.4 Research objectives and thesis outline

The general aim of this thesis was to apply a SES approach towards the assessment of a model West African fishery in order to provide context for how scientists and managers should perceive and deal with recreational fisheries in developing countries and in Africa. To do this, the recreational fishery SES was explored using a combination of traditional techniques and new methodologies, not typical to traditional fisheries science, involving biology, sociology, and economics.

Chapter 2 introduces the model West African recreational fishery for *Polydactylus quadrifilis* on the Kwanza Estuary and provides information relevant to the SESs in which the recreational fishery is nested. It also provides important background information about the social, economic and political settings present within the system and gives a brief review of the family, Polynemidae, and *P. quadrifilis*.

The first two data chapters (Chapter 3 and Chapter 4) focus on the ecosystem components of the fishery and appeal to critical biological 'knowledge gaps' and more traditional fisheries science. This included a reproductive assessment of *P. quadrifilis* (Chapter 3) and an age, growth and maturity study which attempted to investigate the life-history characteristics of the species (Chapter 4). More specifically, Chapter 3 investigates the reproductive style of the species using a multi-method approach in an attempt to provide evidence for the classification of *P. quadrifilis* as sequentially hermaphroditic in this region. A macroscopic and histological description of various stages of development in male, female and transitional fish is provided along with a hypothesised route for sex change. Evidence is also provided for reproductive seasonality through the use of gonadosomatic indices. Chapter 4 focusses on important life-history traits centred around growth and maturity including growth rate, size and age at various developmental stages, including first maturity and sex change, and population structure and investigates the possible 'developmental life-history routes' present within the population. These two chapters are critical for understanding the 'resource unit' subsystem of the SES and also play a role in investigating the 'resource system' and the current 'ecological performance' of the system (Figure 1.1).

Chapter 5 assesses the impact of recreational C&R on the mortality and health of *P. quadrifilis* in the Kwanza Estuary using a multi-disciplinary approach that assesses the reflex impairment and important physiological responses of fish. The recreational fishery relies upon the health of *P. quadrifilis* stocks and, therefore, should aim to minimise the potential impact of recreational C&R fishing on the species. Additionally, this chapter makes recommendations for future best handling practice which aim to reduce C&R-related stress and mortality of *P. quadrifilis*. This chapter is applicable to the resource units core subsystem of the SES and investigates the specific interaction of users and resource units via C&R angling. It also provides insight into the current outcomes of the SES (Figure 1.1).

Chapter 6 provides a comprehensive economic evaluation of the tourist recreational fishery for *P. quadrifilis* on the Kwanza Estuary in order to understand their potential value to various stakeholders and in order to improve the management of the resource system. This information provides a detailed description of the value derived from the domestic and foreign recreational fishery for *P. quadrifilis*. It also accounts for the process of economic leakage and, therefore, assesses the direct economic benefit of the fishery for the local community. This information is important and is used to assess whether or not the fishery is able to meet ecotourism standards and whether it provides significant socio-economic benefits for the local community. Chapter 6 deals with the core subsystems of resource units and users and the interactions and outcomes of the SES (Figure 1.1).

Chapter 7 provides important sociological information on the human dimensions within the artisanal and domestic recreational sectors. More specifically, it aimed to better understand the gears and methods used in each sector, to identify normative user behaviours, to investigate the basic economic cost-benefit of fishing to the different user groups, to understand fisher perceptions about the state and management of the fishery and, lastly, to assess fisher local ecological knowledge (LEK). Various aspects of Chapter 7 were related to the information gathered within other chapters and are discussed here. As such, Chapter 7 will deal with all four of the core subsystems, the interactions, outcomes, related ecosystems and certain social, economic and political settings (Figure 1.1).

Chapter 8, the final discussion chapter, provides the first attempt at understanding an African recreational fishery as a SES. This chapter draws on information collected in each of the other chapters, interrogates contemporary knowledge on SESs in recreational fisheries (in developed countries) and provides context for how scientists and managers should perceive and deal with recreational fisheries in developing countries and in Africa. Additionally, it is centred around the development of an adaptive governance system which aims to promote positive system outcomes and sustainability while building resilience in the Kwanza recreational fishery for *P. quadrifilis*. Ostrom's adapted framework (Figure 1.1) is utilised to provide a route for building resilience and maintaining positive feedbacks between humans and the ecosystem.

# Chapter 2

## Study area and species

### 2.1 Background and study area

*2.1.1 Angola's fisheries*

Angola has an abundance of fisheries resources with an extensive coastline of over 1600 km's. Largescale commercial fishing largely takes place offshore and targets small pelagic fishes with the use of purse-seiners (FAO, 2019). Angola's history of war and unrest led to a lack of basic infrastructure and high levels of poverty which resulted in a large-scale movement of people towards coastal areas in search of food (Belhabib & Divovich, 2015). As a result, coastal areas are dotted with small-scale fishing settlements and there is a high reliance on artisanal and subsistence sectors within the country with an estimated 50 000 dependents in 2010 (FAO, 2019). Small-scale artisanal and subsistence fisheries have been consistently rising with an increasing demand for fish products in line with annual population growth (FAO, 2019). More recently, Belhabib et al. (2015) estimated the artisanal fishing sector in Angola to comprise 135 000 people.

Recreational angling is becoming increasingly popular in West Africa and Angola through the development of foreign angling tourism (Belhabib et al., 2016). Additionally, there is evidence to suggest growth of the domestic or resident recreational angling sector (e.g. see Weir & Nicolson, 2014) which is likely related to increased wealth and a growing middle class (FAO, 2012). However, the recreational fisheries sector is largely unacknowledged and undervalued in West Africa and in Angola (Belhabib et al., 2016).

In terms of governance, Angola has a number of policies and legislation specific to recreational or 'sport' fishing. Chiefly among those is the "Presidential Decree No. 146/13 approving the regulation for sport and recreational fishing" and, to a lesser extent, the "Law No. 6-A/04 on Aquatic Biological Resources" (new Fishing Act). These laws outline 'common provisions' and limit recreational consumption of fish to a "maximum of ten fish with a weight that does not exceed 20 kg, except in the case that a single fish exceeds this weight". Additionally, recreational anglers require an annual permit in order to undertake fishing practices, obtainable from The Ministry of Fisheries. There is evidence that government has recognised the importance of tourism fisheries as they are specifically referred to in the legislation. Here, tourist enterprises are required to apply and pay for a permit to facilitate 'tourist fishing'. However, despite the policy and legislation being in place, there is a lack of implementation by governing bodies and, as a result, many laws are non-functional. For example, recreational fishermen regularly keep more than 20 kg of fish per person on a single outing and many recreational anglers are unaware of the fact that they need a recreational angling licence (pers. obs., pers. comm.). Therefore, there are realistically few governance systems in place that actively manage recreational fisheries in Angola currently.

### *2.1.2 Study area*

The recreational fishery for *Polydactylus quadrifilis* on the Kwanza (commonly also referred to as Cuanza) Estuary provides a typical example of a highly valuable complex SES which is prone to overuse. Extremely little scientific research has taken place within the system and, therefore, there is limited information about the fishery. The resource system appears to be relatively healthy as anecdotal fishing reports suggest that the fishery is highly productive, producing both large numbers of fish and trophy fish. The health of the fishery is likely a result of historically low levels of localised fishing. This was driven by a long history of unrest in Angola which, while having a negative impact on human livelihoods and wellbeing, likely had a *de facto* conservation action for fish populations in Angola and in the Kwanza Estuary (see Thorpe et al., 2009 as an example of the effect of civil war on Sierre Leone fisheries). During the Angolan civil war (1975–2002), the bridge which crosses the Kwanza Estuary, approximately three km upriver from the mouth and sea, was a major military strategic point as it was the main route connecting the capital, Luanda, to areas in the south of the country. As a result, there was strong military presence occupying the bridge and this likely limited the amount of fishing taking place in the area (Dr Iain Nicolson: International Game Fish Association (IGFA) representative, Angola - pers. comm). However, despite relatively high catches in the recent past, anecdotal evidence suggests that catches have begun declining and it would appear that the open-access nature of the fishery needs to be addressed to promote sustainability.

The study area was located between the mouth region and first four kilometres of the Kwanza Estuary in Angola (Figure 2.1). The Kwanza is one of Angola's largest river systems and drains into the Atlantic Ocean just south of the capital city, Luanda. The estuary is tidal and outward flow is halted for a very short period around high tide. The river runs towards the ocean between two sets of cliffs before turning northwards and running parallel to the sea, separated from it only by a thin sand spit (Figure 2.1). The location of the estuary mouth changes periodically, caused by rough seas, which results in a restructuring of the sand spit (pers. obs., see Figure 2.2).

The Kwanza Estuary appears to have significant ecological importance and is one of few large estuarine habitats in northern Angola (Longa Estuary - ±120 km south, Dande Estuary - ±134 km north, Congo Estuary – ±440 km north). The banks of the estuarine section of the Kwanza are host to dense mangrove forests which likely serve as ecologically important areas for both aquatic and terrestrial animals (Kathiresan & Bingham, 2001) and probably provide a vital nursery function for many species (Nagelkerken et al., 2008). Furthermore, the system appears to have significant ecological relevance for large adult fish and consistently produces exceptionally large individuals of a variety of species. For example, *P. quadrifilis* in the Kwanza Estuary are renowned for their large size and all of the International Game Fish Association (IGFA) world recreational angling records come from this location (IGFA, 2017). Additionally, there are numerous other IGFA recreational angling records from the Kwanza region for other species including *Megalops atlanticus*, *Caranx hippos*, *Lutjanus agennes* and *Syphraena afra*.

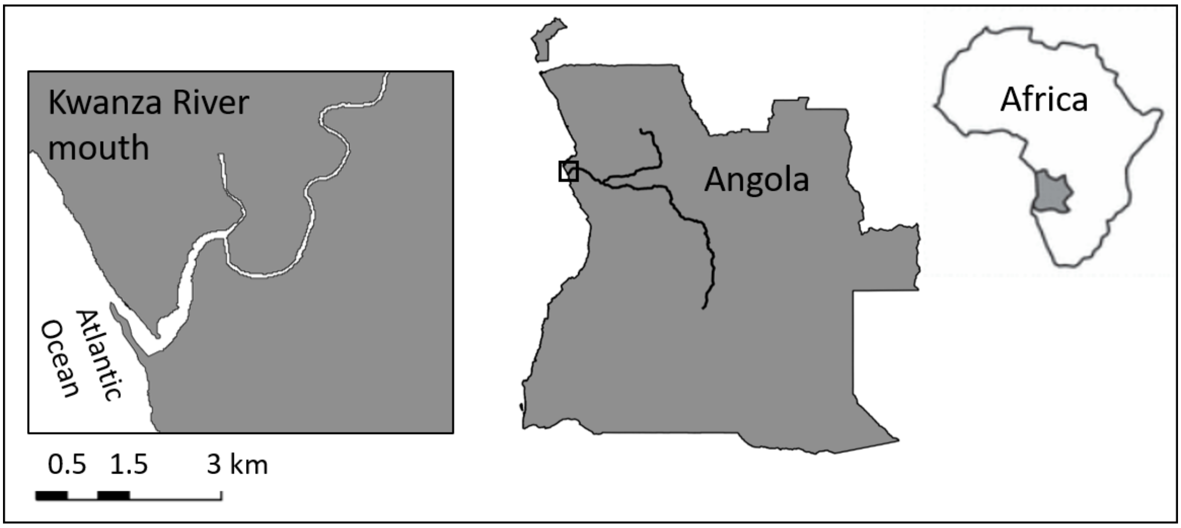


**Figure 2.1:** The Kwanza Estuary mouth in Northern Angola.

As a result of the productivity of the system, the Kwanza Estuary is a famous fishing location for recreational angling and fishermen are attracted to the area from all over the world. The Kwanza River Tarpon Lodge (hereafter referred to as the Kwanza Lodge) was founded in 2007 and is likely to have played a large role in the growth of the recreational fishery in the area. The majority of foreign tourists visit the lodge to target a range of species including *P. quadrifilis*, *C. hippos*, *S. afra, M. atlanticus* and members of the genus *Lutjanus* (primarily *L. agennes*) and *Pseudotolithus* (*P. typus* and *P. senegalensis*). The lodge enforces strict C&R for the majority of fish angled and only a small proportion of fish caught are kept for consumption, usually following accidental fishing-related mortality.

Additionally, there is an increasing market for domestic fishing tourism at the Kwanza Estuary. Many domestic tourists, defined hereon as either Angolan nationals or working expatriates residing in Angola but not in the local area around the lodge, visit the lodge on weekends and public holidays. The majority of domestic fishing tourists travel from the capital city of Luanda (65 km by road) and usually visit the area for the day. However, the lodge does provide accommodation to domestic tourists and, occasionally, fishermen will spend a night or two at the lodge. Many domestic anglers charter fishing trips with the Kwanza Lodge and this includes the provision of a lodge skipper/fishing guide. Alternatively, a growing number of anglers have acquired and begun using their own private vessels. In addition, artisanal fishers have begun making their traditional 'chata' vessels (a chata is a 5–7 m long traditional wooden fishing vessel usually powered by an outboard engine - Sowman et al., 2011) available for recreational charters.

Apart from the recreational fishery, there is a well-developed artisanal fishing community present on the Kwanza Estuary and fishers utilise chatas and other small vessels to fish in the estuary, river and out at sea. Currently, local artisanal fishers use one of four methods to capture fish; gill-nets ('rede'), baited longlines ('kimdamba'), baited hook-and-line ('isca', with or without the use of a rod - handline) and conventional artificial lure angling (use of a fishing rod and reel). Anecdotal evidence suggests that effort for all four methods is on the rise, although angling with artificial lures is thought to have become particularly important. This is thought to have been driven by the development and subsequent growth of the recreational fishery. It has been suggested that interactions between recreational anglers and the local fishers has led to their exposure to new fishing techniques and increased their accessibility to new gears and equipment (Dr Iain Nicolson - pers. comm).

Traditionally, non-foreign anglers (including artisanal and domestic recreational fishermen) would catch fish by trolling lipped crankbait lures behind boats in and around the estuary (Dr

Iain Nicolson – pers. comm.). This method is assumed to have been favoured by fishermen because of their general inaccessibility to alternative fishing equipment and the long lifespan of these lures, which are made of hard materials like wood or plastic. Other techniques popular in the foreign recreational fishery, such as the use of jig-heads and soft plastics, were traditionally less common in local and domestic fishing sectors due to their high expense and general unavailability (Dr Iain Nicolson – pers. comm.). Additionally, soft plastics are not durable and need to be replaced after every fish caught due to damage caused by the fish's mouth and teeth. It's suggested that, more recently, these types of lures have become more freely available in Angola and a small number of non-foreign fishermen have transitioned towards jigging plastics as they believe that it improves their catch efficiency, particularly for *P. quadrifilis* (pers. obs.).

Fishing effort by artisanal and domestic recreational anglers is reported to have increased tremendously over the last ten years (Dr Iain Nicolson -pers. comm.). Increases in domestic recreational effort are likely to be related to the increased economic growth of the country, as is often the case for developing countries (FAO, 2012). Growth of the artisanal sector, however, appears to be largely related to the socio-political characteristics of the country which have resulted in an increase in the number of people living along the coast and relying on fisheries resources (Belhabib & Divovich, 2015). In 2004, only two local chatas were reported to be fishing, using gill-nets, on the estuary and only a small rural village was present in the area (Rico Sakko – Kwanza Lodge owner; pers. comm.). As of 2016, when sampling began, there were likely more than ten chatas operating specifically in the Kwanza Estuary and an entire fishing settlement, with additional chatas used for seagoing fishing, was present at the mouth of the estuary (pers. obs.). Interestingly, Google Earth (Google Inc.) historical satellite imaging from late 2014 shows that the settlement was not present then (Figure 2.2) and demonstrates the increased artisanal fishing pressure in the area. On the 9$^{th}$ of February 2017, 34 chatas were observed on the beach in front of the Kwanza Estuary mouth at the location of the new fishing settlement (pers. obs.) (Figure 2.2).

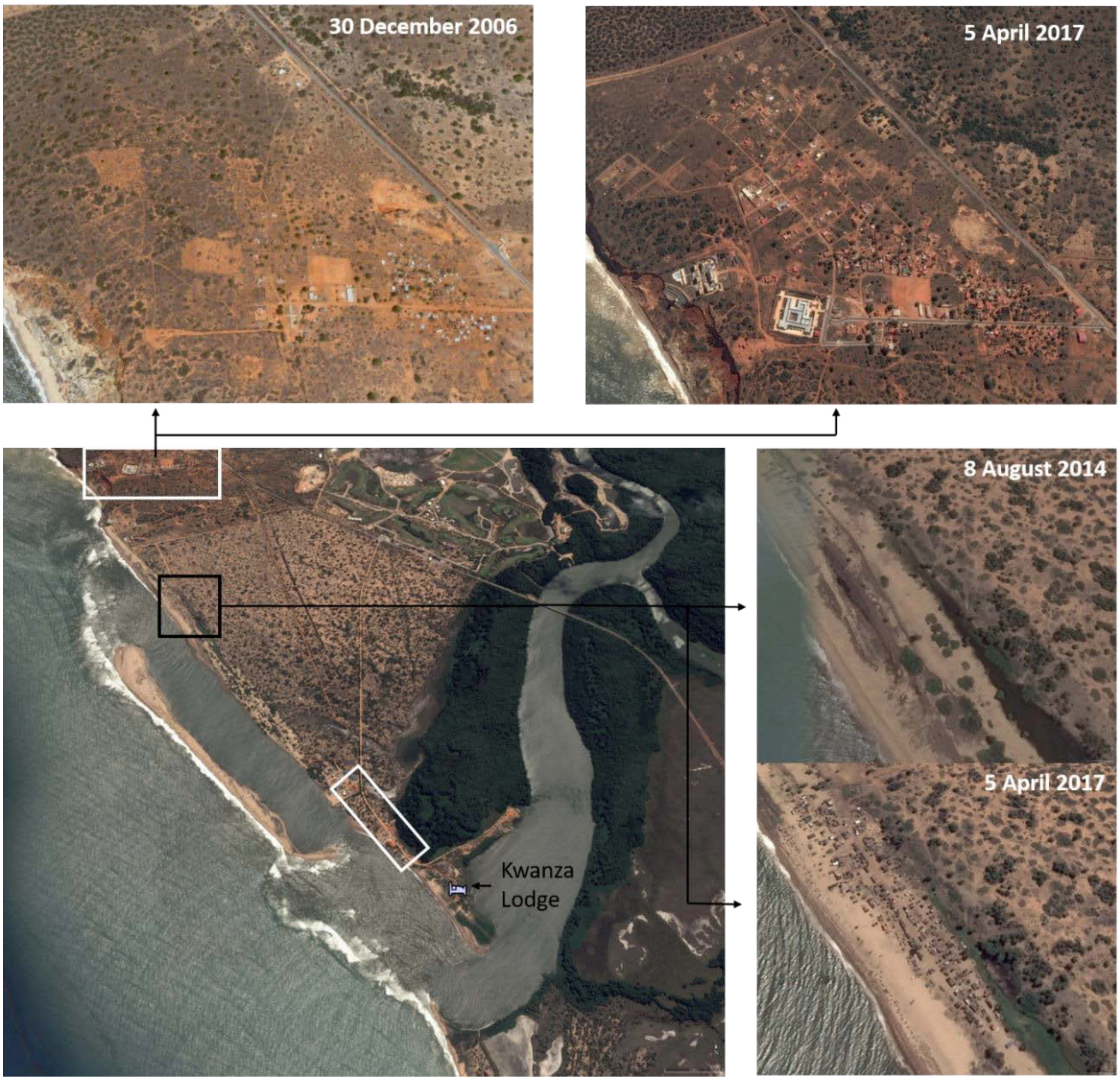


**Figure 2.2:** Google (Google Inc.) satellite images showing the Kwanza Estuary mouth with the original settlements (predating 2007 – white boxes) and the new fishing settlement (black box). The images on the right display a higher zoom image of the new fishing settlement in 2017 and the same location in 2014.

## 2.2 The Polynemidae

The Polynemidae, commonly referred to as threadfins, are a tropical percoid fish family that comprises 43 species in eight genera (Motomura, 2004; Motomura & Tsukawaki, 2006; Lim et al., 2010). Polynemid fishes are famously characterised by the presence of numerous individually separated lower pectoral-fin rays, or 'pectoral filaments' (Pember, 2006). They also possess a distinctive body shape, characterised by a conical snout, inferior mouth and two well-defined and separate dorsal fins (Motomura, 2004). Polynemids display a wide distribution and can be found in all three oceans as well as in certain Asian freshwater rivers and lakes (Motomura, 2004).

The taxonomy of the Polynemidae has largely been based on classical morphometric and cladistic techniques with a particular focus on the number and lengths of pectoral filaments (Motomura, 2004). The family itself is largely distinguished by the presence of pectoral filaments and the systematic relationships between the Polymenidae and other families is poorly understood (Johnson, 1993). It is currently thought that the family is most closely related to the Mugilidae and Sphyraenidae although Johnson (1993) suggested that they may be more closely related to the Sciaenidae based on numerous similarities in osteobiology and larval development, which are not common in other percoid fishes. Overall, there is a lack of taxonomic resolution and a number of papers have looked at the reclassification of certain species and genera within the family (Motomura & Iwatsuki, 2000; Motomura, 2002; Motomura et al., 2002; Motomura & Tsukawaki, 2006) with little focus on the systematic relationship between polynemids and other families (Johnson, 1993). Historically, the family is not well-understood or studied and a total of nine new species have been described since the turn of the century (Motomura & Iwatsuki, 2001; Motomura et al., 2001a, 2001b, 2001c; Motomura, 2003; Motomura & Oijen, 2003; Motomura & Tsukawaki, 2006; Lim et al., 2010)

Polynemids are predominantly marine fishes although certain species inhabit freshwater environments throughout their life-history (certain *Polynemus* spp. & *Polydactylus macrophthalmus*) (Motomura, 2004). Marine polynemids inhabit shallow, often turbid, coastal waters where they favour sand and mud substrate and a number of species are known to move into estuaries at certain stages of their life-history (Motomura, 2004). They are thought to be generalist benthic and epibenthic predators that are well suited to hunting under low light conditions. It has been suggested that the pectoral filaments of polynemid species have a gustatory function and aid in locating prey (Motomura, 2004; Pember, 2006). The diet of most medium to large species is comprised of crustaceans and fish but they have also been found to prey on cephalopods, nematodes, chaetognaths and other invertebrates (Longhurst, 1957). Smaller polynemid species, such as *Fillimanus* spp., and the juvenile stages of larger species (members of the genus *Eleutheronema*) are often planktivorous and utilise numerous gill rakers to sift food from the water (Motomura 2004). In fishes belonging to the genus *Eleutheronema*, the number of gill rakers decrease with increased fish growth and are replaced by tooth plates (Motomura, 2004)

Polynemid reproduction is poorly understood although it is thought to occur in coastal areas or estuaries (Motomura, 2004). Eggs have been described as small and pelagic (Motomura, 2004) and the larval development of some species has been briefly noted (Santerre & May, 1977). Some studies have looked at other aspects of polynemid reproduction such as recruitment (Leber et al., 1998) and hermaphroditism (Dorairaj, 1963; Kagwade, 1976; Pember, 2006). Protandrous hermaphroditism has been suggested for numerous species (Dorairaj, 1963; Kagwade, 1976) although conclusive histological evidence has not been provided and thus sequential hermaphroditism in all polynemid species remains “unconfirmed” (Sadovy De Mitcheson & Liu, 2008). Despite this, protandry is thought to feature prominently within the family and many authors have cited the trait (Longhurst, 1965; Kagwade, 1968; Motomura, 2004; Pember, 2006).

Throughout their distribution, polynemid fishes are important to local fisheries and are considered high-quality food fishes (Motomura, 2004). They form the basis of important commercial, subsistence and artisanal fisheries globally as well as recreational fisheries in Australia and Africa (Motomura, 2004). Certain polynemid fisheries around the world have undergone drastic declines and it is thought to be, at least in part, a result of the failure of fisheries management to appropriately acknowledge and adapt to the complexities involved with managing protandrous species (Abohweyere, 1989; Friedlander & Ziemann, 2003; Pember, 2006).

### *2.2.1 Polydactylus quadrifilis*

The giant African threadfin, *Polydactylus quadrifilis* (Cuvier, 1829), is one of the largest polynemid species, attaining a total length of up to two metres (and approximately 70 kg), and is distributed from Angola to Senegal along Africa's west coast (Motomura, 2004). Like many other marine polynemids, *P. quadrifilis* is frequently found within estuaries (Longhurst, 1957; Moses, 2000; Simier et al., 2004) although their specific usage of estuarine environments is not well understood. While working on the Gambia Estuary, Laë et al. (2004) reported *P. quadrifilis* to be 'abundant' in areas that were over 200 kilometres from the sea and completely fresh (Simier et al., 2004). There is very little information on the biology of the species despite it being a highly important fishery species throughout its distribution (Moses, 2000; Motomura, 2004).

*Polydactylus quadrifilis* contributes towards local subsistence and small-scale fisheries (trawl, gill-net, longline and beach-seine) (Ssentongo and Ansa-Emmim, 1986; Moses, 2000) as well as a well-developed and growing recreational sport fishery (Motomura, 2004) (Figure 2.3). A total reported catch of 12 447 tonnes was recorded for the species in 2001 (Motomura, 2004) although it is likely that this figure is an underestimation due to the presence of many small-scale West African artisanal fisheries which remain unregulated (Belhabib, 2014). Much of the reported landings for *P. quadrifilis* form part of the by-catch of various commercial sectors including inshore demersal and estuarine demersal fisheries, which largely target other polynemids (*Galeoides decadactylus* and *Pentanemus quinquarius*), croakers (*Pseudotolithus* spp.) and grunts (*Brachydeuterus auritus*) (FAO, 2019; Agbeja, 2016), and industrial shrimp fisheries (*Penaeus notialis*, *P. monodon, Parapenaeus longirostris* and *Parapenaeopsis atlantica*) (Ssentongo and Ansa-Emmim, 1986; Laë et al., 2004). West African industrial trawl industries are also known to catch and discard a high number of juvenile non-target species of which polynemids form a large component (Ambrose et al., 2005), thus complicating the management of the species. There is no clear indication that the species is targeted commercially on a large scale.

**Figure 2.3:** A recreationally angled *Polydactylus quadrifilis* from the Kwanza River, Angola. (Angler: Matthew Farthing).

# Chapter 3

## The sexual pattern of *Polydactylus quadrifilis* in the Kwanza Estuary, Angola

### 3.1 Introduction

Fish reproduction is extremely diverse and teleost fishes have the greatest variety of reproductive strategies amongst vertebrates (Munro et al. 1990). Understanding all aspects of fish reproduction is important for the appropriate management of important fishery species. Fisheries scientists will often aim to identify the sizes and ages at which fish spawn, as they are integral to many analytical fisheries assessment methods, and can be used to set restrictions on the fishery in an attempt to achieve sustainable yields. In simple terms, certain fisheries aim to only remove individuals from the fishery from a minimum size and age at which the majority of fish have had the opportunity to reproduce and thereby replenish fish stocks. By targeting fish that have not yet had the opportunity to reproduce, fishermen may drastically reduce recruitment back into the fishery via 'growth overfishing' (Diekert, 2012). Setting such restrictions is further complicated for species with complex reproductive strategies, such as sequential hermaphroditism (Higgins et al., 2015) and therefore it is important that the reproductive strategy of important fishery species is well understood.

Sequential hermaphroditism is a common trait in fishes (Ross, 1990). It is a process that involves the sexual maturation of a fish as one particular sex before undergoing a change to the opposite sex at a certain age or size (Allsop and West 2003) or due to social cues (Avise & Mank, 2009). The evolutionary driver of this phenomenon is most likely related to the preferential selection for larger individuals to be a certain sex (Ghiselin, 1969; Shapiro, 1987;

Warner, 1988; Ross, 1990). The diagnosis of such a reproductive strategy is essential in understanding the life-history and biology of a fish species, particularly for important fishery species whereby the size-selective nature of fishing practices can drastically effect the population structure, and thereby sex-structure of fish stocks (Molloy et al., 2007). The result of this could be a reduction in recruitment and population genetic diversity through either sperm-limitation in protogynous species, or egg-limitation in protandrous species (Alonzo & Mangel, 2004; Molloy et al., 2007).

*Polydactylus quadrifilis* is a member of the family Polynemidae (Motomura, 2004) and is an important fishery species throughout its distribution where it is captured in local subsistence and small-scale fisheries (trawl, gill-net and beach-seine) as well as a growing recreational fishery (Moses, 2000; Motomura, 2004; Carpenter & De Angelis, 2016) (see Chapter 2). However, despite the species' economic importance, there is limited biological information available, which is vital for promoting its sustainable management. Polynemid reproduction is poorly understood (see Chapter 2). However, protandrous hermaphroditism has been suggested for numerous species within the family (Longhurst, 1965; Kagwade, 1968, 1976; Motomura et al., 2002; Motomura, 2004; Pember, 2006), although the trait is considered unconfirmed due to a lack of conclusive evidence (Sadovy de Mitcheson and Liu, 2008). A doctoral thesis (Pember, 2006) suggested significant evidence for sex change in *P. macrochir* and *Eleutheronema tetradactylum* but was possibly not reviewed by Sadovy de Mitcheson and Liu (2008) due to the fact that the work had not undergone peer-review at the time. Since then, an additional paper has suggested protandry in *Eleutheronema tetradactylum* from India (Shihab et al., 2017).

A strict set of guidelines exists for the correct classification of species as functional hermaphrodites (Sadovy and Shapiro 1987; Sadovy de Mitcheson and Liu 2008). Initially, numerous lines of evidence were considered in the diagnosis of sequential hermaphroditism including the simple presence of a bisexual gonadal phase, age- and/or size-sex frequency histograms, sex ratios and sexual dimorphism (Longhurst 1965; Kagwade 1968, 1976; Sadovy and Shapiro 1987). More recently, many of these supporting features have been reconsidered following alternative explanations for the noted observations (Sadovy & Shapiro, 1987). At present, it is suggested that the most significant aspects of diagnosing protandry in wild fish are the presence of degenerating testicular tissue and developing ovarian tissue in the gonads of transitional individuals as well as detailed histological descriptions of various stages of sex reversal (Sadovy and Shapiro 1987; Sadovy de Mitcheson and Liu 2008). Additionally, controlled laboratory or field experiments that can be run over a period of years and using known individuals can provide undeniable evidence for sex change (Guiguen et al., 1994; Micale et al., 2002).

Given the limited biological information available on *P. quadrifilis* (see Chapter 2), the aim of this chapter was to diagnose the sexual pattern of *P. quadrifilis* in the Kwanza Estuary region of Angola. In doing so, particular attention was paid to the guidelines set out by Sadovy and Shapiro (1987) and Sadovy de Mitcheson and Liu (2008).

## 3.2 Methods

Sampling took place in the mouth area and first four kilometres of the Kwanza Estuary in Angola (see Figure 2.1) between the 21$^{st}$ of June 2016 and the 21$^{st}$ of February 2017. Fish were either collected using conventional angling techniques or purchased from local artisanal gill-net and longline fishermen.

Fish were weighed (nearest 0.01 kg) and measured (FL, mm) before being dissected. Fish were sexed as male, female or intersex and the gonads were macroscopically staged according to the eight stages outlined by Laevastu (1965): I = virgin (males only); II = immature/resting; III = developing; IV = maturing; V = mature/pre-spawning; VI = spawning; VII = spent; VIII =

recovering. The gonads were then removed and weighed (nearest 0.01 g). The eviscerated mass of the fish was noted (nearest 0.01 kg) and the gonadosomatic index (GSI) was calculated using the equation:

$$GSI = \frac{100\ x\ gonad\ mass}{eviscerated\ mass}.$$

Mean monthly GSI values were calculated for males and females using non-juvenile individuals (stage II or above).

Representative male gonads belonging to each male macroscopic stage, all intersex and all female gonads were fixed in a 10% formalin solution for between one and four months before histological analysis.

Three 1 mm thick sections were taken transversely through the anterior, median and posterior regions of each gonad using a razor blade. These sections were directly embedded in paraffin wax, sectioned at 5–6 microns, and stained using haematoxylin and eosin (HE) (Austin and Austin 1989). Histological evidence was used to validate the sex of individuals and the macroscopic staging protocol. Validation of macroscopic staging was based on the histological characteristics of the various stage male and female gonads of *Eleutheronema tetradactylum* and *P. macrochir,* which were described by Pember (2006).

To diagnose sexual pattern, the histological sections of male and intersex fish were examined for any signs of testicular degeneration and ovarian development. Ovarian sections were analysed for the presence of residual testicular tissues. All intersex gonads were classified by their functional sex and the diameter of various stage oocytes were measured using the program Leica LAS EZ V3.3 (Leica Microsystems Inc.). From histological sections, the area of the testicular region was calculated as a percentage of the entire gonad using ImageJ freeware (Schneider et al. 2012).

A non-parametric Kruskal-Wallis test with multiple comparisons was performed to assess for differences between the mean length (FL, mm), mass (kg) and GSI values of male, intersex and female fish. Vector images were created using free online graphics software Vectr (Vectr Labs Inc.).

### 3.3 Results

In total, 141 *P. quadrifilis* were sampled ranging in size from 436 to 1360 mm FL and weighing between 1.46 and 38.40 kg (Figure 3.1). Of these, 124 were macroscopically sexed as male, 12 as female and five as intersex. Later histological analysis identified one fish that was initially classed as female to be intersex while all other macroscopic sex classifications were verified (i.e. 124 male, 11 female and six intersex). The mean ± SD fork-length (FL) was 813 ± 129 mm for males (range: 436–1120 mm), 894 ± 57 mm for intersex fish (range: 790–955 mm) and 1202 ± 147 mm for females (range: 825–1360 mm) (Figure 3.1). The average weight was 8.23 ± 3.75 kg (range: 1.46–21.50 kg) for males, 10.37 ± 1.70 kg (range: 7.30–12.18 kg) for intersex fish and 27.45 ± 9.19 kg (range: 7.65–38.4 kg) for females. There was a significant difference between the FL (Kruskall-Wallis: $H(2) = 27.70$, $p < 0.01$) and weight ($H(2) = 27.54$, $p < 0.01$) of fish between sexes and female fish were significantly larger than males in terms of both FL ($p < 0.01$) and weight ($p < 0.01$).

The majority of fish were captured during the winter months (late June, July, August & September), with reduced numbers from October onwards (Figure 3.2). All female fish were encountered between the 1st of July and the 10th of September with only males and one intersex fish encountered outside of this time.

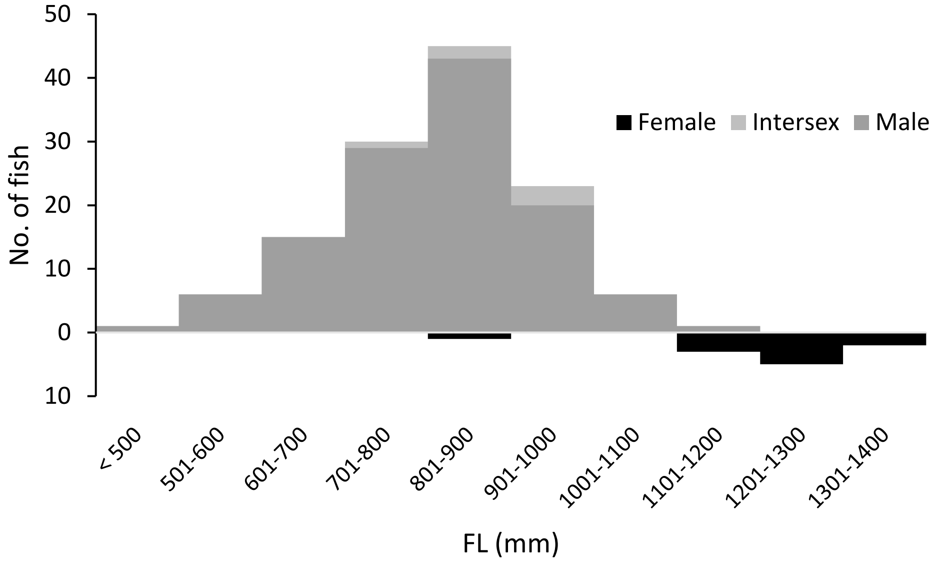


**Figure 3.1:** Sex-specific length frequency histogram of 141 *Polydactylus quadrifilis* sampled from the Kwanza Estuary, Angola.

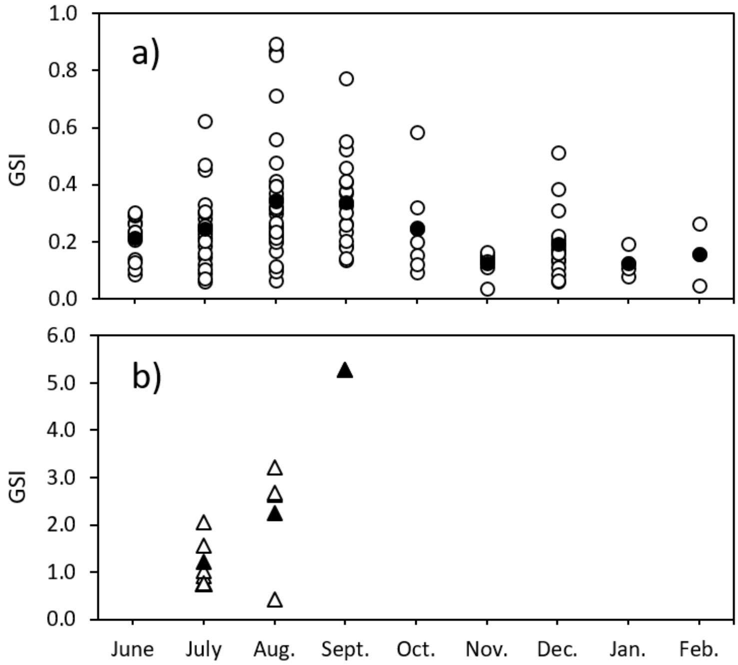


**Figure 3.2:** Monthly gonadosomatic index (GSI) values for male (a) and female (b) *Polydactylus quadrifilis* from the Kwanza Estuary, Angola. Hollow points represent individuals and solid points represent the mean monthly value.

### *3.3.1 Macroscopic appearance of gonads & GSI*

Macroscopic sexing of *P. quadrifilis* proved to be uncomplicated, as male, early- to mid-transitional intersex and female gonads were visually distinct. Late-transitional gonads were difficult to identify as very little testicular tissue was present.

*Males*

Males were observed throughout the sampling period and although developmental stages II through VIII were encountered, no virgin (stage I) fish were observed. Paired male gonads were white in colour and varied in length according to their level of development although they always occupied the majority of the length of the coelomic cavity forwards towards the head (Figure 3.3 a1, a2). Some well-developed testes (stage V–VI) had small lobes (1–4 cm) that branched rearward from the urogenital opening. Early-stage testes (stage II–III) appeared flattened with an oval sectional (transverse) appearance. In contrast, the sectional appearances of more developed gonads (stage IV–VI) were triangular. Spent (stage VII) testes were flaccid and appeared more flattened than testes from the previous two stages. Recovering (stage VIII) testes appeared small and flaccid with a red/brown colouration.

*Intersex*

Early to mid-stage intersex gonads were noticeable macroscopically via the presence of a pink-orange translucent layer that seemed to cover the testicular tissue within (Figure 3.3 b1, b2). They also appeared more rounded compared to the triangular appearance of the well- developed male gonads. Milt was present in all of these individuals and was exuded spontaneously when fish were placed on a hard surface or when pressure was applied to the abdomen of the fish. Late-stage transitional gonads appeared similar to what a typical immature or early developing ovary would look like, bright orange in colour and cylindrical, but with a thin strip of noticeable white tissue on the inner dorsal surface of the gonad (Figure 3.3 c1, c2).

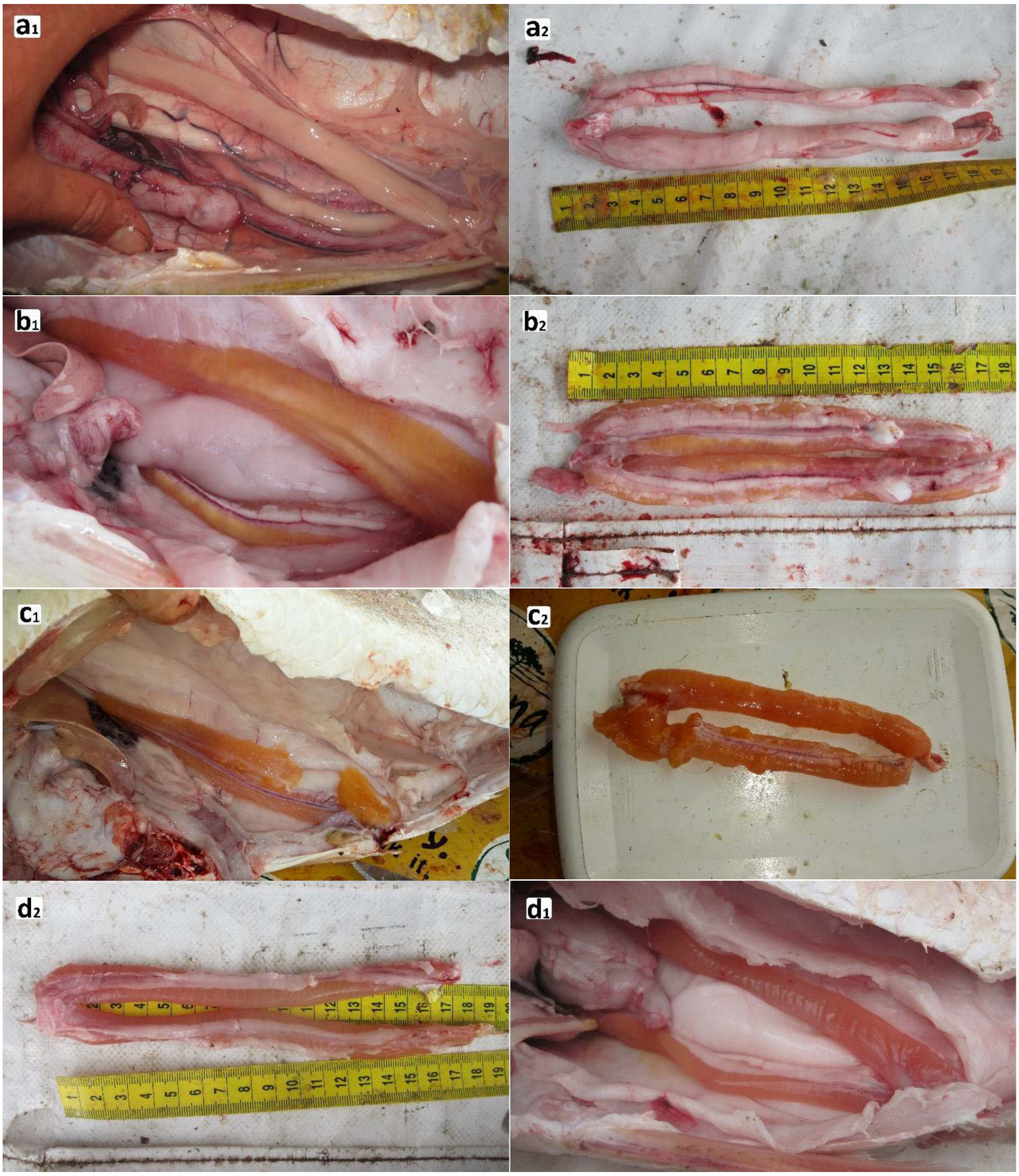


**Figure 3.3:** Macroscopic appearance of various gonads of *Polydactylus quadrifilis* collected from the Kwanza estuary, Angola. Images display a: a mature (stage V) male testis (900 mm FL), b: an early/mid transitional gonad clearly displaying the testicular tissue (white) beneath the ovarian tissue (orange) and the developed sperm duct that runs along the inner dorsal area of the gonad (880 mm FL), c: a late transitional gonad that was initially described as female but later reclassified as intersex (note the thin line of white tissue on the inner dorsal surface where one would expect to find a sperm duct) (955 mm FL), d: a resting ovary (white tissue on the inner dorsal surface of the gonad is lipid) (825 mm FL). Images display gonads inside the coelomic cavity (1) and post-dissection (2).

*Females*

Large female fish were mostly in a mature or spawning condition and only one small, immature female was observed (825 mm FL, 7.65 kg). Ovaries were varying shades of orange-yellow, with clearer orange colour indicative of early-stage ovaries and a creamy-yellow colouration displayed in mature ovaries with oocytes clearly visible through the ovarian wall. A single resting ovary (stage II) appeared fluid-filled and cylindrical in shape (Figure 3.3 d1, d2). Developing ovaries (stage III) were much larger than the single resting ovary and possessed many folds. Maturing and mature ovaries (stages IV–V) were richly vascularised and extremely large, occupying a significant proportion (both forward and backward from the urogenital opening) of the body cavity.

Macroscopic staging was validated for 29 of 31 representative male histological samples. The two gonads that were staged incorrectly included a fish that was reclassified from mature (stage V) to developing (stage III) and another that was reclassified from developing (stage III) to resting (stage II). Of the 11 female fish, macroscopic staging was validated for 10 fish and corrected for one which was macroscopically staged as mature (stage V) but was reclassified as maturing (stage IV).

Mean monthly gonadosomatic indices were highest for both male ($n = 121$ - three male fish did not have values for gonad mass) and female ($n = 10$) *P. quadrifilis* in the months of August and September (Figure 3.2). There was a significant difference between the mean GSI of males ($0.27 \pm 0.18$ (SD)), intersex fishes ($0.27 \pm 0.08$) and females ($1.96 \pm 1.43$) ($H(2) = 28.81$, $p < 0.01$) (Figure 3.4). Between the three sex classes, female GSI was significantly different from both male ($p < 0.01$) and intersex ($p = 0.01$) GSI, while the mean GSI for intersex fishes was similar to that of males ($p = 0.99$) (Figure 3.4). The cumulative mass of all non-juvenile reproductive organs from 121 males was 2778.8 g when compared to 5867.7 g from the 10 females.

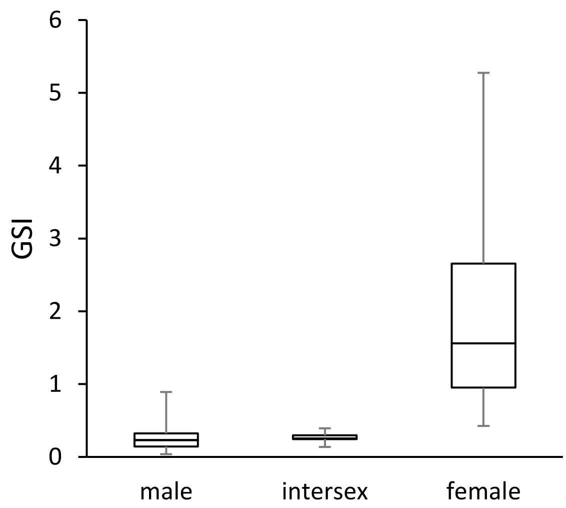


**Figure 3.4:** Gonadosomatic indices (GSI) displayed for male, intersex and female *Polydactylus quadrifilis* sampled from the Kwanza Estuary, Angola.

*3.3.2 Histological characteristics of gonads*

*Males*

The main histological characteristics used to differentiate between the developmental stages of males included the development of the sperm duct and sperm sinuses, the amount of connective tissue present and the composition of specific male germ cells and their location (Figure 3.5 a1, a2). Stage II and III testes were characterized by large amounts of connective tissue. Stage II testes contained spermatocytes, spermatids and spermatozoa which were present in numerous small crypts throughout the testis with no sperm sinuses yet present. Sperm ducts were visible in stage III testes, although they were not always filled with sperm cells. Sperm sinuses that contained spermatids and spermatozoa were noticeable close to the sperm duct. The outer region of the gonad was characterised by crypts (Figure 3.5 a1) that contained cells at various stages of spermatogenesis (as seen in Figure 3.5 a2). In relation to the sperm sinuses and sperm duct, these crypts were located on the outer area of the gonad in all testes belonging to stages III–VII. Stage IV testes could be differentiated from stage III testes by the increased development of the sperm sinuses and sperm duct, which were filled with spermatids and spermatozoa. The sperm sinuses of mature (stage V) and spawning (stage VI) testes extended the majority of the distance towards the gonad wall (Figure 3.5 a1). The spermatids and spermatozoa in spent (stage VII) testes were arranged less densely while recovering (stage VIII) testes were characterised by large amounts of connective tissue and a lack of early-stage spermatogonia.

*Intersex - Transitional gonads*

Transitional gonads were delimited (Sadovy and Shapiro 1987) and characterised by well-defined testicular and ovarian regions that were separated by connective tissue (Figure 3.5 b–e). Ovarian regions were located on the outer ventral surface of the gonad while testicular regions were located on the inner dorsal area (Figure 3.5 b1, c1, d1, e1). Small numbers of early-stage oocytes were often noted within the outer areas of male regions (Figure 3.5 b2) and late-stage spermatids and spermatozoa were present in parts of the ovarian region (Figure 3.5 c2). Ovarian regions were comprised of previtellogenic oocytes. Testicular regions were made up of various male germ cells in crypts, sperm sinuses and the sperm duct. In all transitional gonads, a layer of late-stage spermatids and spermatozoa (in sinuses) was present around the periphery of the male region (Figure 3.5 b1, c1, d1, e1).

Of the six intersex gonads, four were classified as functionally male due to the presence of large functional sperm ducts and testicular cells at various stages of spermatogenesis (Figure 3.5 b1, c1). The remaining two intersex gonads were classified as late transitional with no clear functional sex due to the undeveloped nature of the sperm duct and the presence of few early-stage male cells (Figure 3.5 d1, e1).

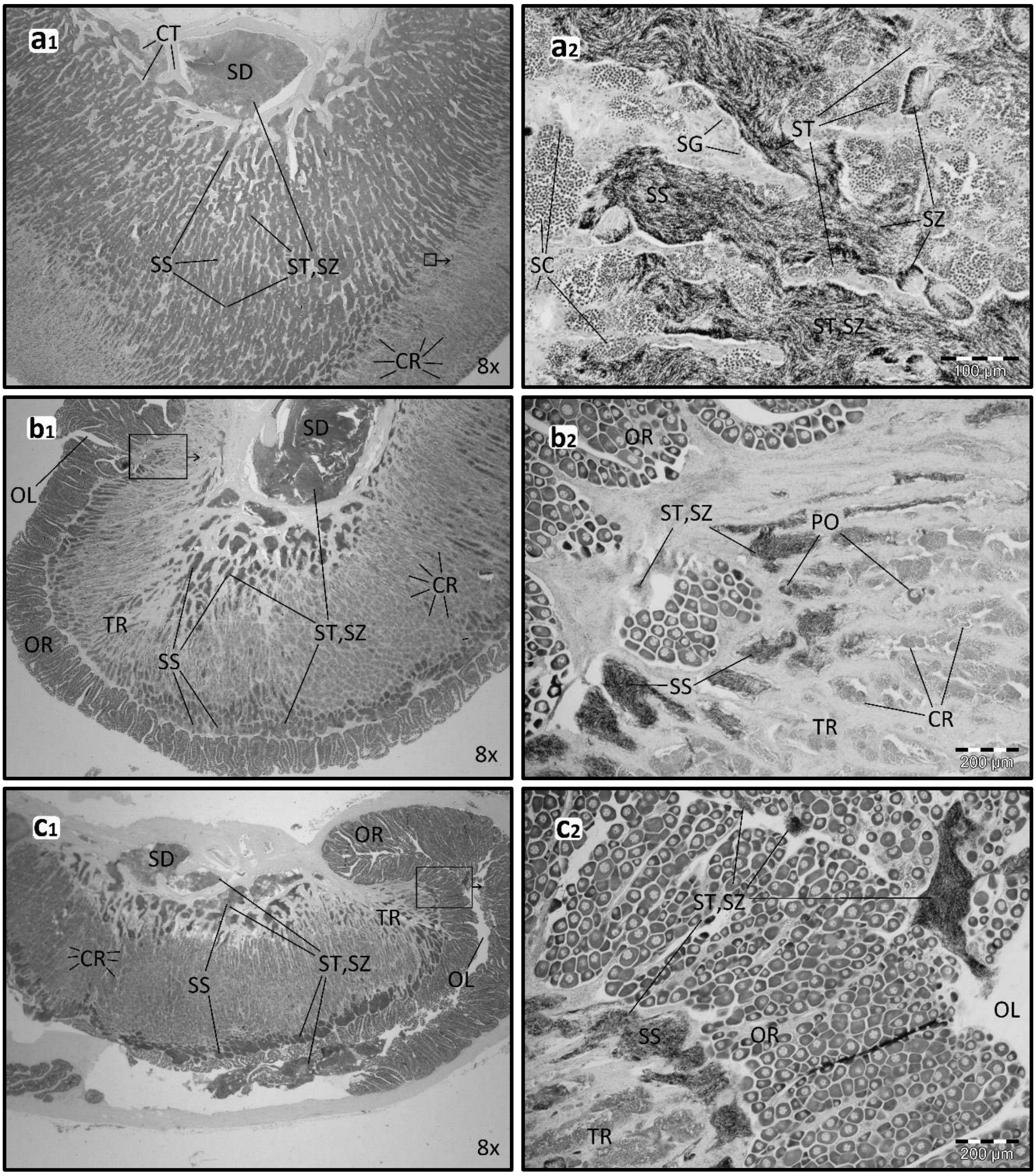


**Figure 3.5:** Low (1) and high (2) power images of transverse microsections through gonads at various stages of sex change in *Polydactylus quadrifilis* including: a) a mature (stage V) testis (890 mm FL); b) an early-transitional intersex gonad with ovarian tissue on the outer ventral surface (1) and early-stage oocytes in the outer testicular region (2) (925 mm FL); c) a mid-transitional intersex gonad displaying ovarian tissues developing from either side of the gonad (1) and residual male tissues in amongst the developing ovarian space (2) (897 mm FL). BV – blood vessel; CR – crypts; CT – connective tissue; OL – ovarian lumen; OR – ovarian region; PO – perinucleolar oocyte; SC – spermatocytes; SD – sperm duct; ST – spermatids; SZ – spermatozoa; TR – testicular region.

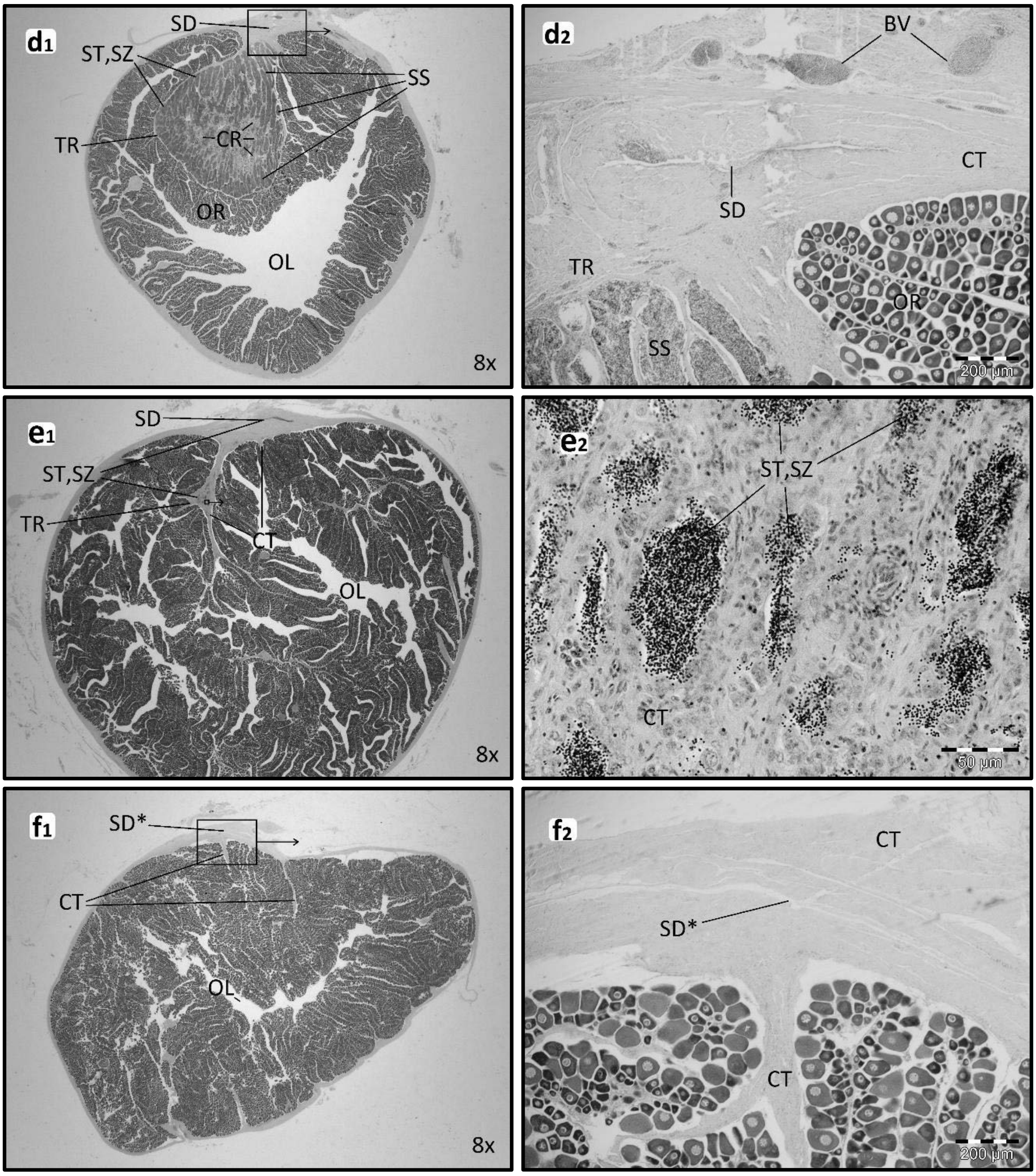


**Figure 3.5 (cont.)**: Low (1) and high (2) power images of transverse microsections through gonads at various stages of sex change in *Polydactylus quadrifilis* including: d) the first late-transitional gonad displaying the greatly reduced male region (1) and degenerated sperm duct (2) (915 mm FL); e) the second late-transitional gonad displaying the remnant male region (1) comprising residual spermatids and spermatozoa in pockets of connective tissue (2) (955 mm FL); f) a resting ovary showing extensions of connective tissue which resemble those of the second late transitional gonad (1) and what may be the remnant degenerated sperm duct* (2). (825 mm FL) BV – blood vessel; CR – crypts; CT – connective tissue; OL – ovarian lumen; OR – ovarian region; PO – perinucleolar oocyte; SC – spermatocytes; SD – sperm duct; ST – spermatids; SZ – spermatozoa; TR – testicular region.

### *Early to mid-transitional* gonads (*functional males*)

For functional male transitional gonads, the ratio of male to female tissue was not always uniform throughout the length of individual gonads and in some cases the transverse sections from one region comprised 90% male tissue while other regions comprised only 40 to 50% male tissue. In two of these cases male tissue dominated the posterior region of the gonad and was least prevalent in the anterior region. However, there was no noticeable difference in the ratio of male to female tissue between the different sections of the other two individuals.

Histological examination of the four functional males revealed well-developed testicular tissue which occupied between 40% and 90% of the gonad (Figure 3.5 b1, c1). This contained obvious sperm ducts and well-defined sperm sinuses that were filled with mature spermatids and spermatozoa (Figure 3.5 b1, c1). Numerous crypts were present that encased male germ cells at various stages of spermatogenesis. The testicular region appeared similar to that of a maturing (IV) or mature (V) male testis (as seen in Figure 3.5 a). However, a layer of sperm sinuses (that were filled with spermatids and spermatozoa) was apparent in the outer area of the testicular region (Figure 3.5 b1, c1). Early-stage oocytes were often located in this outer male region (Figure 3.5 b2).

The ovarian region was largely comprised of early-stage perinucleolar (± 50 μm) and chromatin nucleolar oocytes (<20 μm). In sections that comprised small percentages of female tissue (<15%), a single layer of ovarian tissue was present (Figure 3.5 b1). In further developed sections that comprised more ovarian tissue (20–60%), a second layer of female tissue was present on either side of the ovarian region (Figure 3.5 c1). The second layer appeared to develop from both ends of the ovarian region, eventually meeting in the centre of the ventral surface of the gonad. The gap between the first and second layer formed a luminal space. Residual testicular tissue, in the form of late-stage spermatids and spermatozoa, was commonly found within areas of the developing ovarian lumen (Figure 3.5 c2). No early-stage spermatogenic tissue was apparent in the ovarian component.

*Late transitional*

The gonads of two intersex individuals were categorised as late transitional and appeared to have lost their male function due to the prevailing ovarian tissue which dominated the gonadal area (Figure 3.5 d1, e1). There was no noticeable difference in the ratio of male to female tissues between the anterior, median and posterior regions of either of these gonads.

Testicular tissue comprised 16% of the gonadal space in the first individual (Figure 3.5 d1). This tissue was dominated by late-stage spermatids and spermatozoa which were found in sinuses around the periphery of the testicular region (Figure 3.5 d1). Some early-stage or developing male germ cells were present in the centre of the testicular region and the sperm duct was not well developed (Figure 3.5 d2). The ovarian component of the gonad was characterised by early-stage oocytes, primarily perinucleolar and chromatin nucleolar, of small size (± 50µm). Early-stage oocytes were, as in the functional male gonads, observed in the outer testicular region of the gonad (see Figure 3.5 b2). There was evidence of residual testicular tissue in some areas of the ovarian component of the gonad (see Figure 3.5 c2).

The gonads of the second late transitional fish were dominated (98%) by female tissue (Figure 3.5 e1). Ovarian tissue was at a very early stage of development although stage-one perinucleolar oocytes appeared larger (70–80 µm) than those in the early to mid-transitional gonads and in the previous late transitional gonad. Stage two perinucleolar oocytes (130 µm in diameter) were also visible and were characterised by clear amphophilic vacuoles within the cytoplasm. Male tissue was comprised of residual spermatids and spermatozoa which were situated in pockets of connective tissue (Figure 3.5 e2) and in the degenerated sperm duct (Figure 3.5 e1). No early-stage spermatocytes or spermatogonia were present in the gonad and, like in the first specimen, some residual spermatids and spermatozoa were evident within the luminal space of the ovarian region (see Figure 3.5 c2).

*Females*

The ovary of the single immature female (Figure 3.5 f1) was similar to that of the ovarian section of the second late transitional gonad (see Figure 3.5 e1) and was dominated by small (50 – 70 µm) perinucleolar oocytes, although a few larger late-stage perinucleolar oocytes (120 – 140 µm) were also present. The walls of the gonad appeared thin in comparison to the more developed ovaries, with arms of connective tissue projecting inwards from the ovarian wall in a similar fashion to those observed in the late transitional gonad (see Figure 3.5 e1). A small area of weakly formed connective tissue was present in the gonadal wall where one would expect to find a sperm duct (Figure 3.5 f2).

Developing (stage III) ovaries were histologically characterised by the presence of cortical alveolar oocytes in relatively high numbers along with perinucleolar and chromatin nucleolar oocytes. Thick well-vascularised connective tissue was present in the walls of these ovaries and also extended across regions of the ovary. Stage IV ovaries were similar to those of stage III with the additional presence of yolk granule oocytes. The ovaries of mature females (stage V) were dominated by yolk granule oocytes with cortical alveolar and perinucleolar oocytes also present.

### 3.4 Discussion

Diagnosing the sexual patterns of fish is particularly significant for important fishery species as it has implications for their appropriate management (Law, 2000; Molloy et al., 2007). *Polydactylus quadrifilis* were shown to be protandrous hermaphrodites with a male dominated sex-ratio and the GSI of mature female fish was significantly higher than that of males. Therefore, the population likely has a high reproductive reliance on fewer, larger, highly fecund female fish. Several lines of histological evidence for classifying protandry in *P. quadrifilis* were identified in this chapter. In transitional gonads, residual late-stage spermatogenic tissue within the ovarian component suggests previous male function. The outer testicular region of transitional gonads only contained late-stage spermatogenic tissues, similar to those found within the ovarian component. This is unlike the normal testicular anatomy of mature male fish, whose testes are characterised by the presence of late-stage spermatids and spermatogonia in sinuses near the sperm duct while the outer region is comprised of crypts containing cells at various stages of spermatogenesis. It is therefore likely that this outer testicular region is in the process of degeneration. In addition, the presence of early-stage oocytes in the outer testicular region suggests that this area is in a process of cellular reorganisation towards female function. The degeneration of the sperm duct with increased prevalence of ovarian tissue also suggests that there is a loss of male function that corresponds with ovarian development.

The process of sex change and the development of the ovarian luminal space in *P. quadrifilis* can be explained via a number of steps. An overall reshaping of the gonad from triangular (Figure 3.6a) to circular (Figure 3.6e) takes place. A layer of degenerating male tissue, in the form of late-stage spermatids and spermatozoa, is present on the outer testicular region of all intersex gonads (Figure 3.6b–d). A single layer of ovarian tissue is first noticeable on the ventral surface of the gonad (Figure 3.6b). Thereafter a second layer develops from either end of the ovarian region to form the luminal space (Figure 3.6c). Residual male tissue within the luminal space of the (outer) ovarian component and developing early-stage oocytes in the (inner) male portions, suggest a process of development from the outside inwards. There is a loss of male function with increasing ovarian prevalence shown first by the degeneration of the sperm duct (Figure 3.6d) and then by a loss of all early-stage male germ cells (Figure 3.6e). This sex change process appears to follow a similar process to that of *Inegocia japonica* described by Fujii (1971), whereby the first signs of ovarian tissue appeared on the outer region of the gonad and developed inwards, displacing the testicular tissue over time. The luminal space was formed through a reshaping of the gonad to form a second layer of ovarian tissue on the outer surface of the gonad (Fujii 1971).

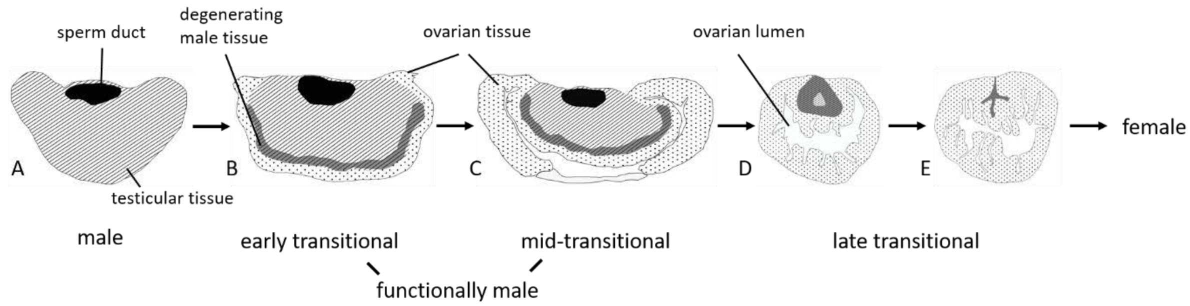


**Figure 3.6:** Schematic diagram showing the process of sex change in *Polydactylus quadrifilis*, from male (A) through intersex (transitional gonads) (B–E) to female. Vector images are based on the histological sections of transitional gonads.

The characteristics of the bisexual gonads of *P. quadrifilis* display many similarities to those of other polynemids. In many species, including *P. macrochir* and *Eleutheronema tetradactylum* (Pember, 2006), *Leptomelanosoma indicum* (Kagwade, 1976), *Galeoides decadactylus* (Longhurst, 1965) and *P. microstoma* (Dorairaj, 1963), ovarian tissue is located on the outer ventral region of the gonad and testicular tissue on the dorsal inner region. In fact, while working on *Leptomelanosoma indicum* (previously known as *Polydactylus indicus*), Kagwade (1976) noted that "*It may be said that it* (testicular tissue) *is not noticeable anywhere on the outer surface of the gonad. It appears that the proliferation of the ovarian lamellae extends so much over the greatly reduced testicular part that the latter which remains concealed inside the former cannot be taken notice of*". Furthermore, the male and female regions of bisexual gonads have been consistently reported as being separated by connective tissue (Dorairaj 1963; Kagwade 1976) and gonads comprising various amounts of testicular and ovarian tissues have often been suggested to be at different stages of transition (Longhurst, 1965; Pember 2006). Thus, it is possible that protandry may feature in other polynemid species and reproductive studies that use conclusive histological approaches are necessary to appropriately diagnose the trait.

With regard to the population structure of *P. quadrifilis* in this study, the presence of large male fish can be explained using two separate lines of reason, either they are yet to undergo sex change (monogyny) or they are not going to. Both scenarios are common in confirmed protandrous species (Moore, 1979). Some protandrous species display a wide size range at which sex change can occur (Pember, 2006). For *P. quadrifilis*, intersex fish were observed over a fairly broad size range (790 – 955 mm FL, 7.30 – 12.18 kg). Despite this, male fish were observed at sizes up to 1120 mm FL and 21.50 kg, far larger than that of the observed intersex fish. Therefore, it is possible that some proportion of male fish do not undergo sex change, although age and growth information is necessary to rule out the possibility that differential individual growth may explain the observed patterns, as sex change may be more closely correlated with age and not size. For example, in the rudimentary hermaphrodite, *Diplodus cervinus hottentotus*, age was found to be a more meaningful predictor for juvenile bisexual individuals than size (Winkler et al., 2014). Similarly, age was found to be a better predictor of sex change in the protandrous *Pagellus bogaraveo* (Micale et al., 2002). The potential for partial protandry in *P. quadrifilis* is investigated further in Chapter 4.

The relatively low occurrence of intersex fish sampled is worth noting. The fact that sampling was not undertaken during each calendar month may have led to a disproportionate observation of intersex individuals. In a study on *Galeoides decadactylus*, Longhurst (1965) found female sex ratios of less than 16% (compared to 7.8% for *P. quadrifilis* in the present study) in any given monthly sample while the ratio of intersex fish varied between 0.3 and 39.9% depending on the month. Furthermore, several studies have observed a higher proportion of intersex fish following the reproductive period (Fujii, 1971; Moore, 1979) and in a study on *Polynemus heptadactylus* (Polynemidae), the occurrence of intersex fish in monthly samples varied between 2 and 45% depending on the time of year (Nayak, 1959 cited by Kagwade, 1968). Although the reproductive period for *P. quadrifilis* in this area is undocumented, the GSI results from this study suggest that it may peak in August and September (see Figure 3.2). This is also when the large mature females were observed in the area. Seeing as the majority of fish were sampled during this period, it is possible that intersex individuals may have been underrepresented in the sample.

Diagnosing the sexual pattern of *P. quadrifilis* is crucially important due to the value of the species towards local fisheries. Size selective fishing on sequentially hermaphroditic species has been known to lead to recruitment overfishing and a reduction of the age and size at which sex inversion takes place (Molloy et al., 2007; Moore et al., 2011). Although no quantitative fishing effort data is available for the region, anecdotal evidence suggests that the number of people fishing in the area has increased substantially over the past 10 years and that fishermen, including local gill-net fishermen, have begun using selective fishing methods, such as the use of artificial plastic lures, to target large *P. quadrifilis* (see Chapter 2). The result of this may be that the species has already begun to shift towards a smaller size at which sex change occurs, although currently it is impossible to approve this statement without baseline biological information from before fishing began. However, if true, this may have caused the observed gap between the size range of intersex individuals and larger males. Similarly, increased fishing may also partially explain the highly male-dominant sex ratio as increasing levels of exploitation remove the larger (in this case female) individuals first from the population (Law, 2000).

This same line of reasoning may also help to explain the presence of a single small female of 825 mm FL, and 7.65 kg, well below the size of the next largest female (1110 mm FL, 18.75 kg). The gonads of this fish appeared extremely similar to those of the late transitional fish, whose transitional state only became apparent after histological examination. Histologically, the gonads of these two fish appeared similar, both displaying a near-identical composition of ovarian cells as well as projections of connective tissue which, in the transitional fish, were filled with residual spermatogenic tissue. In the female, an area of weakly formed connective tissue was also noticeable close to where one would expect to find a residual sperm duct. Therefore, it is likely that this fish may have only recently been derived from a transitional fish, with the testicular tissue not apparent. The fact that it is of a smaller size may be a result of slow growth.

Alternatively, it is also possible that this small fish is a primary female (an individual which developed as a female without ever occupying a male or intersex reproductive stage) in an immature or resting state. If we consider the possibility that it may be an immature primary female, it would indicate that primary female maturation occurs at a far larger size compared to that of males due to the fact that mature male fish were observed at relatively small sizes (smallest mature male – 436 mm FL, 1.46 kg). It is also unlikely that this fish would be resting as the ovaries of all other female fish were categorized as stage-III or higher during what appears to be their peak reproductive period (based on monthly GSI values). Despite this, we cannot rule out the possibility that primary females are present within the population, although it seems highly unlikely. Indeed, digyny (where females have dual pathways of development) has been observed in other confirmed and suggested protandrous species (Longhurst, 1965; Fujii, 1971; Moore, 1979).

*Polydactylus quadrifilis* in the Kwanza Estuary are renowned for their large size and all of the International Game Fish Association world recreational angling records come from this location (IGFA, 2017). Anecdotal evidence from the local community suggests that the largest fish are always female (see Chapter 7) and the results from this study support this notion. Female *P. quadrifilis* displayed significantly higher GSI values (mean – 1.96, max – 5,28) when compared to those of mature males (mean – 0.27 and maximum of 0.89). The higher GSI of females combined with their larger average body size indicates that they hold high reproductive potential. The fact that the population structure is dominated by many smaller male fish may be balanced by the high fecundity of large female fish. To further illustrate this, the 10 developed females observed in this chapter held more than two-fold more cumulative gonadal mass than all 121 non-juvenile males combined. The observation is striking and the population of *P. quadrifilis* in this region are undoubtedly highly dependent on large females for successful reproduction and recruitment. Furthermore, through natural selection, females that have survived long enough to reach large sizes are likely to be the most well-adapted individuals in the population and therefore hold immense genetic value.

It is important to note that sample sizes for intersex and female fish during this study were relatively low. It is hypothesised that the cause for this is related to natural population structure, resulting in fewer individuals within the sample group. This is common for protandrous hermaphrodites and male-dominated sex-ratios have been reported in a number of species (Sadovy & Shapiro, 1987). Additionally, it may be possible that the low number of intersex and female fish may be a result of increased fishing pressure which has begun reducing the number of larger, older fish (Alonzo & Mangel, 2004). Unfortunately, the only means in which sample sizes of intersex and female fish could be increased would be via further biological sampling. The sampling technique, which utilised fishing as a collection method, is unlikely to have selected against larger individuals, although it is likely to have contributed towards the lack of very small juvenile fish. Although sample sizes remain reasonably low, each sex is adequately represented within this study in order to draw realistic conclusions about the sexual pattern of *P. quadrifilis* and thus further biological sampling would not be warranted. However, further analysis of other populations in different locations may provide useful information about population specific trends and aid in the effective management of the species across its distribution.

Protandrous fishery species are becoming increasingly acknowledged as highly susceptible to overexploitation (Molloy et al., 2007). The stock collapse of *Polydactylus sexfilis*, a suspected protandrous polynemid species from the Indo-Pacific, has largely been attributed to recruitment overfishing (Friedlander & Ziemann, 2003). The reliance of *P. quadrifilis* on large highly-fecund female fish for reproductive success is likely to make the species sensitive to overfishing. Appropriate management strategies need to be implemented and should aim to protect large adult females through the use of either maximum legal limits or slot sizes. The fact that many *P. quadrifilis* fisheries make use of gill-nets would seemingly make the targeting of specific sized individuals fairly uncomplicated. However, the large individuals captured using less selective gears, such as beach seines and hook and line should be revived and released rather than harvested. The seasonal nature of the fishery for large females may reduce the difficulty of implementation and enforcement of these regulations. Unfortunately, the compliance with regulations in the artisanal and subsistence sectors may be complicated due to their reliance on fish for their livelihoods. However, emphasis on compliance in the recreational sector, whose participants are not dependent on the capture of fishes for their livelihoods, may be the best way forward for the species in the short-term. Further investigation of the life-history of *P. quadrifilis*, through the incorporation of age and growth data, will provide critical information for the potential management of the species.

# Chapter 4

## The age, growth and life-history pattern of *Polydactylus quadrifilis* in the Kwanza Estuary, Angola

### 4.1 Introduction

In fisheries management, it is widely acknowledged that there is a need for a comprehensive understanding of the biology and life-history of the fishery species at hand (Beverton & Holt 1957; King & McFarlane, 2003). An important facet of this understanding relies upon the accurate aging of fish, as it allows researchers to investigate the growth patterns of individual species and populations and is valuable for the assessment of population productivity, reproductive potential and sustainability over time (Higgins et al., 2015). Fish growth is often plastic, both within and amongst individuals, and can change in response to fishing pressure or other ecosystem or environmental change (Jennings, 1998; King & McFarlane, 2003; Moore et al., 2011). Monitoring for these biological changes can often give us the first indications that populations may be under pressure and therefore population-specific baseline estimates of important life-history characteristics need to be established as reference points to guide management decisions.

Traditionally, the life-history of species has been modelled under the assumption that the majority, if not all, members of the same species develop in the same way and maintain a similar life-history. However, it is evident that there is inherent variability in the evolutionary, ecological and behavioural characteristics within a species (Munday et al., 2006; Higgins et al., 2015; Crook et al., 2017, Reid et al., 2018). The most commonly addressed of those is the species-specific variability in life-history traits between male and female fish. This is often the result of marked differences in the behavioural and reproductive traits of males and females and thus their allocation of resources towards somatic growth is not the same (Gross, 1996).

Many fish species have complex life-histories and it is becoming increasingly acknowledged that there are often numerous pathways for individual fish growth and sexual development both between and within sexes (Gross, 1996; Munday et al., 2006; Crook et al., 2017). This is further complicated in fish species with elaborate sexual patterns such as hermaphroditism. In hermaphroditic fishes, growth often varies according to the gender state of the individual and sex reversal is acknowledged as an energetically expensive process affecting somatic growth (Higgins et al., 2015). In sequential hermaphrodites, growth may differ between the primary and the terminal sex (Garratt et al., 1993; Munday et al., 2004) and the size and age at which sex change occurs is often highly variable (Munday et al., 2006; Pember, 2006). Sequentially hermaphroditic fishes may undergo sexual development through a variety of pathways. In some cases, not all individuals of the primary sex will transition into the terminal sex (Pajuelo et al., 2008), a phenomenon known as partial protandry in male-first hermaphrodites or partial protogyny in female-first hermaphrodites. Additionally, not all members of the terminal sex will be derived from the primary sex (diandry in protogynous species and digyny in protandrous species) (Sadovy & Shapiro, 1987). These phenomena complicate the modelling of fish growth because it is only possible to assess the sexual state of an individual at the time of capture and it is most often impossible to accurately estimate the prior or future sexual function of said individual.

Despite this, growth models have been developed for many sequentially hermaphroditic fishes (Garratt et al., 1993; Munday et al., 2004; Pember, 2006), yet few publications have made any attempt at modelling and understanding the inherent life-history complexity present. Many of these models adopt the same technique that would be applied to a typical gonochorist species, producing a singular correlation between fish length and age based on all of the individuals within a population (e.g. Davis, 1984; Pember, 2006). In some cases, it may be argued that this is perhaps because the investigated species have not shown significant differences in growth which would have warranted further investigation. It may also be explained by the possibility that many of these species only (or at least largely) displayed one developmental pathway from the primary to the terminal sex at a specific age or size. Thus, a growth model describing the whole population would adequately represent a high enough proportion of the population to ignore outliers created by a select few individuals with alternative life-history tactics or strategies (Higgins et al., 2015). Additionally, many researchers have provided separate correlations for fish of either sex, disregarding the fact that a proportion (or all) of the fish of the terminal sex are derived from the primary sex (e.g. Munday et al., 2004; Choat et al., 2006). For example, in a protandrous fish species, how is it possible to model female growth exclusively when females were in fact once males?

Regardless of the reasoning, the consequences of these techniques should be considered as we attempt to adequately describe the complex biological traits of fish species (Higgins et al., 2015). For example, certain sequential hermaphrodites may have numerous pathways for sexual development, each of which is affected differently by external selection pressures (Crook et al., 2017). If individuals on a specific developmental pathway exhibit slower growth rates, for example, it is likely that management recommendations may not favour these fish. Since the maintenance of diversity, whether genetic, physiological, behavioural or life-history, is a central tenet of preserving the resilience of a species through the promotion of adaptive capacity (Elmqvist et al., 2003), the removal of fish belonging to a specific pathway will have consequences for the species. Therefore, describing the growth patterns of different developmental pathways and incorporating these into fisheries management is critical for the promotion of resilient fisheries.

*Polydactylus quadrifilis* is a protandrous hermaphrodite and plays an important role in recreational, subsistence and small-scale fisheries across its distribution (Loubens, 1964; Moses, 2000; Motomura, 2004; Butler et al., 2018) (see Chapter 2). Despite the fisheries value of the species, it's biology is largely understudied, excepting for a doctoral study undertaken in Gabon in the mid-1960's (Loubens, 1966). Furthermore, the protandrous nature of the species increases its susceptibility to overexploitation, via recruitment overfishing, as fishing practices can selectively remove larger, often female, fish first from the population resulting in egg-limitation (Law, 2000) (see Chapter 3).

The protandrous nature of *P. quadrifilis* is likely to affect the growth between individuals over time. To understand these differences, it is important to identify the various pathways that exist for individual sexual development. In Chapter 3, *P. quadrifilis* was identified as a protandrous hermaphrodite and it was also noted that there were a small number of large males within the population whose size exceeded the size range in which sex changing fish were observed. Based on this observation, it was hypothesised that some proportion of primary male fish do not change sex and become female (partial protandry). In order to confirm this trait, it was recommended that accurate age estimates are utilised to investigate the growth of the species (Butler et al., 2018) (Chapter 3). Furthermore, no small or juvenile female fish below the size range in which transitional individuals were found. Therefore, it seemed unlikely that primary females existed within the sampled group of fish, although it was not possible to confirm with certainty whether the species is mono- or dygynic.

This chapter aimed to investigate the life-history characteristics of *P. quadrifilis* in the Kwanza Estuary and interrogate the manner in which growth rates are measured in hermaphroditic fishes. To do this, we examined the size- and age-at-maturity and size- and age-at-sex-change for *P. quadrifilis*. We thereafter investigated alternative methods for adequately describing the growth of *P. quadrifilis* individuals belonging to either one of two distinct hypothetical life-history pathways: pathway I ('changers') – initial maturation as a primary male followed by a sex change to female; pathway II ('non-changers') – initial maturation as a male fish with no subsequent sex change. In doing so, we analysed length-at-age data according to the common techniques utilised in the contemporary literature, which included modelling the entire population as a whole and modelling the separate sexes using the Von Bertalanffy Growth Function (VBGF). Thereafter, we attempted to model the two developmental pathways (i.e. the 'changers' and the 'non-changers'). To do so, a number of assumptions were required in order to place younger primary male fish into either pathway, as it was not possible to ascertain whether or not they would later change sex. Two hypothetical approaches were taken and presented models that placed younger male fish using increased growth rate as the effect of sex change, in the first case, and as the cause of sex change in the second. Additionally, important life-history estimates were calculated for *P. quadrifilis* in the Kwanza Estuary including the length- and age- at-maturity and at-sex-change.

## 4.2 Methods

Sampling took place in the mouth area and first four kilometres of the Kwanza Estuary in Angola (Figure 2.1) between the 21$^{st}$ of June 2016 and the 31$^{st}$ of March 2018. Two hundred and twenty-one fish were either collected using conventional angling techniques or purchased from local subsistence gill-net and longline fishermen.

Once acquired, fish were weighed (nearest 0.01 kg) and measured (FL and TL, mm) before being dissected. Fish were sexed and the gonads were staged according to the eight stages outlined by Laevastu (1965): I = virgin (males only); II = immature/resting; III = developing; IV = maturing; V = mature/pre-spawning; VI = spawning; VII = spent; VIII = recovering (Butler et al., 2018) (Chapter 3). The sagittal otoliths were removed and stored in paper envelopes for further processing and analysis.

Additionally, the sagittal otolith pairs from 83 *P. quadrifilis* (with measurement data; FL, mm) were collected from the same location between 2007 and 2014. This data was only included in assessing the overall growth of *P. quadrifilis* (Von Bertalanffy Growth Functions – VBGF's).

*4.2.1 Otolith preparation*

To determine the optimal otolith sectioning protocol, a pilot study was conducted using a sub-sample of 60 otolith pairs. Otoliths from the same fish were either analysed whole in methyl salicylate, or after transverse or longitudinal sectioning at 500 µm. Otoliths were set in clear polyester resin before being sectioned using a twin-blade diamond-edged geological saw and mounted on microscope slides using DPX mountant. For each analysis, the number of opaque zones between the otolith nucleus and edge were recorded microscopically using reflected light by three independent readers. Additionally, each otolith reading was assigned a readability index value of between 0 (unreadable) and 5 (easily readable). The ideal sectioning method was selected based on the average of the readability indices and the calculated index of average (absolute) percentage error (IAPE - Beamish and Fournier 1981):

$$IAPE = \frac{1}{n}\sum_{j=1}^{n}[\frac{1}{R}\sum_{i=1}^{R}|\frac{X_{ij} - \overrightarrow{X_J}}{\overrightarrow{X_J}}|]$$

where n fish are aged, R is the number of times each fish j is aged, $X_{ij}$ is the *i*th age determined for the *j*th fish, and $\overrightarrow{X_J}$ is the average age calculated for the *j*th fish.

Based on the results of the pilot study, all subsequent otoliths were sectioned transversely at 500 µm. The entire otolith collection was read by two readers independently and thereafter reread by the first reader following a period of several weeks. On each occasion, the number of visible opaque bands were counted and the otolith edge type was classified according to Harris et al. (2007) and Burton et al. (2015): 1 – opaque zone on otolith edge; 2 – narrow translucent zone (<30% of the width of the previous translucent zone); 3 – moderate translucent zone (30%-60% of the width of the previous translucent zone); 4 – wide translucent zone (>60% of the width of the previous translucent zone). For all sections, the age of a fish was accepted when a) at least two of the three opaque zone counts were the same (e.g. 4, 4, 5 = 4) and b) for fish that were aged as 10 years or older, when the three counts were consecutive (e.g. 10, 11, 12), the middle reading (11) was accepted. The classification of otolith edge type was only considered if it was consistent across all three readings.

Age values were adjusted according to the edge type for each otolith. Individuals that were captured during or soon after the period of opaque zone formation were assigned an age equivalent to the opaque zone count (edge types 1 – opaque zone on otolith edge; and 2 – narrow translucent zone). Otoliths with edge types 3 (moderate translucent zone) and 4 (wide translucent zone) were given an age equivalent to the opaque zone count plus one (Harris et al., 2007; Burton et al., 2015).

*4.2.2 Age validation*

To validate the periodicity of opaque ring formation, a representative sample of 91 *P. quadrifilis* captured using conventional angling gear were injected intramuscularly with high-tet 120 oxytetracycline (OTC; 0.1 $ml.kg^{-1}$), tagged and released at the capture site. A single fish was recaptured after a period of 333 days at liberty. The otoliths from this individual were removed, transported and sectioned (as above) in the dark and observed and photographed at 40x magnification under ultraviolet (UV) light and under normal reflected light.

As further endorsement, the periodicity of opaque zone formation was indirectly validated using the mean edge type per month (Harris et al., 2007).

*Models*

*Length- and age- at-maturity and at-sex-change*

Macroscopic staging data was used to assess the length- and age-at- sexual maturity of sampled *P. quadrifilis*. Fish were considered mature when gonads were staged as III or above, based on the assumption that they would mature within the same spawning season. A modified logistic regression model (Walker, 2005) was used to estimate length- and age-at-maturity according to the following equations:

$$P(L) = P_{MAX}.(1 + e^{-\ln(19)\left(\frac{L-L_{50}}{L_{95}-L_{50}}\right)})^{-1}$$

$$P(A) = P_{MAX}.(1 + e^{-\ln(19)\left(\frac{A-A_{50}}{A_{95}-A_{50}}\right)})^{-1}$$

where $P$ is the proportion of mature fish at a given length ($L$) or age ($A$), $L_{50}$ (or $A_{50}$) is the length (or age) at which 50% of the fish have reached maturity, $L_{95}$ (or $A_{95}$) is the length (or age) at which 95% of the fish have reached maturity and $P_{MAX}$ is the asymptote of the ogive. A generalised linear model (GLM) with a binomial error structure and logit-link function was used to estimate $L_{50}$ /$A_{50}$ and $L_{95}$/$A_{95}$ using R version 3.3.3 (R Development Core Team) (Harry et al., 2013).

The lengths and ages at which 50% of individuals had either initiated or completed sex-change was calculated using the same logistic regression model. In the first case, intersex fish were grouped with females due to the fact that they had either initiated (intersex) or completed (female) sex-change. In the second case, intersex fish were grouped with males to assess for the $L_{50}$ at which sex change was completed. Because the aim of this analysis was to accurately estimate the $L_{50}$ and $A_{50}$ for fish that undergo sex-change, males over the age of 10 were excluded from the analysis under the assumption that they would not change sex.

*4.2.3 Growth*

The VBFG was chosen to model growth due its successful prior application for the majority of aged polynemid species (Longhurst, 1965; Dentzau & Chittenden, 1990; Prasad et al., 2005; Pember, 2006; Sossoukpe et al., 2016). The VBGF was fitted to the length-at-age data using the following formula:

$$L(t) = L_\infty(1 - e^{-k(t-t_0)})$$

where $L(t)$ is the fork-length of a fish at age $t$, $L_\infty$ is the asymptotic maximum length for the population, $k$ is the growth coefficient and $t_o$ is the y-intercept or 'size-at-age 0'. The model parameters were estimated by minimising the sum of squares of the residuals using the Microsoft Excel function SOLVER. Model variability was calculated using parametric bootstrapping in which 1000 iterations for the parameter estimates were randomly computed. The 95% confidence intervals for the parameters were calculated from the bootstrap data as the 2.5 and 97.5 percentiles of the corresponding estimated values (Buckland, 1984).

The growth of individuals from the two hypothesised developmental pathways (pathway I, 'changers' – initial maturation as a primary male followed by a sex change to female and pathway II, 'non-changers' – initial maturation as a male fish with no subsequent sex change) was investigated using VBGF's. However, it was not possible to ascertain which pathway small male fish would utilise, as it is possible that they may still change sex to female at a later stage. Therefore, two different model approaches were taken, each with different model assumptions for the hypothetical pathways. These two approaches investigated increased growth as the effect (approach 1) and as the cause (approach 2) of sex change (Figure 4.1).

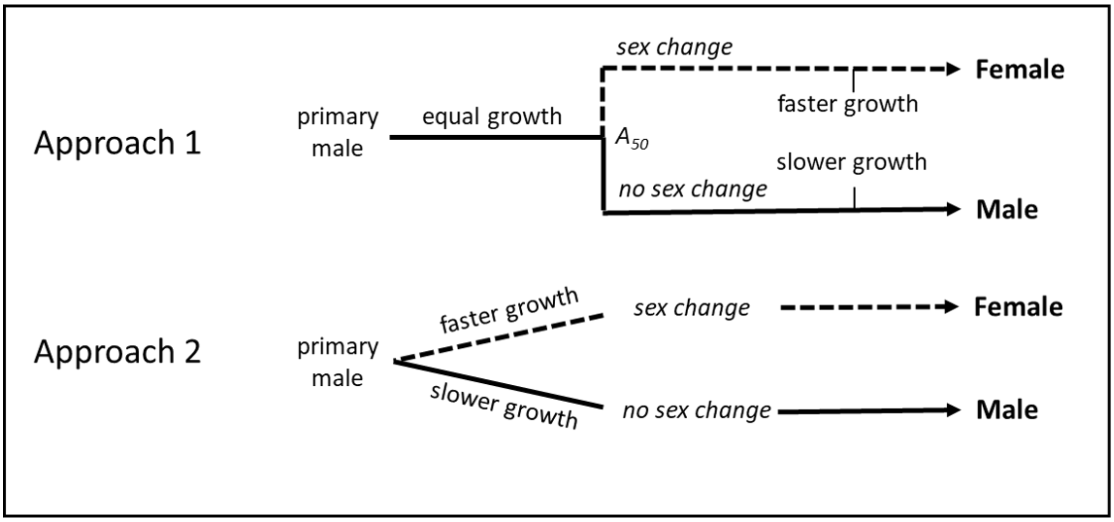


**Figure 4.1:** Schematic diagram displaying the two approaches utilised to assess the potential drivers for sex change in *Polydactylus quadrifilis* and used to explain the various developmental pathways present. Approach 1 assumes that protandric sex-change results in an increase in growth rate. The second approach assumes that growth varies naturally and that the fastest growing individuals change sex. Dotted lines represent pathway I ('changers') and solid lines represent pathway II ('non-changers').

Approach 1: Sex-change causes an increase in growth rate

The first approach investigated the possibility that sex-change influences growth. In doing so, it was assumed that primary male growth was equal for both pathways up to the calculated $A_{50}$ at which sex change is initiated (Figure 4.1). Therefore, male fish with ages below $A_{50}$ were grouped into both pathways. The model assumptions were as follows:

(i) all intersex and female fish are derived from males,

(ii) fish lifespan and mortality are equal for both pathways,

(iii) growth is monophasic for both pathways,

(iv) fish growth up to the $A_{50}$ for sex change is equal for both pathways (i.e. increased growth takes place after sex-change), and

(v) male fish above the $A_{50}$ for sex change will remain male.

Approach 2: Increased growth of primary males is the cause of sex-change

The second approach investigated the possibility that sex change is the result of differential individual growth. The ratio of female to male fish above the $A_{95}$ for sex change completion was calculated as 3:1. All fish in each age class below the age corresponding with the $A_{95}$ for sex change completion were divided according to size with the larger three-quarters of the data points grouped into pathway I and the smallest quarter into pathway II. All intersex and female fish were grouped into pathway I and only male fish were considered in pathway II. Model assumptions were as follows:

Assumptions (i), (ii) and (iii) as outlined in Approach 1, and

(iv) the ratio of fish belonging to each pathway is equal across all age classes and that the ratio is 3:1, changers:non-changers,

(v) sex change is the result of accelerated growth, and

male fish above the $A_{95}$ for sex change will remain as males.

*4.2.4 Statistical analyses*

A likelihood ratio test (LRT) (Kimura, 1980) was performed to assess for difference between the model parameters and the models themselves between the two approaches. Likelihood ratio tests were also used to assess for difference between the conventional models (the 'full model', 'all males' and 'all females') and the two separate pathways modelled in the two hypothetical approaches. This was performed so as to assess whether utilising the 'full model', 'all males' and 'all females' would adequately represent individual growth of sex changing fish and the growth of non-changing fish. The coefficient of determination was calculated for all models according to the following formula:

$$R^2 = \frac{SSR}{SST}$$

where SSR is the sum of squares of the model residuals and SST is the sum of squares of the total error. Model standard deviation was also calculated before and after the calculated $A_{50}$ and the $A_{95}$ for sex change in all cases.

**4.3 Results**

A total of 226 *P. quadrifilis* were sampled from 2016 to 2018 ranging in size from 160.0 mm to 1360.0 mm fork-length (FL), in mass from 0.05 kg to 40.7 kg and in age from one to 23 years (Figure 4.2). Of these, the majority (n = 170, 75.2%) were males (mean ± SD FL = 814.7 ± 138.2 mm; range: 436.0–1185.0 mm). The remaining fish sampled were comprised of females of larger size (n = 21; mean ± SD FL = 1193.1 ± 159.7 mm; range: 825.0–1360.0 mm), intersex fish (n = 9; mean ± SD FL = 954.1 ± 104.0 mm; range: 790.0–1125.0 mm) and juveniles (n = 26; mean ± SD FL = 244.2 ± 30.7 mm; range: 160.0–313.0 mm) (Figure 4.2).

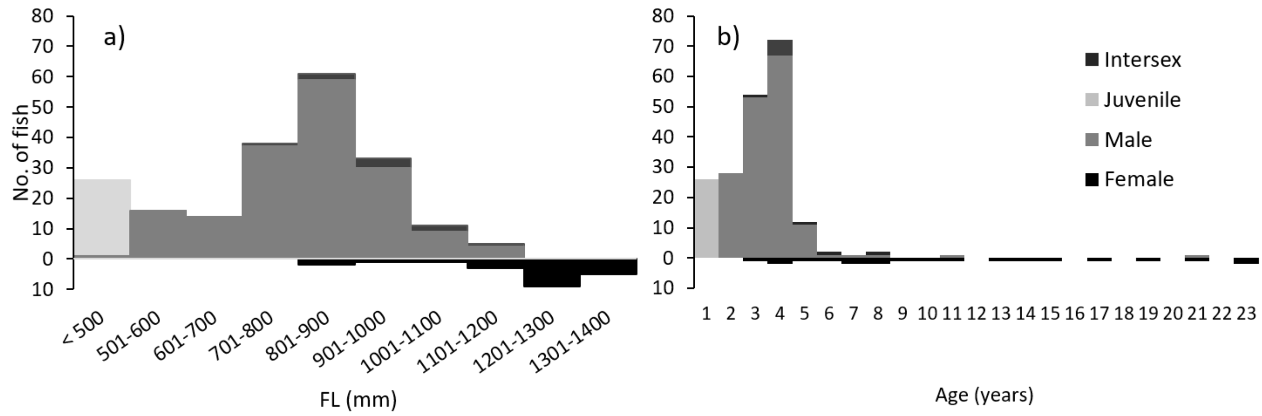


**Figure 4.2:** Sex-specific length (a) and age (b) frequency histograms of 226 *Polydactylus quadrifilis* sampled from the Kwanza Estuary, Angola.

The additional 85 *P. quadrifilis* samples collected between 2007 and 2014 comprised fish ranging in size from 475 mm to 1525 mm FL and in age from two to 23 years. Of these, 24 fish were sexed as male, six as female and 55 were unsexed. These individuals were only included in the overall growth equation (VBGF's).

Body-size relationships adhered to the following equations:

$$TL = 1.1 \times FL + 27.2 \quad (n = 226, r^2 = 0.99)$$

$$W = 5 \times 10^{-9} FL^{3.14} \quad (n = 226, r^2 = 0.99)$$

*4.3.1 Otolith preparation*

Results of the pilot study indicated that transverse otolith sections provided a higher ARI value (4.0; longitudinal – 2.4; whole otoliths – 2.2) and a lower IAPE value (6.76) than longitudinal sections (25.05) or whole otoliths (40.13). Thus, all remaining otoliths were sectioned transversely.

*4.3.2 Age validation*

Otolith sections displayed broad translucent zones and narrow opaque zones during the first 3 to 4 years of growth (Figure 4.3a, b). Thereafter opaque zone formation occurred closer together resulting in narrower translucent zones (Figure 4.3b). Agreement was good between readers and there was consensus between at least two of the three readings for the majority of otoliths (96.69%). For the remaining 10 otoliths (3.31%), where none of the three readings coincided, the three readings were consecutive (10, 11, 12) and the middle value was accepted. The IAPE score across the three readings for all otolith sections was 4.27%.

A single clear fluorescent band appeared in the sectioned otolith of the recaptured specimen (Figure 4.3d). This fish was tagged on 4 August 2016 and recaptured on 3 July 2017 (333 days at liberty). During this time, the fish grew 125.0 mm from a FL of 905.0 mm at tagging to 1030.0 mm at recapture. The fluorescent band was positioned on the outer edge of a distinctive opaque zone (Figure 4.3c, d). While there was no clear opaque zone present between the fluorescent band and the outer edge of the otolith, the distance between the fluorescent band

and the otolith edge was equivalent to the distance between the two outer opaque zones (Figure 4.3c, d).

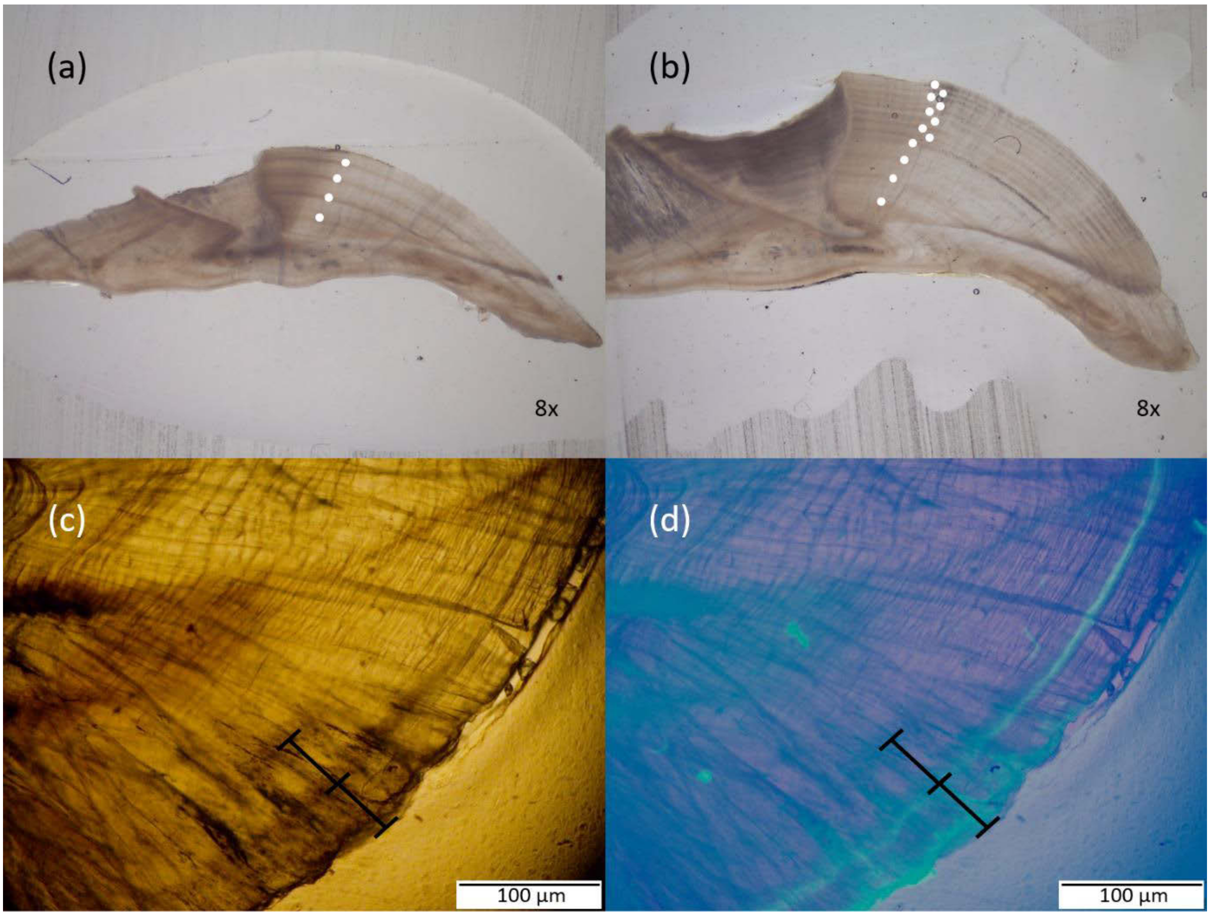


**Figure 4.3:** Photomicrographs of sectioned *Polydatylus quadrifilis* otoliths from a) a 5-year old (4 increments plus 1 – otolith edge type 4) 1010 mm FL male (August 2016), b) a 13-year old 1340 mm FL female (September 2017) and c) & d) a 6-year old recaptured intersex specimen following intramuscular injection of oxytetracycline (OTC; 0.1 $ml.kg^{-1}$)(July 2017) under normal transmitted light (c) and ultraviolet light (d). The recaptured individual spent 333 days at liberty and grew from a FL of 905 mm at tagging to 1030 mm at recapture.

Otolith edge analysis revealed that opaque zone formation occurred once annually (Figure 4.4). *Polydactylus quadrifilis* in the Kwanza Estuary deposited opaque zones on the otolith marginal edge from July to February with a peak in November (Figure 4.4). Narrow translucent zones (edge type 2) predominantly appeared in otoliths harvested from December to March. Moderate translucent zones (edge type 3) were identified in otoliths collected in the months from January until September (edge type 3) while wide translucent zones (edge type 4) predominantly appeared in otoliths collected from April until October prior to peak opaque zone formation in November (Figure 4.4).

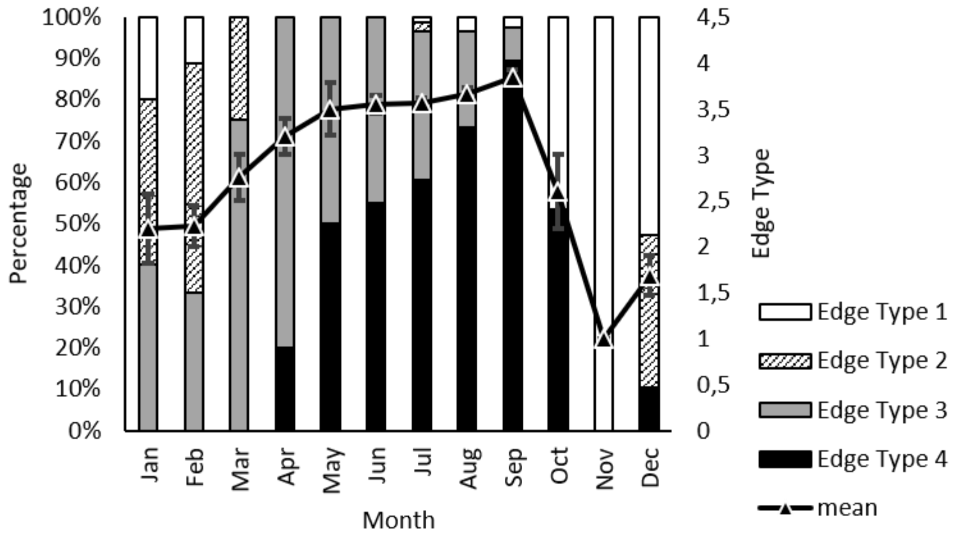


**Figure 4.4:** Monthly percentage composition of otolith edge types and mean monthly edge score with standard error of *Polydactylus quadrifilis* sampled from the Kwanza Estuary, Angola. Edge types: 1 – opaque zone on otolith edge; 2 – narrow translucent zone (<30% of the width of the previous translucent zone); 3 – moderate translucent zone (30%–60% of the width of the previous translucent zone); 4 – wide translucent zone (>60% of the width of the previous translucent zone). N-values are displayed above each month.

*Length- and age- at-maturity and at-sex-change*

*Polydactylus quadrifilis* displayed rapid maturation with all juvenile fish sampled (range: 160 – 313 mm FL) belonging to the 1-year age class. All fish belonging to subsequent age classes were mature (436 – 1360 mm FL). The length and age at which 50% of the population were mature was calculated as 399.2 mm FL and 1.50 years. The length and age at which 95% of the population were mature was calculated as 512.2 mm FL and 1.86 years, respectively.

The size and age at which sex change occurred within *P. quadrifilis* varied over a moderately wide range. Intersex individuals were observed at sizes ranging from 790 to 1125 mm FL and ages ranging from 3 to 8 years (Figure 4.2). The length and age at which 50% of the population had initiated or completed sex change was calculated to be 1082.3 mm FL and 1127.4 mm FL and 6.2 years and 7.06 years, respectively (Figure 4.5a–d). The length and age at which 95%

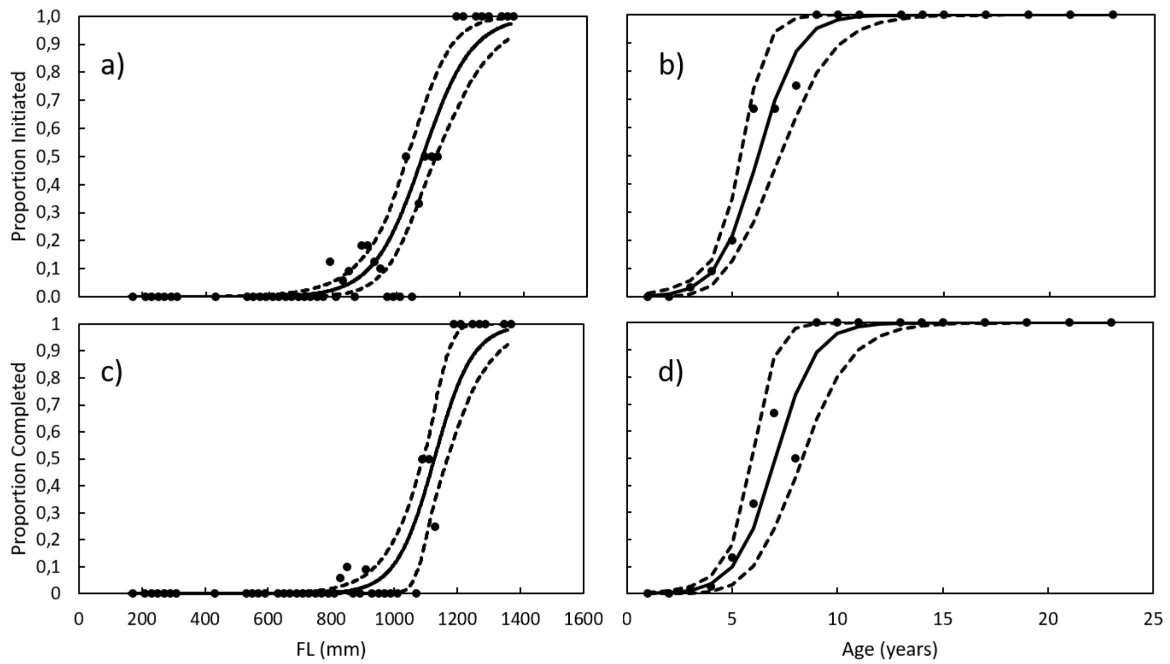


**Figure 4.5:** Length- (a, c) and age- (b, d) at-sex change initiation (a, b) and completion (c, d) for *Polydactylus quadrifilis* collected from the Kwanza Estuary, Angola. Dotted lines represent the 95% confidence intervals.

of the population had initiated or completed sex change was calculated as 1309.4 mm and 1306.2 mm and 9.0 years and 9.8 years, respectively.

*4.3.3 Growth*

Growth in *P. quadrifilis* was adequately modelled by the VBGF (Figure 4.6a, Table 4.1) providing an overall $R^2$ value of 0.55 (Table 4.2). The full model predicted the length-at-age particularly well below the $A_{50}$ and $A_{95}$ for sex change completion, demonstrated by lower model standard deviation (Figure 4.6a, b, Table 4.2). However, the model predicted length-at-age poorly above the $A_{50}$ and $A_{95}$ for sex change completion (Table 4.2) caused by noticeable differences in mean size-at-age between male and female fish above 10 years of age. (Figure 4.6b). In contrast, when modelling all males and all females together, the model predicted the

**Table 4.1:** Statistical values of the Von Bertalanffy growth parameters for *Polydactylus quadrifilis* sampled from the Kwanza Estuary, Angola. Values are displayed for the full dataset 'full model', for all male fish, all female fish and for the two developmental pathways, pathway I 'changers' and II 'non-changers', under the two hypothetical approaches seen in Figure 4.6.

| | | Summary Statistics | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Parameter | Point estimate | Mean | Coefficient of variation | Standard error | Lower 95% CI | Upper 95% CI | Min | Max |
| | **Full model (n = 311)** | $L\infty$ (mm, FL) | 130.79 | 130.85 | 0.01 | 1.27 | 128.42 | 133.25 | 126.61 | 135.59 |
| | | $K$ (years$^{-1}$) | 0.32 | 0.31 | 0.03 | 0.01 | 0.30 | 0.33 | 0.29 | 0.35 |
| | | $t_0$ (years) | 0.23 | 0.23 | 0.21 | 0.05 | 0.14 | 0.33 | 0.06 | 0.39 |
| | **All females (n = 27)** | $L\infty$ (mm, FL) | 134.63 | 134.88 | 0.02 | 2.24 | 130.88 | 139.72 | 129.11 | 143.97 |
| | | $K$ (years$^{-1}$) | 0.30 | 0.30 | 0.21 | 0.06 | 0.19 | 0.44 | 0.14 | 0.59 |
| | | $t_0$ (years) | -0.08 | -0.21 | -4.54 | 0.94 | -2.36 | 1.20 | -5.25 | 1.80 |
| | **All males (n = 220)** | $L\infty$ (mm, FL) | 113.28 | 113.25 | 0.01 | 1.68 | 109.99 | 116.43 | 108.19 | 117.90 |
| | | $K$ (years$^{-1}$) | 0.44 | 0.44 | 0.04 | 0.02 | 0.41 | 0.48 | 0.39 | 0.51 |
| | | $t_0$ (years) | 0.43 | 0.43 | 0.08 | 0.04 | 0.36 | 0.50 | 0.32 | 0.54 |
| **Approach 1** | **Pathway I 'changers' (n = 246)** | $L\infty$ (mm, FL) | 133.24 | 133.32 | 0.01 | 1.47 | 130.47 | 136.19 | 128.08 | 137.91 |
| | | $K$ (years$^{-1}$) | 0.31 | 0.31 | 0.03 | 0.01 | 0.29 | 0.32 | 0.27 | 0.34 |
| | | $t_0$ (years) | 0.26 | 0.26 | 0.17 | 0.04 | 0.17 | 0.34 | 0.09 | 0.39 |
| | **Pathway II 'non-changers' (n = 220)** | $L\infty$ (mm, FL) | 113.28 | 113.30 | 0.01 | 1.61 | 110.12 | 116.47 | 108.22 | 118.23 |
| | | $K$ (years$^{-1}$) | 0.44 | 0.44 | 0.04 | 0.02 | 0.41 | 0.48 | 0.39 | 0.51 |
| | | $t_0$ (years) | 0.43 | 0.43 | 0.08 | 0.04 | 0.36 | 0.50 | 0.31 | 0.54 |
| **Approach 2** | **Pathway I 'changers' (n = 195)** | $L\infty$ (mm, FL) | 132.55 | 132.59 | 0.01 | 1.26 | 130.21 | 135.06 | 128.67 | 136.78 |
| | | $K$ (years$^{-1}$) | 0.32 | 0.32 | 0.03 | 0.01 | 0.30 | 0.34 | 0.29 | 0.35 |
| | | $t_0$ (years) | 0.25 | 0.25 | 0.17 | 0.04 | 0.17 | 0.33 | 0.09 | 0.36 |
| | **Pathway II 'non-changers' (n = 61)** | $L\infty$ (mm, FL) | 113.65 | 113.61 | 0.01 | 1.46 | 110.84 | 116.55 | 109.64 | 117.92 |
| | | $K$ (years$^{-1}$) | 0.38 | 0.38 | 0.04 | 0.02 | 0.35 | 0.41 | 0.34 | 0.43 |
| | | $t_0$ (years) | 0.46 | 0.45 | 0.11 | 0.05 | 0.35 | 0.55 | 0.26 | 0.59 |

length-at-age particularly well for ages above the $A_{50}$ and $A_{95}$ for sex change completion but poorly for ages below the $A_{50}$ and $A_{95}$ for sex change completion, particularly for females (Table 4.2).

When modelling the separate developmental pathways, the growth curves for pathway I and pathway II in approach 1 (Figure 4.6c) appeared similar to those found in approach 2 (Figure 4.6d). However, there was a significant difference between the models for pathway II in approach 1 versus pathway II in approach 2 (likelihood ratio test, $p < 0.01$, Table 4.3), although there was no significant difference between the parameters $L_\infty$, k and $t_0$ (Table 4.3). There was

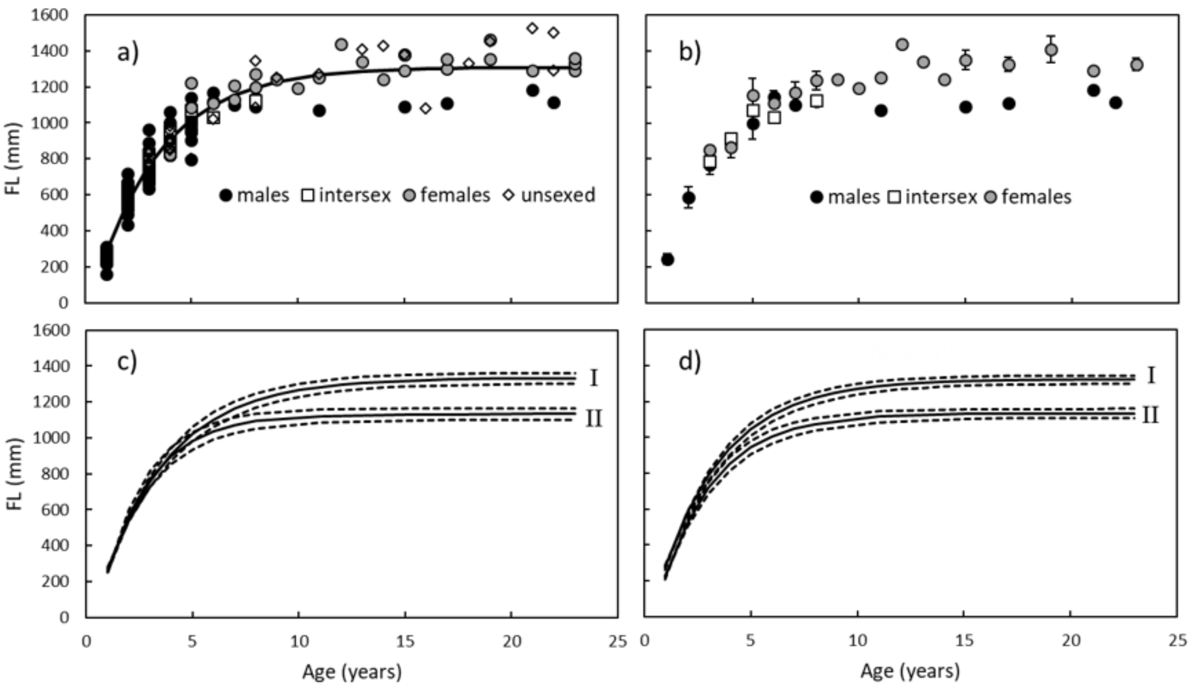


**Figure 4.6:** Length-at-age (a) and mean length-at-age (with standard deviation) (b) of 331 *Polydactylus quadrifilis* sampled from the Kwanza Estuary, Angola. A Von Bertalanffy growth equation is fitted to all fish sampled ('full model') (a) and to the two hypothetical developmental pathways, pathway I ('changers') and pathway II ('non-çhangers') for Approach 1 (c) and Approach 2 (d). For Approach 1 (c), all male fish below the calculated $A_{50}$ for sex change initiation (6.2 years) are grouped under both pathways (I and II) and for Approach 2 (d), male data points (up until the age of 10 years) are grouped into either pathway according to size-at-age with the upper three-quarters grouped into pathway I and the lower quarter grouped into pathway II.

no significant difference between the models or their parameters for pathway I (Table 4.3) under either approach. When compared with the full model ($R^2$ = 0.55), a better fit was achieved for pathways I ($R^2$ = 0.63) and II ($R^2$ = 0.61) using approach 1 and for pathway II when using approach 2 ($R^2$ = 0.69). In contrast, the model fit for pathway I under approach 2 was similar ($R^2$ = 0.54) to the full model (Table 4.2). Furthermore, when compared to the full model, greatly reduced model standard deviation was observed before and after the $A_{50}$ and $A_{95}$ for sex change for pathways I and II in approach 1 and 2 (Table 4.2).

**Table 4.2:** Model standard deviation and the coefficient of determination ($R^2$) of the Von Bertalanffy growth function for *Polydactylus quadrifilis* sampled from the Kwanza Estuary, Angola. Standard deviation is provided for the model above and below the calculated $A_{50}$ and $A_{95}$ for sex change completion. Values are displayed for the full dataset 'full model', all male fish, all female fish and for either developmental pathway, pathway I 'changers' and II 'non-changers', under the two hypothetical approaches seen in Figure 4.6.

| | | | Total | Before A50 | After A50 | Before A95 | After A95 |
|---|---|---|---|---|---|---|---|
| | **Full model** | n | 311 | 261 | 50 | 278 | 33 |
| | | σ | 6.86 | 5.94 | 10.40 | 6.04 | 11.67 |
| | | $R^2$ | 0.55 | | | | |
| | **All females** | n | 27 | 6 | 21 | 10 | 17 |
| | | σ | 6.70 | 9.08 | 5.85 | 7.53 | 6.16 |
| | | $R^2$ | -0.28 | | | | |
| | **All males** | n | 220 | 210 | 10 | 215 | 5 |
| | | σ | 5.32 | 5.38 | 3.61 | 5.34 | 3.97 |
| | | $R^2$ | 0.61 | | | | |
| **Approach 1** | **Pathway I 'changers'** | n | 246 | 224 | 22 | 229 | 17 |
| | | σ | 5.77 | 5.75 | 6.00 | 5.74 | 6.19 |
| | | $R^2$ | 0.63 | | | | |
| | **Pathway II 'non-changers'** | n | 220 | 210 | 10 | 215 | 5 |
| | | σ | 5.32 | 5.38 | 3.59 | 5.34 | 3.99 |
| | | $R^2$ | 0.61 | | | | |
| **Approach 2** | **Pathway I 'changers'** | n | 195 | 171 | 24 | 178 | 17 |
| | | σ | 5.07 | 4.87 | 6.32 | 4.93 | 6.32 |
| | | $R^2$ | 0.54 | | | | |
| | **Pathway II 'non-changers'** | n | 61 | 53 | 8 | 56 | 5 |
| | | σ | 3.52 | 3.43 | 4.05 | 3.49 | 3.81 |
| | | $R^2$ | 0.69 | | | | |

Likelihood ratio tests revealed that the 'full model' was significantly different from the models for 'all males' and for the 'non-changers' (pathway II) in approach 1 and approach 2, although differences in values for k (p = 0.8) and $t_0$ (p = 0.14) were not significant in the latter (Table 4.3). There were no significant differences between the 'full model' and models for 'all females' and the 'changers' (pathway I) in approaches 1 and 2 (Table 4.3).

**Table 4.3:** Likelihood ratio test results (p-values) for the comparison of the various Von Bertalanffy age-growth models and their parameters for *Polydactylus quadrifilis.* The symbol † is present where a comparison was foregone because the two models being compared were the same (i.e. all values = 1).

| | | | | | | **Approach 1** | | **Approach 2** | |
|---|---|---|---|---|---|---|---|---|---|
| | | | **Full model** | **All females** | **All males'** | **Pathway I 'changers'** | **Pathway II 'non-changers'** | **Pathway I 'changers'** | **Pathway II 'non-changers'** |
| | **All females** | *model* | 0.41 | - | - | - | - | - | - |
| | | *L∞* | 0.28 | - | - | - | - | - | - |
| | | *k* | 0.87 | - | - | - | - | - | - |
| | | *t⁰* | 0.78 | - | - | - | - | - | - |
| | **All males** | *model* | **< 0.01** | **< 0.01** | - | - | - | - | - |
| | | *L∞* | **< 0.01** | **< 0.01** | - | - | - | - | - |
| | | *k* | **< 0.01** | 0.10 | - | - | - | - | - |
| | | *t⁰* | **0.03** | 0.56 | - | - | - | - | - |
| **Approach 1** | **Pathway I 'changers'** | *model* | 0.78 | 0.64 | - | - | - | - | - |
| | | *L∞* | 0.40 | 0.69 | - | - | - | - | - |
| | | *k* | 0.67 | 0.94 | - | - | - | - | - |
| | | *t⁰* | 0.80 | 0.73 | - | - | - | - | - |
| | **Pathway II 'non-changers'** | *model* | **< 0.01** | - | † | **< 0.01** | - | - | - |
| | | *L∞* | **< 0.01** | - | † | **< 0.01** | - | - | - |
| | | *k* | **< 0.01** | - | † | **< 0.01** | - | - | - |
| | | *t⁰* | **0.03** | - | † | **0.03** | - | - | - |
| **Approach 2** | **Pathway I 'changers'** | *model* | 0.06 | 0.87 | - | 0.14 | - | - | - |
| | | *L∞* | 0.33 | 0.57 | - | 0.81 | - | - | - |
| | | *k* | 0.74 | 0.77 | - | 0.44 | - | - | - |
| | | *t⁰* | 0.82 | 0.71 | - | 0.96 | - | - | - |
| | **Pathway II 'non-changers'** | *model* | **< 0.01** | - | **< 0.01** | - | **< 0.01** | - | - |
| | | *L∞* | **< 0.01** | - | 0.92 | - | 0.92 | - | - |
| | | *k* | 0.08 | - | 0.11 | - | 0.11 | - | - |
| | | *t⁰* | 0.14 | - | 0.81 | - | 0.81 | - | - |

The model for 'all males' was significantly different from the model for the 'non-changers' in approach 2, although values for $L_\infty$, k and $t_0$ were not significantly different (Table 4.3). The models for 'all males' and 'non-changers' in approach 1 were not compared as they were the same. The model and the parameters for 'all females' were not significantly different from the models and the parameters of the 'changers' in both approaches (Table 4.3). There was a significant difference in the models and the $L_\infty$ values between 'all males' and 'all females'.

Within the two hypothetical approaches, there was a significant difference between the models and the respective model parameters $L\infty$, k and t0 for the 'non-changers' versus the 'changers' in the first approach (Figure 4.6c, Table 4.3). Models for the 'non-changers' and the 'changers' in approach 2 were not compared because younger male fish were grouped into either pathway according to size and therefore there was a possibility that differences between the models were an artifact of the methodology.

**4.4 Discussion**

The age-growth data presented, in combination with the sexual pattern information provided in Chapter 3, provides strong evidence for partial protandry in *P. quadrifilis*. This was evident via the presence of several extremely old male fish, including one individual of 22 years, one year younger than the oldest fish recorded. There also appeared to be a relationship between somatic growth and sex change whereby differences in the size of fish of the same age were observed between those that likely changed sex and those that did not, with older male fish noticeably smaller than females of the same age. This suggests that *P. quadrifilis* have at least two developmental pathways and it is likely that growth rate and asymptotic size of individuals varies between either pathway. In attempting to accurately model the two developmental pathways, further support was provided in that there were significant differences in the values for $L_\infty$ and k between the two pathways in the first approach. Therefore, it is likely that fish that changed sex grew to larger sizes and at a faster rate than fish that did not change sex.

Somatic growth in *P. quadrifilis* was rapid in the first four years, with individuals reaching approximately 277.9, 552.6, 754.1 and 901.9 mm FL in their first, second, third and fourth years of growth respectively (based on the 'full model'). Individuals also displayed rapid sexual maturation as primary males after their first year of growth. Despite the grossly understudied nature of the biology of the majority of the Polynemidae, it would seem, from well-studied species, that fast growth and early maturation is common (Longhurst, 1965; Dentzau & Chittenden, 1990; Motomura, 2004; Pember, 2006). For example, Pember (2006) found that *P. macrochir* in Australia attained a size of approximately 827.8 mm TL in their fourth year of growth and reached maturity between 202 and 412 mm TL and at an age of between one and two years old.

In this chapter, sex change in *P. quadrifilis* was shown to occur within a broad size and age window ranging from 790 to 1125 mm FL and from 3 to 8 years. This broad window for sex-change is common and has been observed in a number of sequential hermaphrodites (Munday et al., 2006) including members of the Polynemidae (*P. macrochir* range: 313–1139 mm TL and 2–8 years) (Pember, 2006). However, this suggests that sex-change in *P. quadrifilis* is not closely related to age or size and is therefore more likely conditional to some other aspect of the individual state. If individual reproductive fitness is taken into consideration, then sex change would most likely be related to some property of the mating group and is probably associated with the ratio of primary males to secondary females and total egg to sperm biomass (Munday et al., 2006). However, sex change is also often related to social cues (Robertson, 1972; Shapiro, 1979) and without adequate information on other behavioural traits for *P. quadrifilis*, it is difficult to effectively understand what these may be.

The social environment that often effects sex change in sequential hermaphrodites is usually linked to complex mating systems (Todd et al., 2016). Therefore, it is important to understand how spawning takes place in protandrous species. In well-studied protandrous animals, spawning is either monogamous (as seen in anemone fishes - *Amphiprion* and *Premnas* spp.) or random (Munday et al., 2006), which has been observed in some broadcast spawners such as barramundi (*Lates calcarifer*) (Todd et al., 2016). The mechanisms and behaviour of the former are well studied although the cues for sex change in group spawning protandrous fishes are unclear (Todd et al., 2016). Spawning in *P. quadrifilis* is not well documented, although nearshore spawning aggregations of large adults have been anecdotally reported from Gabon (Loubens, 1964). This, in conjunction with the fact that *P. quadrifilis* display high fecundity with moderately small egg-size (Loubens, 1966; Butler et al., 2018) may lead one to assume that they are likely group, broadcast spawners.

From the two hypothetical models, it was clear that there is a relationship between sex-change and somatic growth in *P. quadrifilis*. However, it was difficult to ascertain if this difference in growth between the two developmental pathways was the cause or the effect of sex change, i.e., is increased initial growth a cue for sex-change? Or do fish that change sex have increased growth rates as a result of their secondary female state? The evolutionary drivers involved in larger female size, in protandrous fishes, are most likely related to increased reproductive output (Ghiselin, 1969; Shapiro, 1987; Warner, 1988; Ross, 1990; Munday et al., 2006). Female *P. quadrifilis* exhibit significantly higher reproductive investment (higher GSI) when compared to males (Butler et al., 2018). As there is normally a trade-off between growth and reproductive output (Gross, 1996), it is surprising that secondary females, when compared with males, maintain faster growth and larger asymptotic size, despite having dedicated large energy reserves to the process of sex-change as well as increased reproductive output. Hence, the most likely explanation for the increased growth rates of secondary female fish would be that increased growth took place prior to sex change. This scenario was hypothetically modelled in approach 2 and although it provided a very good coefficient of determination value for pathway

II, the ‘non-changers’, ($R^2 = 0.69$), it modelled pathway I, the more dominant pathway, poorly ($R^2 = 0.54$).

While fast growth may be a trigger for sex change in this species, it is also possible that growth may accelerate after sex change, as demonstrated in approach 1. In this case, improvements in model fit were seen for both pathways I ($R^2 = 0.63$) and II ($R^2 = 0.61$). If sex change is related to accelerated growth, then it would become critical to understand the factors affecting growth rate and whether they are determined by facultative or obligate drivers. In other words, is the variation in growth rate that leads to a change of sex, or lack thereof, a result of the immediate surrounding environment (i.e. resource availability, favourable conditions, competitive ability etc.) and an individual’s resultant state or is it caused by other factors stemming from a predestined genetic polymorphism? Essentially, this is an argument over the classification of strategy as ‘conditional’ in the first case versus ‘alternative’ in the second (see Gross, 1996).

Variable reproductive phenotypes related to differential growth are common in fishes and have been shown to result from both genetic polymorphism (e.g. *Xiphiphorous nigrensis*) and conditional strategy (e.g. *Salmo salar*), although the latter is far more common (Gross, 1996). A typical example would be that of male ‘sneaking’. A number of fish species display two or more male phenotypes (Gross, 1996). Generally speaking, the first, and often more common, strategy involves high investment in growth over a longer period of time. This is directed at increasing desirable attributes related to display, courtship and fighting ability and often aimed at winning over females and reproductive rights. The second strategy invests highly in gonadal development with less investment in growth. These individuals are unable to compete directly with dominant males, but successfully reproduce by ‘sneaking’ mating opportunities.

Keeping this example in mind, it is possible that male *P. quadrifilis* that utilise developmental pathway II (‘non-changers’) invest more highly in reproductive output and less in somatic growth than those that utilise pathway I ('changers'). For example, it is possible that the majority of young *P. quadrifilis* primary males invest highly in somatic growth, with minor investment in reproduction; which is supported by the low relative GSI of small males compared with larger females (Butler et al., 2018) (Chapter 3). This is driven by the objective of growing rapidly, changing sex and then investing heavily in reproductive output at a larger size and as the sex with the reproductive advantage. However, this strategy is risky, as individuals will need to survive long enough to change sex and function as females in order to benefit. Therefore, a small proportion of primary male fish may invest relatively more energy into gonadal development as a tactic to combat sperm competition and increase individual reproductive success in the short-term. This 'choice' of strategy may be the result of two genetic phenotypes or it may be driven by conditional strategy (Gross, 1996) and may explain the observed patterns of growth in this study.

Alternatively, growth may simply vary naturally within the population, the result of both individual competitive ability (genetics) and resource availability, and individuals that grow rapidly change sex and become female while those that do not, remain male. In this case, two alternative tactics are displayed within a 'conditional strategy' (Gross, 1996). In the lower age cohorts, there is an obvious skew in sex ratio towards males. This may create an incentive for faster growing individuals to change sex and function as females due to the reproductive advantage it would provide them. However, at larger sizes, where the majority of primary males have completed sex change, the sex ratios are reversed and are skewed towards females. Within these cohorts, slower growers that have yet to change sex may not receive significant benefit by undergoing the energetically expensive process of sex change. These larger males also maintain higher reproductive output compared to small males due to their larger body size. Therefore, they may easily outcompete small males during spawning events, incentivising their male state. This theory also ties in well with the broad size and age range observed for sex change in *P. quadrifilis* and may therefore be the most likely scenario.

A similar theory was presented by Munday et al. (2004) for the protogynous parrotfishes *Scarus frenatus* and *Chlorurus sordidus*. Here, secondary males displayed faster growth and larger size than that of primary females. Otoliths for both sexes of both species were shown to increase in size consistently throughout life and not in direct accordance with somatic growth. The otoliths of secondary males were found to be smaller than those from females of the same size and this was put forward as evidence for a sex-specific growth effect, whereby the otoliths of faster growing individuals (changers) are smaller than in slower growers (non-changers). This effect was most pronounced during early life and it was therefore concluded that initial growth most likely dictated which fish changed sex, with faster growers changing, and slower growers remaining as females. Unfortunately, preliminary studies do not identify any similar size differentiation in the otoliths of *P. quadrifilis*.

The dearth of scientific research on *P. quadrifilis* inhibits the formation of robust conclusions about its life-history and there are undoubtedly numerous other aspects affecting an individual's growth. It would seem, from the little published information available, that the species has a strong dependency on the estuarine environment (Longhurst, 1957; Loubens, 1964, 1966) and migrates long distances up individual river systems (at least 250 km) (Laë et al., 2004; Simier et al., 2004). While sampling extensive Gabonese estuarine systems, Loubens (1966) reported extremely few juvenile fish below 20 cm standard length and therefore hypothesised that *P. quadrifilis* only migrate into the estuarine environment (from marine origin) at this size. Thereafter, he observed an increasing trend in the mean size range of fish as he sampled upstream, suggesting an upstream migration with initial development. However, larger, mature individuals were commonly located in close proximity to the ocean. From this, it would appear that *P. quadrifilis* likely undertake largescale ontogenetic migrations and this is likely to have a large effect on somatic growth (Higgins et al., 2015).

*Polydactylus quadrifilis* utilise numerous highly variable habitats throughout their life-history and therefore it is possible that differences in the movement patterns between individuals may explain the observed variation in growth and an individual's resultant 'choice' of developmental pathway (Crook et al., 2017). Ontogenetic migrations are critical aspects that affect the life-history of fishes and have been found to have a significant relationship with the conditional strategy of an individual (Gross, 1996; Crook et al., 2017). The migratory behaviour of animals has received increasing amounts of attention in recent times and is acknowledged as being extremely complex (Secor, 2015; Reid et al., 2018). However, estuarine species provide unique opportunities for migratory study due to the fact that they are restricted to a narrow pathway upstream and downstream while within a system. In addition, movement into and out of the estuarine environment is easily monitored at a single location (Thorstad et al., 2013). This, in turn, greatly increases the ability of researchers to detect fish movement when using technology such as acoustic telemetry. Otolith microchemistry is also particularly useful for investigating ontogenetic movement between the marine and estuarine environment and it is recommended that the combination of these two fields, in a multi-method study of movement behaviour, would provide invaluable insights into the life-history of *P. quadrifilis* going forward.

The classification of life-history strategy is critical towards gaining an understanding of the evolutionary biology of a species but it is also, and perhaps more importantly, critical for fisheries conservation and management (Crook et al., 2017). Anthropogenic disturbances to the immediate environment including river abstraction, habitat alteration, climate change and harmful fishing practices have the potential to affect the composition of reproductive phenotypes within the population through their impact on the conditional strategies of individual fish (Crook et al., 2017). Through this, they can shift the points at which important life-history events, such as sex change, occur, thus affecting population growth rate, asymptotic size and overall reproductive capacity and population sustainability (Moore et al., 2011). Therefore, research focusing on the life-history of *P. quadrifilis* is critical for the appropriate management of the recreational, subsistence and small-scale fisheries of the region.

If we consider the conventional techniques used to model fish growth, the 'full model' and the separate models for 'all males' and 'all females' in this study displayed higher model standard deviation than the two hypothetical methods. When compared to the two developmental pathways, it was shown that the 'full model' would adequately represent fish on pathway I, i.e. the 'changers', because there was no significant difference between the models or their parameters. However, this was not the case for pathway II ('non-changers'). Therefore, when utilising the 'full model', a stock assessment may only represent a proportion of the population and, although the proportion of sex changers is greater (estimated to be 75%), it would run the risk of selecting against individuals from pathway II and thereby reduce intrapopulation variability.

Separate models for all males and all females provided a better alternative in this case, although some differences were still noted. The models for 'all females' represented individuals from pathway I well in both approaches, however, pathway II was not adequately represented by the model for 'all males' in approach 2. Despite this, it provided similar model parameters in all cases, although it may not hold true for other hermaphroditic species. For example, if sex change did not occur over a wide age range, females may have only been encountered in large sizes and at old ages. Thus, modelling 'all females', without the small males that would inevitably change into females, would likely produce different results as there would be no data-points for young or small fish. Similarly, the modelling for 'all males' would be skewed by the data-points of young 'changers' which would later become female.

It is important to mention the caveats within a study such as this, whereby numerous assumptions are required in order to estimate the life-history pathways individual fish will follow. For example, when calculating the length and age at which sex change occurs, the model is likely to be affected by the numerous younger male fish within the data set which may not change sex. These individuals will affect the proportion of 'changed' to 'changing' fish in each age class and therefore likely affect the results and calculated reference points.

Going forward, it is important that fisheries scientists appreciate the complexities involved with analysing important life-history reference points and modelling the growth of sequentially hermaphroditic species. Life-history variability needs to be further investigated and thereafter acknowledged and conserved through dynamic management plans. Adequate investigations of fish life-history need to be promoted so that they may be used simultaneously in age-and-growth studies. Without the acknowledgement and appreciation of population diversity, we stand to drastically reduce the ability of fish populations to function and adapt to the ever-changing world we live in today. Through the appreciation and conservation of population diversity, it is possible that we may preserve the resilience of fish species through the promotion of adaptive capacity, thereby building sustainable fisheries. While understanding life-history complexities is vital for appropriate management, so too is understanding the potential impacts users may have through their interactions with fish stocks. Catch-and-release (C&R) angling is a critical conservation action in recreational fisheries (Brownscombe et al., 2019) and, therefore, it is imperative that we have an appropriate understanding of the threat it may pose to the health and survival of *P. quadrifilis.*

# Chapter 5

## A rapid assessment of the impact of catch-and-release by the foreign recreational fishery for *Polydactylus quadrifilis* on the Kwanza Estuary

### 5.1 Introduction

In West Africa, and many other developing regions, small-scale artisanal and subsistence fisheries are highly important for food security and poverty alleviation (Béné, 2003; Béné et al., 2010; Belhabib et al., 2015). However, while benefiting local communities, small-scale fisheries have the potential to exhaust fisheries resources leading to an exacerbation of poverty (Allison & Ellis, 2001). Recreational fisheries in developing countries are often overlooked as sources of alternative livelihoods for local communities, despite their considerable contributions towards local economies and human welfare through the provision of livelihoods, food security and poverty alleviation (Wood et al., 2013; Belhabib et al., 2016). In addition, they often maintain a less exploitative use of fisheries resources as recreationally captured fish are often released after being caught (Barnett et al., 2016; Belhabib et al., 2016).

Despite these potential benefits, even 100% catch-and-release (C&R) recreational fisheries pose a threat to local fish species through C&R-related stress (Arlinghaus et al., 2009; Arkert et al., 2018), injury (Burkholder, 1992; Ferter et al., 2015) and the impairment (Danylchuk et al., 2007; Davis, 2005) and alteration (Cooke & Schramm, 2007; Philipp et. al, 1997) of natural behaviour, which have been shown to contribute to mortality (Brownscombe et al., 2015). However, it is evident from the multitude of C&R studies globally, that the impacts and outcomes of recreational fishing vary greatly among fisheries (Arlinghaus et al., 2007). This variability stems from differences in the biology of the target species, the environmental conditions associated with the fishery and the techniques and behaviours of the anglers (Bartholomew and Bohnsack, 2005). For example, common biological aspects of importance include fishery species' sensitivity towards C&R and local predator densities (Danylchuk et al., 2007b), while important environmental conditions include water temperature (Brownscombe et al., 2014) and water depth (Ferter et al., 2015). Each fishery also employs different angling techniques, driven by the cultural, socio-economic and regulatory aspects of the fishery, which thereby influence important C&R factors such as hooking injury and fight time and intensity (Brownscombe et al., 2015) and can negatively impact overall fish health (Cooke et al., 2016).

It is critical to understand the social-ecological systems (SESs) within which recreational fisheries are nested (Ostrom, 2009; Arlinghaus, 2017) (see Figure 1.1). For example, the outcomes of recreational fishing have the potential to vary in their level of impact, based on various qualities of the ecosystem. In order to adequately understand this, we need to assess the human dimensions involved within that ecosystem and value them as a critical component. This will, in turn, allow for the maintenance of positive feedbacks between fishery user groups and the environment (Arlinghaus, 2017) and may facilitate pro-environmental behavioural changes (Mannheim et al., 2018). All in all, knowledge of the species- and fishery-specific impacts of C&R practices on the survival of fishes is critical for fisheries managers to better estimate mortality and manage their fisheries.

The fishery on the Kwanza Estuary in Angola is complex and comprises various sectors. These include an informal artisanal gill-net, longline and line fishery and a growing domestic and foreign tourist recreational fishery (see Chapter 2). The recreational fishery changes seasonally and while the primary target species in the austral summer is *Megalops atlanticus* (the Atlantic tarpon), *Polydactylus quadrifilis* is the dominant target species in winter (Chapter 7). Unlike *M. atlanticus*, *P. quadrifilis* is an important target species in the artisanal sector. The domestic fishery sectors, both artisanal and recreational, are highly consumptive with very little releasing of fish (Chapter 7). However, the foreign tourism sector, which primarily operates out of the Kwanza Lodge, practices exclusive C&R angling, with exceptions made for badly damaged individuals (see Chapter 2).

Within the recreational fisheries present on the Kwanza Estuary, a number of angling techniques have been observed, including the trolling of lipped crankbait lures, the use of artificial lures and jigs and the use of bait, including live fish, dead fish, crustaceans and cephalopods (pers. obs.). However, foreign recreational anglers almost exclusively use live-fish-bait and light-medium tackle artificial lure and jig angling. The Kwanza Estuary hosts some of the largest (over 50 kg) *P. quadrifilis* individuals recorded globally and is a critical area of importance for the species (Butler et al., 2018) (Chapter 2 and 3). Relatively speaking, these very large fish are targeted on extremely light tackle (strength-rated as low as 10 lb), as it is appealing to fishing enthusiasts based on the difficulty of the challenge it presents. However, this tackle choice is problematic and often results in lengthy fight times, which are commonly understood to negatively impact fish health and survival following C&R (Skomal, 2007; Suski et al., 2007; Cooke et al., 2016). Furthermore, anecdotal evidence suggests that *P. quadrifilis* do not fare well following C&R with fish commonly observed struggling to regain equilibrium in the water when released.

Given the anecdotal evidence of poor survival following a C&R event, it is critical that the health and survival of *P. quadrifilis* is assessed within the foreign recreational fishery in order to understand the potential threat it may pose to the sustainability of the fish stock and other reliant user groups. Additionally, an understanding of the major contributing factors to C&R stress in this species will aid in the development of appropriate handling practices which can be implemented within the foreign and domestic recreational fisheries to optimise fish survival following C&R. This chapter aimed to assess the sensitivity of *P. quadrifilis* to recreational C&R within the foreign recreational fishery using a rapid assessment approach. To do this, a number of C&R variables including fight time, air exposure, hook placement, hooking injury, total time of the stress event, river depth and angling method were measured and related to two indicators of fish health and survival. These included the secondary physiological stress indicators blood glucose and blood lactate concentration (see Cooke et al., 2013) and reflex action mortality predictors (RAMPs, see Davis, 2010).

**5.2 Methods**

The experiments were carried out on the lower reaches of the Kwanza Estuary in Angola (Figure 2.1) from the 2nd of June until the 19th of August 2017 and again from the 4th of June until the 8th of August 2018. A temperature logger, that was placed close to the fishing area at a depth of one metre (low-tide), recorded water temperature every three hours throughout the study. This provided a temperature range during the study period but could not facilitate the estimation of specific temperatures during catch events.

Data collection was undertaken on boats operated by the Kwanza Tarpon Lodge and fish were either angled by lodge fishing guides or by foreign fishing tourists. Angler behaviour was not manipulated by researchers and fish handling was allowed to take place as it naturally would. Anglers utilised light-medium-/medium-weight spinning rods and fixed spool reels and either targeted fish by casting and retrieving artificial lures (3/4–1.5 oz jigs with barbed 6/0–8/0 J-hooks) or by casting out live-fish-bait (4/0–6/0 circle hook).

For each capture event, the angling method (as either artificial lure or live-bait) and the "fight time" was recorded, using a stopwatch, as the time from when an angler hooked a fish to the time that it was landed. Hook placement was then noted (hook embedded in the jaw, throat or on the head or body of the fish) along with a ranking of hook-related injury which was categorised between 0 and 3 (0 = no bleeding/ minimal bleeding, insufficient to create a blood trail within the water, 1 = noticeable bleeding, sufficient to cause a light trail of blood in the water, 2 = bleeding sufficient to create a moderate blood trail and light discolouration of the water and 3 = profuse bleeding, staining the water around the head area of the fish a deep red/brown colour with blood often seen pumping out of the mouth and gills). "Air exposure" (the total amount of time the fish was outside of water between landing and release) was recorded with a stopwatch. During this time, fish were measured (fork-length – FL, cm) and photographs were commonly taken of the angler and the fish. At this point, fish were handed over to a researcher for either blood extraction or RAMP analysis. In order to avoid confounding factors, the assessments of physiological and physical impairment were never performed on the same individual fish. Because blood extraction took place outside of the water, time taken to extract blood was recorded and included in the air exposure time. The "total time" (of the stress event) was recorded from the time of hooking until the time at which either blood was extracted, or a RAMP assessment was performed.

### *5.2.1 Blood chemistry*

Blood (< 2 ml) was taken from the caudal vasculature of the fish using a 20G, 88mm spinal needle and syringe. Point of care devices were utilised to measure blood lactate ($mmol.l^{-1}$, Lactate-Pro 2, Arkray Inc., Kyoto, Japan) and blood glucose ($mmol.l^{-1}$, Accu-Chek Active, Roche Diagnostics, Basel, Switzerland) (Cooke et al., 2008).

### *5.2.2 Reflex action mortality predictors (RAMPs)*

Four common RAMPs (Davis, 2010; Raby et al., 2012) and one additional new RAMP were performed on fish obtained from anglers, immediately after the C&R event in a large floating mesh net that was attached to the side of the boat (Figure 5.1). The four traditional RAMP assessments included “head complex”, “tail grab”, “equilibrium” and “body flex” and were chosen due to their common use (Brownscombe et al., 2014; Lennox et al., 2015; Bower et al., 2016a; Cooke et al., 2016) and validation (Raby et al., 2012) in other C&R studies. “Head complex” involved assessing the regularity of the fish’s opercula beats (regular = 0, irregular or none = 1). “Tail grab” involved gently grabbing the fish’s tail and noting the fish’s response (reactive swimming action = 0, no response = 1). “Equilibrium” involved gently inverting the fish and recording whether or not it was able to right itself within three seconds (positive response = 0, no response = 1). “Body flex” involved gently lifting the fish and holding it on its side, above the water. Fish that responded by flexing their torso within three seconds were given a score of 0, while those that did not were given a score of 1.

**Figure 5.1:** Performing a RAMP assessment on a large (126 cm fork-length) *Polydactylus quadrifilis* individual next to the boat in a floating soft mesh net. Note how the fish is orientated upside-down and appears to be positively buoyant – this behaviour was often noted following C&R (post-release – i.e. following handling, not when landed).

A new, additional RAMP indicator termed “maintenance of equilibrium” was employed. This test was an extension of the test for the reflex equilibrium and was performed directly thereafter

(Figure 5.2). It involved placing the fish in its natural upright position and observing whether it was capable of remaining upright for a period of three seconds (maintenance of equilibrium = 0, an inversion back to an upside-down position = 1). Where individuals were already in an upright position (i.e. they regained equilibrium during the previous RAMP / scored 0 for equilibrium), fish were gently handled or moved slightly to simulate the handling effect of inverting upside-down fish (Figure 5.2). The reasoning behind the inclusion of this new indicator was that *P. quadrifilis* displayed difficulty maintaining equilibrium once released (see Figure 5.1). It is hypothesised that this behaviour may be related to the extremely large size of their swim bladder (Motomura, 2004), and even fish caught at modest depths experienced some form of minor barotrauma.

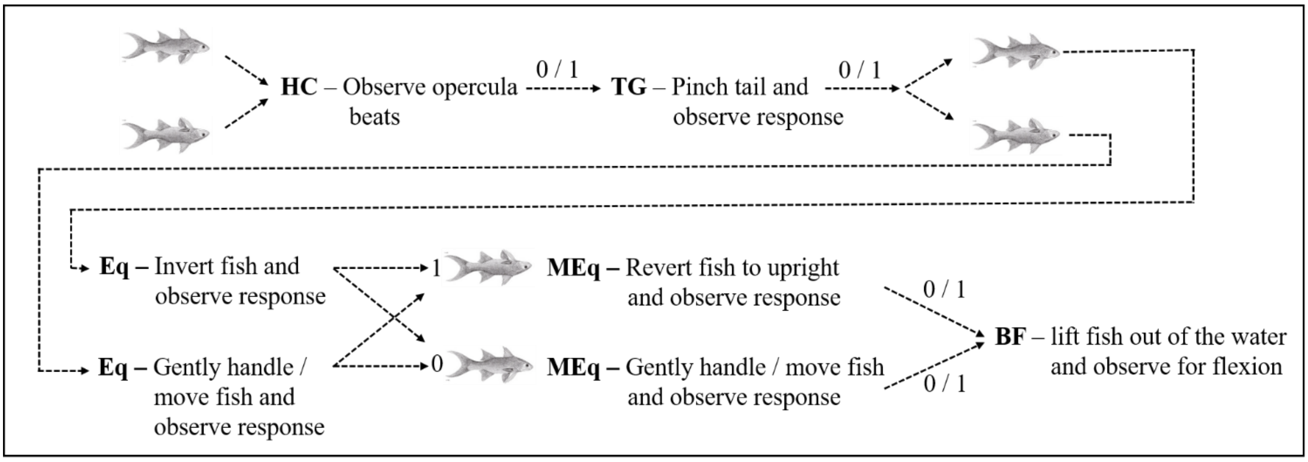


**Figure 5.2:** Schematic diagram demonstrating the order and process in which reflex action mortality predictor (RAMP – Davis, 2010) tests were performed on *Polydactylus quadrifilis* following recreational catch-and-release angling and in accordance with the orientation of the fish at the time. HC – head complex, TG – tail grab, Eq – equilibrium, MEq – maintenance of equilibrium & BF – body flex.

It is argued that although equilibrium and maintenance of equilibrium rely on similar reflexes, they are still varied enough to include within a cumulative RAMP scoring system. In this case, the two equilibrium-related RAMP assessments vary in their difficulty of achievement (for the fish) and in their utilisation of different muscle groups. For example, regaining equilibrium (especially with an overinflated swim bladder) would require far more muscle usage than maintaining equilibrium. Additionally, the two indicators have different ecological relevance and this may guide best practice when releasing fish. For example, if fish show high rates of impairment for equilibrium but low rates of impairment for maintenance of equilibrium, then it would be important that fish are released in an upright position and are allowed to swim off in a controlled manner rather than being thrown back into the water.

In terms of its validation, Davis (2010) stated that the validation of a new RAMP indicator involves comparing the impaired state of fish following a stress event with that of fish that have had no stress or have made a full recovery from stress. In this instance, unstressed, healthy fish would maintain an upright position, which is common for *P. quadrifilis* and most other fish species. Therefore, if *P. quadrifilis* display impairment following C&R, we can intuitively validate this new indicator based on the obvious difference between impaired and non-impaired individuals. Furthermore, since the RAMP indicator 'equilibrium' is commonly associated with increased risk of mortality (Danylchuk et al., 2007b; Brownscombe et al., 2015), logic would dictate that maintenance of equilibrium would also be linked to increased mortality, although perhaps with a greater risk factor.

The RAMP values for all measures were summed for each fish, to give a score ranging from 0 to 5, with 5 indicating a high level of predicted mortality. As with other studies (e.g. Bower et al., 2016), RAMP values were treated as objective measurements.

### *5.2.3 Statistical analyses*

To determine the relationship among all measured variables, Pearson's $r$ and Spearman's Rank correlations were performed between C&R (fight time, air exposure, total time and river depth) and fish-specific variables (fish length, blood glucose concentration, blood lactate concentration and RAMP score). Pearson's $r$ correlations were used to compare continuous variables while Spearman's Rank correlations were used for ordinal data (RAMP score). Values for fight time were log-transformed to conform to normality.

*Blood chemistry*

A linear model (LM) was used to model the effect of the C&R variables on blood glucose and blood lactate concentrations. Blood lactate and blood glucose concentration were considered the response variables and fight time, air exposure and total time were considered the explanatory/predictor variables. The variables river depth, hooking position, hooking injury and angling method were excluded from the model due to the low variation in values. Additionally, total time was excluded from the model due to its high level of collinearity with fight time (variance inflation factor > 20). The interaction of air exposure and fight time was included in the full model. A model selection process was conducted using the '*dredge*' function in the '*MuMIn*' package (Barton, 2019) (R Core Team, 2017) and was based on the generation of individual models using all combinations of predictor variables. All models were compared using second order Akaike Information Criterion (AIC)c and models with $\Delta$AIC < 2 were considered as 'top scoring models' (Burnham & Anderson, 2004). The final model selection was based on the 'top scoring model' with the highest number of variables.

*Reflex action mortality predictors (RAMPs)*

Given that RAMP score is an ordinal categorical multinomial response variable**,** cumulative link models (CLM) with logit link functions were used to model the effect of C&R variables on the RAMP score of *P. quadrifilis* using the package '*ordinal'* (Christensen, 2019). The RAMP score, ordered from 0–5 (0 = no impairment, 5 = high impairment), was considered the response variable. The continuous independent variables fight time, air exposure, total time, river depth and categorical variable 'angling method' were considered the explanatory/predictor variables. Hooking position and hooking injury were excluded from the model due to low variation in values and total time was excluded due to its high level of collinearity with fight time (variance inflation factor > 20). The interaction of air exposure and fight time was included in the model. A model selection process was conducted using the functions ‘*drop1*’ and ‘*Chi*’ test, and the best fit was chosen according to the model with the highest number of variables within ΔAIC < 2 of the best-fit model.

A generalised linear model (GLM) with binomial distribution and logit-link function was used to model the effect of the C&R variables on individual RAMP indicators (head complex, tail grab, equilibrium, maintenance of equilibrium and body flex) using the package ‘*MASS*’ (Venables & Ripley, 2002). The binomial indicator score (0 = impaired, 1 = unimpaired) was considered the response variable while fight time, air exposure, river depth and angling method were considered explanatory/predictor variables. Again, the interaction of air exposure and fight time was included in the model. Hooking position and hooking injury were excluded from the model due to low variation in values and total time was excluded due to its high level of collinearity with fight time (variance inflation factor > 20). The interaction of air exposure and fight time was included in the full model. Model selection procedures followed the same as presented in the blood analysis section above.

The model assumptions required to run the various models were tested and met. All analyses were conducted in Rstudio (version 1.1.463).

### 5.3 Results

A total of 94 *P. quadrifilis* were sampled from the Kwanza Estuary ranging in size from 45 to 135 cm FL (mean 78.4 cm, SD 17.9 cm). Of these, 34 were blood sampled and 60 undertook RAMP assessments. Fish were captured in water ranging in depth from 3.5 to 7.0 m (mean 5.1, SD 0.6) and in temperature ranging from 23.1 to 28.4ºC (mean 25.2, SD 1.01). Of the 94 fish, 83 (88.3%) were captured using artificial lures (jig with single barbed J-hook), while 11

(11.7%) were captured using live-bait with circle hooks. The hook placement was in the jaw of the fish for 82 of the 83 fish angled on artificial lure and 11 of the 11 fish caught on circle hooks. One fish that was caught on artificial lure was hooked at the back of the mouth close to the throat. A hooking injury score of 0 was given to all fish and bleeding was never sufficient to create a blood trail in the water. The average fight time (± SD) for all fish was 229.0 ± 536.4 s (range: 16–5133 s) while air exposure averaged 112.7 ± 69.8 s (range: 0–330 s) and total time of the stress event averaged 379.3 ± 559.9 s (range: 83–5358 s).

There were high levels of correlation between a number of the variables (Table 5.1). Amongst the independent variables, fight time, air exposure and total time were significantly correlated with fish length with larger individuals subject to longer fight (r = 0.88) and air exposure times (r = 0.41) (Figure 5.3, Table 5.1). Additionally, river depth was significantly correlated with

**Table 5.1:** Pearson's *r* (all comparisons except for RAMP) or Spearman's Rank correlation coefficients (RAMP comparisons), shown on the bottom left, and corresponding p-values (top right) for the various catch-and-release (C&R) variables and fish metrics measured during C&R angling for *Polydactylus quadrifilis*. All comparisons of blood glucose and blood lactate have 28 degrees of freedom, all other relevant comparisons have 90 degrees of freedom.

| | Log (fight time) | Air exposure | Total time | River depth | Fish length | Glucose | Lactate | RAMP* |
|---|---|---|---|---|---|---|---|---|
| Log (fight time) | - | <0.001* | <0.001* | 0.41 | <0.001* | 0.22 | 0.75 | <0.001* |
| Air exposure | 0.39 | - | <0.001* | 0.39 | <0.001* | <0.01* | 0.72 | <0.001* |
| Total time | 0.41 | 0.53 | - | 0.51 | <0.001* | 0.02* | 0.51 | <0.001* |
| River depth | 0.09 | 0.09 | -0.07 | - | 0.04* | 0.85 | 0.06 | 0.16 |
| Fish length | 0.88 | 0.41 | 0.78 | 0.22 | - | 0.23 | 0.68 | <0.001* |
| Glucose | 0.23 | 0.52 | 0.42 | -0.04 | 0.23 | - | 0.04* | - |
| Lactate | 0.06 | 0.07 | 0.12 | 0.35 | 0.08 | -0.37 | - | - |
| RAMP* | 0.44 | 0.62 | 0.56 | 0.19 | 0.44 | - | - | - |

fish length but with a weak correlation coefficient (r = 0.22 – Table 5.1). Similarly, yet unsurprisingly, total time was significantly correlated with its two constituents – air exposure and fight time (Table 5.1).

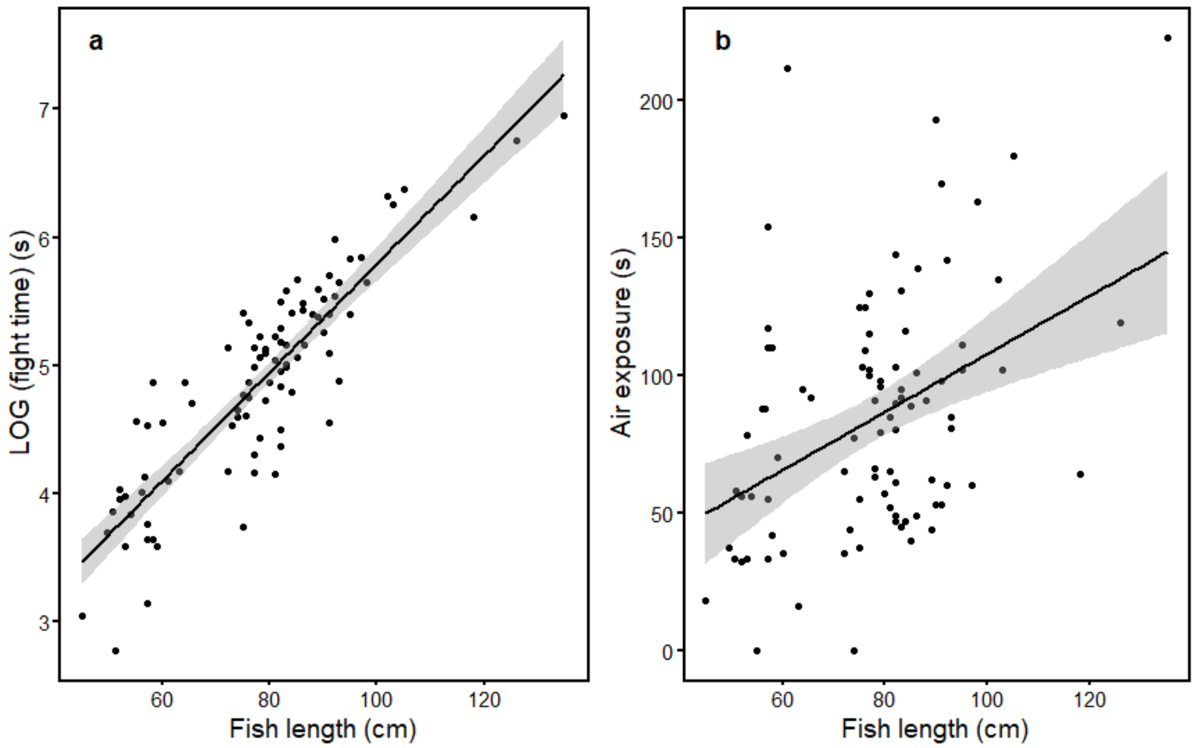


**Figure 5.3:** Relationship between the variables fish length and (a) fight time and (b) air exposure for *Polydactylus quadrifilis* following recreational catch-and-release angling on the Kwanza Estuary, Angola.

*5.3.1 Blood chemistry*

Blood data was collected from a total of 34 fish, with blood glucose values attained for 32 individuals and blood lactate values for 31 individuals (due to instrument failure). Mean fish length was 79.6 ± 14.5 cm FL (range: 50.5–105 cm). The average fight time was 209.7 ± 138.1 s (range: 38–588 s) and the average air exposure was 176.7 ± 65.9 s (range: 30–330 s). The time taken to extract blood averaged 67.3 ± 49.2 s (range: 5–196 s) while the total time of the stress event averaged 417.9 ± 139.8 s (range: 200–840 s). Blood glucose concentration averaged 2.52 ± 0.72 mmol.mm$^{-1}$ and ranged from 1.4 to 4.8 mmol.mm$^{-1}$ while blood lactate concentration averaged 2.76 ± 0.97 mmol.mm$^{-1}$ and ranged from 1.4 to 5.5 mmol.mm$^{-1}$ (Figure 5.4). Air exposure and total time were significantly correlated with blood glucose concentration (Table 5.1). Additionally, blood glucose and blood lactate concentrations were negatively correlated with each other (Table 5.1).

Following the model selection process for the LM, all relevant variables were included in the final model. The LM identified air exposure as a significant predictor of blood glucose with longer exposure times correlated with higher glucose concentrations (d.f. = 1, Wald $\chi2$ = 2.54, p = 0.017, Figure 5.4b, Table 5.2). Fight time and its interaction with air exposure did not significantly predict blood glucose concentration (Figure 5.4a, Table 5.2). Blood lactate concentration was not significantly predicted by any of the C&R variables used in the LM (Figure 5.4c & d, Table 5.2).

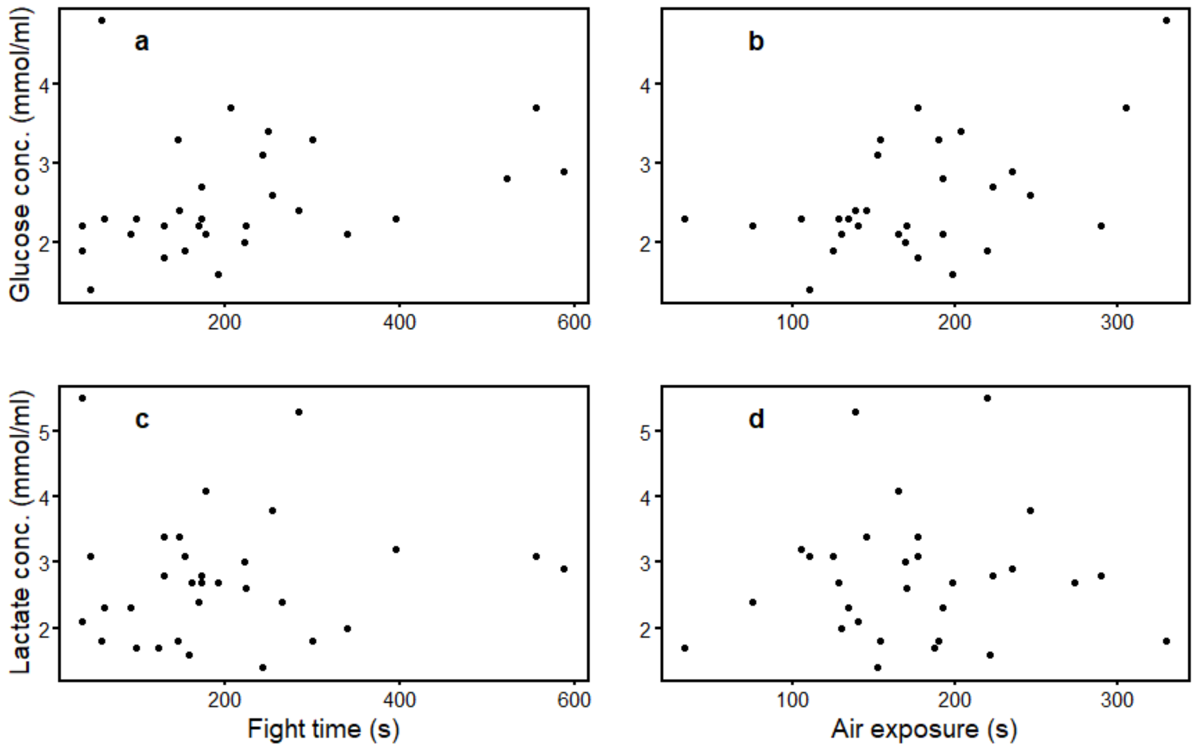


**Figure 5.4:** Relationship between fight time (a, c) and air exposure (b, d) and blood glucose (a, b) and blood lactate concentrations (c, d) of *Polydactylus quadrifilis* following recreational catch-and-release angling on the Kwanza Estuary, Angola.

**Table 5.2:** Summary results of the Linear Models (LM) describing the relationship between blood glucose and lactate concentration and air exposure, fight time and the interaction of air exposure and fight time for *Polydactylus quadrifilis* following catch-and-release angling. Significant p-values are indicated by bold text.

| Variables | df | Estimate | SE | Wald $X^2$ | p-value |
|---|---|---|---|---|---|
| *Model - glucose concentration* | | | | | |
| Intercept | | 0.849 | 0.595 | 1.428 | 0.165 |
| Air exposure | 1 | 0.008 | 0.003 | 2.537 | **0.017** |
| Fight time | 1 | 0.004 | 0.003 | 1.297 | 0.206 |
| Air exposure : fight time | | 0.000 | 0.000 | -0.904 | 0.374 |
| *Model - lactate concentration* | | | | | |
| Intercept | | 2.270 | 0.978 | 2.317 | 0.028 |
| Air exposure | 1 | 0.002 | 0.005 | 0.428 | 0.672 |
| Fight time | 1 | 0.002 | 0.005 | 0.372 | 0.713 |
| Air exposure : fight time | | 0.000 | 0.000 | -0.274 | 0.786 |

*5.3.2 Reflex action mortality predictors (RAMPs)*

Reflex action mortality predictor assessments were undertaken on a total of 60 fish ranging in size from 45 to 137 cm FL (mean 77.7, SD 19.6). Fight time averaged 239.9 ± 665.3 s (range: 16–5133 s), air exposure 76.4 ± 39.5 s (range: 0–223 s) and total time of the stress event 357.4 ± 694.1 s (range: 83– 5358 s). Cumulative RAMP score was significantly correlated with fight time, air exposure, total time and fish length (Table 5.1). A total of 47 fish (78.3%) displayed some level of reflex impairment (RAMP > 0) and the mean RAMP score across all fish was 1.78 ± 1.43. Of the RAMP indicators, equilibrium was the most commonly impaired (73.3%). This was followed by body flex (45.0%), maintenance of equilibrium (40%) and tail grab (20%). No fish displayed impairment for the RAMP head complex (0%).

In the binomial logistic regression models, following the model selection processes, the interaction between air exposure and fight time was excluded from the final model in all cases. Air exposure was identified to be a significant predictor of reflex impairment for the indicators tail grab (d.f. = 1, $z = 1.97$, $p < 0.05$), equilibrium (d.f. = 1, $z = 2.13$, $p = 0.03$), maintenance of equilibrium (d.f. = 1, $z = 3.31$, $p < 0.01$) and body flex (d.f. = 1, $z = 2.94$, $p < 0.01$) (Figure 5.5,

Table 5.3). River depth, angling method and fight time were not identified as significant in any of the models (Table 5.3).

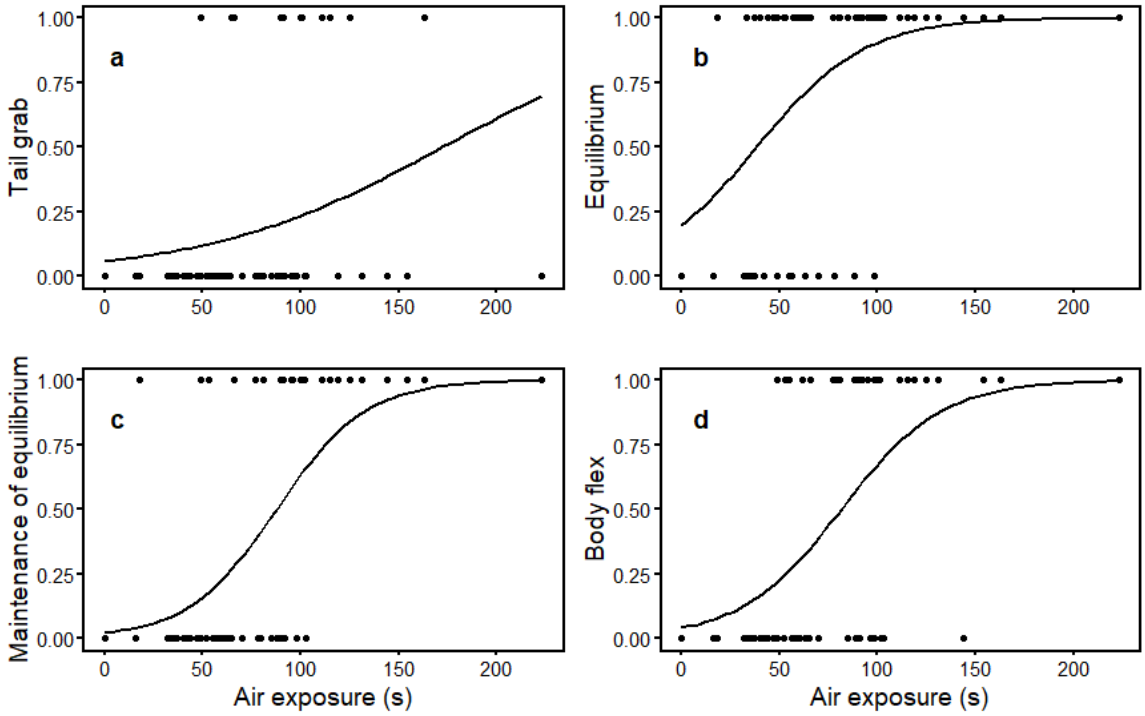


**Figure 5.5:** The occurrence of reflex impairment is displayed for the reflex action mortality predictor (RAMP – Davis, 2010) indicators 'tail grab', 'equilibrium', 'maintenance of equilibrium' and 'body flex' with increasing air exposure for *Polydactylus quadrifilis* following catch-and-release angling. Lines of best fit were fitted using a binomial logistic regression model.

Following the model selection process for the CLM, all relevant variables were included in the final model. The CLM identified air exposure to be a significant predictor of cumulative RAMP score with higher RAMP scores observed for individuals with long air exposure times (Figure 5.6, Table 5.4). Fight time alone was not identified by the CLM as significant in this instance (Figure 5.6a), however the interactive effect of fight time and air exposure was shown to significantly predict RAMP score (Table 5.5). The negative model estimate (Table 5.4) indicates that the two predictors have a cumulative effect on RAMP score up until a threshold, above which there is no longer a combined effect.

**Table 5.3:** Summary results of the binomial logistic regression models used to describe the relationship between the probability of reflex impairment in *Polydactylus quadrifilis*, using four reflex action mortality predictors (RAMP – Davis, 2010), and the catch-and-release variables air exposure, fight time, angling method and river depth. Significant p-values are indicated by bold text.

| | Variables | df | Estimate | SE | z value | p-value |
|---|---|---|---|---|---|---|
| *Model - tail grab* | | | | | | |
| | Intercept | | -7.563 | 4.694 | -1.611 | 0.107 |
| | Air exposure | 1 | 0.021 | 0.011 | 1.973 | **0.049** |
| | Fight time | 1 | -0.003 | 0.002 | -1.188 | 0.235 |
| | Angling method - live bait | 1 | 0.474 | 0.892 | 0.531 | 0.595 |
| | Depth | 1 | 0.874 | 0.860 | 1.016 | 0.310 |
| *Model – equilibrium* | | | | | | |
| | Intercept | | -4.861 | 3.583 | -1.357 | 0.175 |
| | Air exposure | 1 | 0.028 | 0.013 | 2.134 | **0.033** |
| | Fight time | 1 | 0.009 | 0.005 | 1.769 | 0.077 |
| | Angling method - live bait | 1 | 0.452 | 1.224 | 0.370 | 0.712 |
| | Depth | 1 | 0.550 | 0.685 | 0.804 | 0.422 |
| *Model - maintenance of equilibrium* | | | | | | |
| | Intercept | | -4.235 | 3.717 | -1.139 | 0.255 |
| | Air exposure | 1 | 0.043 | 0.013 | 3.312 | **0.001** |
| | Fight time | 1 | 0.002 | 0.003 | 0.752 | 0.452 |
| | Angling method - live bait | 1 | 0.224 | 0.822 | 0.272 | 0.785 |
| | Depth | 1 | 0.013 | 0.696 | 0.018 | 0.985 |
| *Model - body flex* | | | | | | |
| | Intercept | | -7.156 | 4.028 | -1.777 | 0.076 |
| | Air exposure | 1 | 0.034 | 0.012 | 2.944 | **0.003** |
| | Fight time | 1 | 0.002 | 0.003 | 0.707 | 0.479 |
| | Angling method - live bait | 1 | 1.437 | 0.934 | 1.540 | 0.124 |
| | Depth | 1 | 0.712 | 0.739 | 0.963 | 0.335 |

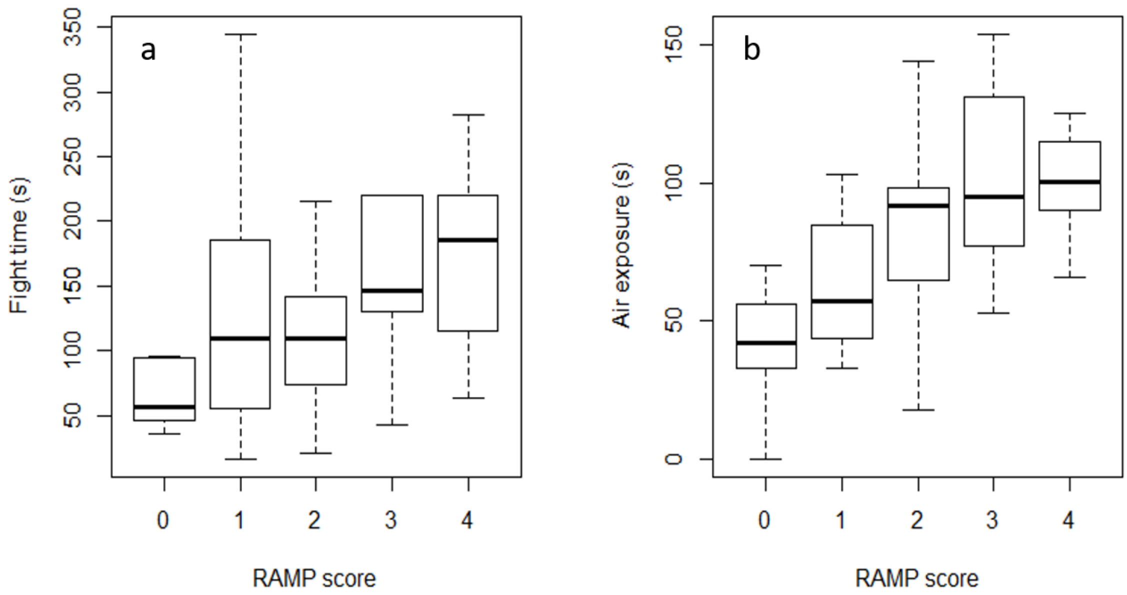


**Figure 5.6:** The relationship between cumulative RAMP score and (a) fight time and (b) air exposure for *Polydactylus quadrifilis* following recreational catch-and-release on the Kwanza Estuary, Angola.

**Table 5.4:** Summary results of the Cumulative Link Model (CLM) describing the relationship between RAMP and air exposure, fight time, river depth, angling method and the interaction of air exposure and fight time for *Polydactylus quadrifilis* following recreational catch-and-release on the Kwanza Estuary, Angola.

| Variables | Estimate (βi) | SE | z value | P-value |
|---|---|---|---|---|
| *Model - RAMP* | | | | |
| Air exposure | 0.034 | 0.008 | 3.990 | **0.000** |
| Fight time | 0.002 | 0.002 | 1.207 | 0.228 |
| Depth | 0.685 | 0.539 | 1.271 | 0.204 |
| Angling method (live bait) | 0.923 | 0.660 | 1.399 | 0.162 |
| Air exposure : fight time | 0.000 | 0.000 | -2.377 | **0.017** |
| *Threshold coefficients* | Estimate (θ^j) | | | |
| *0\|1* | 1.862 | 2.853 | 0.653 | |
| *1\|2* | 3.859 | 2.886 | 1.337 | |
| *2\|3* | 4.801 | 2.903 | 1.654 | |
| *3\|4* | 5.889 | 2.921 | 2.016 | |
| *AIC* | 173.020 | | | |
| *Log-likelihood* | -77.510 | | | |

## 5.4 Discussion

It has been well established that various aspects of C&R angling lead to both the physiological and physical impairment of fishes (Danylchuk et al., 2007a; Cooke et al., 2008, 2013a; Gallagher et al., 2014; Brownscombe et al., 2015; Arkert et al., 2018). However, it has also been shown that these effects differ between species, and the ultimate fate of fishes following C&R is largely impacted by the way in which they are handled (Brownscombe et al., 2015; Cooke et al., 2016) and the environment in which they are released (Cooke & Philipp, 2004; Raby et al., 2014), thus making studies fishery specific. *Polydactylus quadrifilis* in the Kwanza Estuary demonstrated substantial sensitivity towards C&R practices primarily through motor impairment. This was indicated by the significant positive relationships between RAMP indicator and cumulative score and air exposure and fight time. Their impairment following C&R is likely to lead to higher rates of direct C&R-related mortality as well as higher rates of indirect mortality via predation.

In terms of physiological impairment, there was a significant relationship (LM, $p = 0.02$) between air exposure and blood glucose concentration for *P. quadrifilis.* However, the gradient of the relationship was particularly low (Figure 5.2, Table 5.2) and therefore suggested that air exposure did not significantly increase blood glucose concentrations. Interestingly, no other C&R variables were identified as significant contributors towards physiological stress during this study and blood lactate concentrations were not correlated with any of the C&R variables, including air exposure. This is fairly common (Martinez-Porchas et al., 2009) and several similar studies have failed to observe trends between one or both of the physiological responses and various C&R variables (Arkert et al., 2018; Arlinghaus et al., 2009; Brownscombe et al., 2014). It is likely that this is a consequence of a range of factors which increase the potential for error. Error can arise from a variety of sources and can be increased by the incorrect timing of blood extraction (Cooke et al., 2013a) and by a host of internal and external conditions of the study animal (Martinez-Porchas et al., 2009).

When using secondary stress response indicators, such as blood glucose and blood lactate, significant delays between the stressor and peak response are common (see Perrier et al., 1977; Arends et al., 1999; Arkert et al., 2018). Therefore, the immediate measurement of blood parameters may produce unreliable estimates of stress as the secondary indicators may not yet have sufficiently accumulated in the blood (Wendelaar Bonga, 2011). Additionally, sample sizes play an important role and need to be sufficiently large to encompass individual variability in baseline glucose and lactate concentrations. The baseline concentrations of these physiological indicators may differ between individuals based on a number of factors including the timing of the individual's last meal, recent energetic expenditure and the fish's nutritional status, amongst others (see Martinez-Porchas et al., 2009). Therefore, it is suggested that where funding and experimental design allow, species-specific laboratory studies, that examine the time course of the secondary stress response, should precede field studies. Experiments should then maintain fish in appropriate holding facilities for this predetermined time before blood sampling (Cooke et al., 2013a). In addition, the inclusion of primary stress response indicators, such as blood cortisol, may provide more complete information on the stress response and sample sizes should be large enough to incorporate individual variation in baseline concentrations.

While these best practices for estimating physiological stress have been outlined previously (Cooke et al., 2013a), they are not always possible to implement, particularly in the field, where appropriate laboratory and holding facilities are unavailable or far from the study site. While potentially biased, the use of blood physiology with immediate sampling, as utilised in this study, still provides useful information, although the potential consequences of the bias should be acknowledged.

The RAMP analyses identified air exposure to be of importance for the wellbeing of released *P. quadrifilis*. This was demonstrated by the significant relationships between reflex impairment and air exposure and the interaction between air exposure and fight time. Both the CLM and binomial logistic regression models identified air exposure as a significant predictor of reflex impairment in all cases (Table 5.3, Table 5.4). This supports the notion that air exposure is the critical aspect of the C&R process for *P. quadrifilis* in this fishery. Additionally, this finding aligns with many similar studies as air exposure has been found to significantly impact reflex impairment in a number of recreational angling species (Brownscombe et al., 2013; Bower et al., 2016b; Gagne et al., 2017).

The effect of air exposure on *P. quadrifilis* was further exacerbated by extended fight times (up to 85 minutes), whereby these two variables combined to have a cumulative effect on reflex response. This effect was observed up until a threshold, above which the effect of air exposure seemingly overshadowed fight time. This was demonstrated by the interaction between air exposure and fight time in the CLM and suggests that reducing fight times may aid in reducing overall physical impairment. Interestingly, however, the CLM did not identify fight time alone as a significant predictor of reflex impairment. This was unexpected as *P. quadrifilis* during this study endured relatively long fight times (averaging approximately 4 minutes) when compared with other studies (Brownscombe et al., 2014; Lennox et al., 2015; Bower et al., 2016a; Arkert et al., 2018) and fight duration is often expected to be of increased importance with larger fish species (Skomal, 2007) such as *P. quadrifilis*. This may suggest that *P. quadrifilis* are physically resilient to extended fight times, if and when air exposure is kept to a minimum.

When looking at the individual RAMP indicators, it is interesting to note that many authors have found a similar pattern of impairment between the common indicators for different species and in different studies (Brownscombe et al., 2015; Bower et al., 2016a). Traditionally, the commonly used indicators body flex and tail grab are the most sensitive and produce the highest rates of impairment while head complex and equilibrium produce lower rates of impairment (Brownscombe et al., 2015). Thus, and because reflex impairment has been successfully correlated with fish health, it has been proposed that impairment for the indicators body flex and tail grab may be indicative of minor physical impairment with fairly limited consequences for fish health (Bower et al., 2016a). In contrast, impairment of the less sensitive indicators equilibrium and head complex may suggest more serious physical impairment (Bower et al., 2016a).

Interestingly, during this study the most sensitive of the common RAMP indicators was found to be equilibrium with 73.3% of angled fish displaying impairment. This is not typical and is thought to be related to the large size of the swim bladder in *P. quadrifilis* and resultant barotrauma, despite the relatively shallow angling depths (mean of 5.1 m). Under normal circumstances, a loss of equilibrium (that is not the result of barotrauma) indicates major motor impairment (Brownscombe et al., 2015). However, in this instance, it is suggested that a loss of equilibrium is indicative of minor impairment, based on the difference in causation.

When compared with the traditional indicator equilibrium, the new indicator maintenance of equilibrium appeared to be less sensitive for this species, with only 40% of individuals displaying reflex impairment. Although the two indicator tests are similar, the results illustrate their varied nature for *P. quadrifilis* and solidify the new RAMP as a relevant and useful addition to the experimental design. As further support, the binomial logistic regression found a highly significant correlation between the RAMP maintenance of equilibrium and the most influential C&R factor, air exposure, demonstrated by a p-value of 0.001 (Table 5.2). It is likely that maintenance of equilibrium will prove useful in other experimental designs where fish are unable to easily regain equilibrium on the surface and may be particularly useful during studies assessing the effects of barotrauma. Additionally, the assessment may also allude to the potential for higher rates of post-release mortality via predation. In instances where fish are unable to maintain an upright position, they will likely remain upside-down on the water surface for long periods where they are extremely vulnerable to predation (Danylchuk et al., 2007b) from both above (e.g. avian and human predators) and below (e.g. piscivorous teleosts, elasmobranchs and reptiles).

The indicators body flex (45% impairment) and tail grab (20% impairment) presented moderate levels of impairment in *P. quadrifilis*. This falls within the range of expectation and is similar to what has been found in other C&R studies (e.g. Gagne et al., 2017). Both of these reflex indicators have been linked with the escape response and are therefore thought to be indicative of the fish's ability to avoid predators (Brownscombe et al., 2015). In many cases (n = 19, 31.7% of fish) during this study, fish would display impairment for equilibrium yet would still respond positively to the indicator tests body flex and tail grab. In these cases, *P. quadrifilis* individuals likely maintained the basic ability to escape from predation but were being severely impacted by their inability to regain equilibrium. Based on this findings, it is suggested that handling practices should aim to address this via the use of techniques such as venting of the swim bladder or rapid recompression, which have been shown to aid recovery (Drumhiller et al., 2014). Additionally, it was observed that fish that were allowed to recover in a protected environment (within the floating mesh net in which RAMP assessments were undertaken – Figure 5.1) would regain equilibrium naturally within a few minutes. This is similar to what has been observed in angled bonefish, *Albula* spp., whereby fish held in recovery bags for a period of 15 minutes displayed significantly less motor impairment compared with fish that were released immediately following C&R (Brownscombe et al., 2013).

Within the individual RAMP indicators, *P. quadrifilis* did not display any impairment for the indicator "head complex". This may lead one to believe that head complex is not well suited to this species. However, it appears that "head complex" is the least sensitive of all of the traditional reflex indicators, (Brownscombe et al., 2014, 2015; Bower et al., 2016b; Gagne et al., 2017). From a mechanistic perspective, a positive response for “head complex” (regular breathing) is governed by the autonomic nervous system. Therefore, an impairment of this response indicates an extreme neurological impact (Brownscombe et al., 2015) and may indicate a significant level of predicted mortality (Bower et al., 2016a). Therefore, the lack of impairment in this study may indicate that major impairment to the autonomic nervous system of *P. quadrifilis,* as a consequence of C&R, was minimal.

It is important to acknowledge that the RAMP indicators used within this study have not been linked to C&R-induced mortality for *P. quadrifilis* specifically. Therefore, there is a need for a further study aimed at understanding how RAMP is linked to mortality for this species. This would improve the meaningfulness of the RAMP results reported within this study. However, RAMP is thought to have general applicability across numerous different angling species and has produced similar relationships between indicator score and biological relevance and predicted mortality in a number of cases (reviewed in Brownscombe et al., 2015). Therefore, its use within this study is warranted, although further investigations regarding the species-specific link between RAMP impairment and mortality should be carried out in the future.

Although it was not possible to estimate rates of direct mortality following C&R in this study, it appears that there are low rates of hook-related injury in the foreign recreational fishery for *P. quadrifilis* on the Kwanza Estuary. This is directly related with the techniques employed by anglers within this fishery and the current practice is likely to be the best possible approach towards reducing hooking injury for this species. For example, single-hook lures are less likely to result in deep-hooking and hooking-related bleeding and injury when compared with treble hooks (Burkholder, 1992). Similarly, for fishing practices that employ bait, circle hooks have been shown to promote hook placement in the jaw of the fish (Cooke & Suski, 2004; Bartholomew & Bohnsack, 2005).

While hooking injury appeared to be a less important factor contributing to direct mortality, the findings of this study suggest that direct (and indirect) mortality arising from C&R would likely be attributed to the exhaustion associated with extended air exposure and, to a lesser extent, fight times. Therefore, to promote survival of *P. quadrifilis* in this fishery, it is suggested that guides and anglers focus on reducing fight and air exposure times. This is particularly relevant for larger individuals as it was demonstrated that they are subjected to extended fight and air exposure times (Figure 5.3). A reduction in fight time can be achieved through the use of heavier fishing tackle (Brownscombe et al., 2015). This would include stronger rods, reels and lines with higher breaking strains. However, the use of heavier tackle may negatively impact the attractiveness of the fishery to recreational anglers who are drawn to the appeal of catching large fish on light tackle. Therefore, a balance needs to be found whereby tackle is appropriately strong enough to limit fight time, but sufficiently light to appeal to recreational fishermen.

In contrast, extended air exposure times are more difficult to reduce as they are directly reliant on the angler and their level of preparedness and willingness to conserve the fish's health. It is suggested that a temporary knotless silicone holding net should be utilised in which the hook can be removed and where fish can be held while anglers prepare their camera for photographs. Once fish are removed from the water, they should be held low to the ground and a maximum air exposure time should be enforced by the guide or skipper at the time. Based on the logistic regression models developed in this study (Figure 5.5, Table 5.3), it is suggested that a maximum air exposure of 40 seconds is enforced. This time correlates with the approximate time at which 50% of the sampled fish displayed minor reflex impairment (equilibrium) and low rates of moderate to major impairment.

To address the loss of equilibrium, which may have a considerable impact on post-capture predation, it is suggested that individuals displaying these symptoms should be allowed to recover in a suitable holding net until they regain equilibrium naturally. Additionally, the use of a clean hypodermic needle may aid in venting the swim bladder and allowing the fish to recover quickly but should only be attempted by qualified or suitably trained anglers or guides. If C&R is promoted and resultant mortalities are adequately minimised, recreational angling for *P. quadrifilis* may justifiably contribute towards conservation through ecotourism (Zwirn et al., 2005). However, it is also critical to appreciate other social and economic characteristics of the fishery in order to understand the benefits they may have for the local community. If ecotourism is to take place, it is important that there are significant socio-economic benefits for locals and the fishing community is placed in a better position than it would be without the development of the recreational fishery.

# Chapter 6

# An assessment of the total direct economic contribution of the recreational fishery targeting *Polydactylus quadrifilis* on the Kwanza Estuary

## 6.1 Introduction

Globally, recreational fisheries have been identified as significant contributors towards national economies (Henry & Lyle, 2003; Cisneros-Montemayor & Sumaila, 2010; DFO, 2015). However, much of the research within this field has taken place in the developed world, where there are high rates of participation and a lower reliance on fish stocks for food (Mora et al., 2009; Cooke et al., 2018). Recreational fisheries in the developing world are, on average, less well developed and therefore receive less scientific attention (Bower, 2017; Arlinghaus et al., 2019). Here, fisheries research has traditionally focussed on small-scale artisanal sectors (Smith et al., 2005; Mora et al., 2009), due to their potential for poverty alleviation (Belhabib et al., 2016), and large industrialised fisheries, based on their economic importance. Therefore, the recreational fisheries of much of the developing world are not well understood, with many countries disregarding their impact, both economically and environmentally (Bower, 2017).

Recreational fisheries are characterised by heterogeneous human-nature relationships and a social-ecological systems (SESs) approach (see Chapter 1) has been advocated to fully appreciate their complexity (Hunt et al., 2013; Arlinghaus, 2017). Traditionally, systems of natural resource, such as forestry or fisheries, have been analysed with oversimplified theoretical models that have not taken all aspects into account (Ostrom, 2009; Ostrom & Cox, 2010). Therefore, complexity theory and adaptive SES science is now receiving attention as a more holistic approach towards resource management (see Chapter 1). If we are to improve our understanding of recreational fisheries in the developing world, it is critical that we apply a SES approach to our investigations (Bower, 2017). In terms of Africa, the majority of recreational fisheries work has focussed separately on the biological traits of the angling species (Butler et al., 2017; Arkert et al., 2018) or on the traits of the user groups (Kirchner et al., 2000; Potts et al., 2009; Mannheim et al., 2018). These studies have largely taken place in southern Africa with little to no formal information available for the West African region, despite increased evidence of the importance of foreign recreational fishing tourism there (Belhabib et al., 2016; Arlinghaus et al., 2019).

It has been widely suggested that recreational fisheries (including those in West Africa - Belhabib et al., 2016) have the potential to increase the value of fish catches based on the high 'willingness to pay' for recreational fishing (Wood et al., 2013) (see Chapter 1). Additionally, recreational fisheries often maintain a non-consumptive or 'reduced-impact' use of fisheries resources, through catch-and-release (C&R) angling, and therefore a number of authors have identified recreational angling as a potential vector for ecotourism (Zwirn et al., 2005; Wood et al., 2013; Barnett et al., 2016) and conservation (Jensen et al., 2009; Everard & Kataria, 2011). However, it has also been acknowledged that many integrated conservation and development projects which utilise ecotourism as a strategy have been prone to failure in the medium- to long-term (Garrod, 2003; Wood et al., 2013). This is largely because projects are often theorised to be ecotourism ventures (i.e. the concept works on paper) but are not adequately understood or tested from a practical standpoint. This is because researchers have largely failed to appreciate that ecotourism acts within complex SESs. Thus, recreational fisheries which aim to achieve ecotourism goals should be understood and managed according to their unique social and ecological traits (Wood et al., 2013).

Ecotourism is increasingly popular in the developing world based on the remoteness of the locations and the perception that they harbour 'unspoilt' environments (Wood et al., 2013). In many cases, ecotourism has created incentives for national governments to protect and expand wildlife areas where they contribute towards local economic productivity (Durbarry, 2004). Similarly, as West African recreational fisheries are increasing in popularity with foreign fishermen due to their remote location, new and attractive angling species and the perceived pristine state of their stocks (Potts et al., 2009; Belhabib et al., 2016), they present an opportunity to contribute to local economic productivity. Unlike harvest fisheries, foreign West African recreational fisheries are often non-consumptive (Belhabib et al., 2016). Therefore, it is possible that their development may incentivise the protection of recreationally important species, with knock-on effects via the protection of associated ecosystems and thereby non-target species. This has been the case in the developed world. For example, in Florida, USA, the strict management and protection of Atlantic tarpon (*Megalops atlanticus*), bonefish (*Albula vulpes*) and important associated ecosystems has been driven largely through the recreational value of the species (Barbieri et al., 2009; Adams & Cooke, 2015). Additionally, recreational fisheries have the potential to contribute towards human welfare and provide a source of income and livelihoods for local communities (Potts et al., 2009; Wood et al., 2013; Tufts et al., 2015; Barnett et al., 2016). If such benefits are available to consumptive fishery stakeholders, such as artisanal fishermen, they will be more likely to protect the species or habitats that are important to the recreational fishery.

Ecotourism ventures are, however, complicated endeavours and require the commitment and cohesion of numerous stakeholders (Garrod, 2003; Barnett et al., 2016). Similarly, for recreational fisheries to operate as ecotourism ventures, it is critical that there is local participation and that all user groups are committed to, and benefit from, the process. In West Africa, fisheries have diverse user groups and there is a critical reliance on artisanal fisheries for livelihoods and food-security (Belhabib et al., 2015). The development of recreational fisheries in these areas is likely to place additional pressure on local ecosystems (McPhee et al., 2002) and may result in conflict between user groups (Bower et al., 2014; Nguyen et al., 2016). Therefore, it is necessary to understand the ways in which recreational fisheries are able to generate sources of income and livelihoods for local communities whilst promoting sustainability and conservation (Bower, 2017). It is suggested that an investigatory approach that views recreational fishing as a tourism activity and views fishermen as 'tourists' will be able to harness new methodologies and the wealth of knowledge that is available within tourism studies and apply them within a SES framework.

A major problem with the development of tourism in developing countries is the potential for leakage of value out of the local economy, thus rendering the contribution made to poverty alleviation insignificant (Smith & Jenner, 1992; Sandbrook, 2010b, 2010a). This leakage may take place on both the national and local scale. Leakages out of the national economy have been shown to be significant and are largely through a need for increased importation of goods and services and through the repatriation of profits by foreign tourism operators and owners (Smith & Jenner, 1992). Leakage out of local economies is even more significant and is driven by the reduced capacity of local communities to produce skilled staff and quality operational supplies (Sandbrook, 2010b). In certain cases, the local economic benefit from tourism has been shown to be as low as 1% (Walpole & Goodwin, 2000). From the perspective of recreational fishing tourism, it is imperative that leakage is reduced so that local fishing communities receive the maximum possible benefit and can persist even if consumptive fishing is shifted away from the recreational target species.

Therefore, it is necessary to provide comprehensive economic evaluations of tourist recreational fisheries in order to understand their potential value to various stakeholders and in order to improve the management of the resource system. This chapter aims to assess the direct economic contribution of the recreational fishery for *P. quadrifilis* on the Kwanza Estuary. In doing so, it provides values in terms of direct economic contribution as well as estimates of local economic benefit following estimated leakage. Additionally, the catch-per-unit-effort (CPUE) for the various species in the area was assessed and used to provide an economic benefit (in US$) per fish and per kilogram of fish caught in the recreation fishery. These values were then compared to the market value of fish caught within the artisanal fishery using the principle of 'recreational to commercial ratio' or RCR (see Belhabib et al., 2016).

## 6.2 Methods

The Kwanza Lodge was founded in 2007 to cater to foreign fishing tourists and has been involved with the development of the recreational fishery for *P. quadrifilis* on the Kwanza Estuary (see Chapter 2). The majority of lodge-caught fish are released due to strictly enforced C&R rules and only a small proportion of fish are kept for consumption, usually following accidental fishing-related mortality (Chapter 5).

Additionally, domestic fishing tourism has become more popular at the lodge (see Chapter 2). Domestic tourists are defined as either Angolan nationals or working expatriates residing in Angola but not in the local area around the lodge (see Chapter 2).

Apart from fishing tourists, both foreign and domestic tourists (non-fishing) also benefit from the establishment of the lodge whereby they are attracted by the other appealing attributes and activities that have resulted from the lodge's establishment. These include a swimming pool, boat cruises, meals, accommodation and general tranquillity and relaxation.

In addition to lodge-based tourism, a number of domestic fishing tourists visit the area to fish recreationally using private or charter vessels owned by local artisanal fishermen. Many of these anglers travel from Luanda on weekends and public holidays and usually visit the area for the day. Domestic tourists may pay inflated prices for use of the lodge's facilities based on the shorter duration of their stays and their smaller group sizes when compared to foreign guests, who commonly receive package deals. As a result, many domestic fishing tourists that initially used the lodge vessels and guides have subsequently either switched to the artisanal charter boat services as a cheaper alternative or have purchased and begun using their own vessels. Therefore, at least some of the recent increases in recreational effort can be attributed to the lodge and thus, it is likely that recreational angling effort in this fishery would be reduced if the lodge did not exist.

### *6.2.1 Defining the fishery 'sectors'*

For the purposes of this chapter, the recreational fishery for *P. quadrifilis* on the Kwanza Estuary will be divided into two main sectors. These will include the recreational fishery operating out of the lodge (the 'lodge fishery') and the domestic recreational fishery which operates separately from the lodge through the use of private vessels and artisanal charter vessels (the 'non-lodge fishery') (Figure 6.1a). The lodge fishery can be further divided into three separate sub-sectors. These include the 'domestic lodge fishery', the 'foreign lodge fishery' and 'lodge casuals', or hereon referred to as 'casuals', who are defined as domestic and foreign tourists who visit the lodge for purposes other than fishing (Figure 6.1a).

### *6.2.2 Catch-per-unit-effort (CPUE)*

#### *CPUE – lodge fishery*

Catch-per-unit-effort was recorded for the lodge fishery on the Kwanza Estuary during the winter fishing seasons (approximately 1 June – 30 September) in 2016, 2017 and 2018. Fishing took place on boats owned by the lodge and the skipper of the boat was responsible for recording catch and effort data. Skippers took note of the location and time at which fishing began and ended for each session and on each day. The type of fishing (trolling/artificial lure/bait) and number of rods was recorded. The number of *P. quadrifilis* and other species

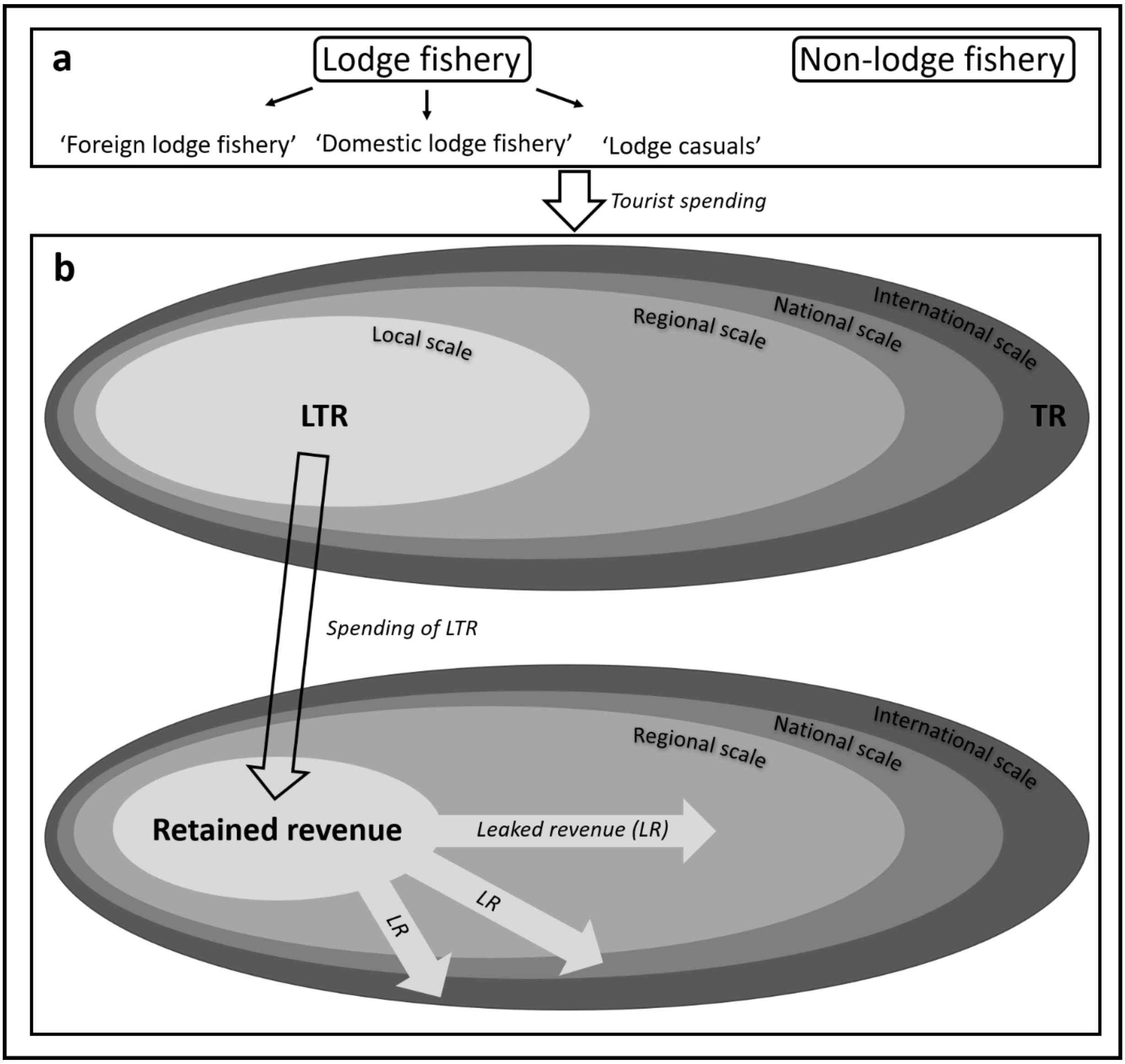


**Figure 6.1:** Schematic diagram illustrating the two main sectors of the recreational fishery present on the Kwanza Estuary and the three further subsectors within the 'lodge fishery' (a). Tourist spending from the fishery sectors contributes to total revenue (TR) on a local, regional, national and international scale. Local expenditure contributes to local total revenue (LTR) and is either retained (retained revenue) or leaked to the regional or national economy or out of Angola (international scale) (b).

caught was recorded for each session and each fish was measured (mm, FL/TL depending on species). Catch of the primary species was converted into weight in kilograms using the equations developed for the relevant species or, in the case where no length-weight relationships were available, a closely-related species:

*Polydactylus quadrifilis*: $W(g) = 0.0069 \times FL(cm)^{3.14}$ (Chapter 4)

*Caranx hippos*: $W(g) = 0.0207 \times FL(cm)^{2.987}$ (*C. ignoblis* – Maggs and Mann, 2013a)

*Sphyraena afra*: $W(g) = 0.0192 \times FL(cm)^{2.84}$ (*S. barracuda* - Maggs and Mann, 2013b)

*Lutjanus* spp.: $W(g) = 0.028 \times FL(cm)^{2.84}$ (*L. argentimaculatus* - Maggs and Mann, 2013c)

*Pseudotolithus* spp.: $W(g) = 0.0075 \times TL(cm)^{3.029}$ (Tia et al., 2017)

The CPUE was calculated using the formula $CPUE = \sum_i (\frac{C_i}{E_i})$ where $C_i$ is the quantity or mass (kg) of fish captured by the $i$th fisher and $E_i$ is the effort expended by the $i$th fisher (angler-hours).

*CPUE – non-lodge fishery*

For boats operating separately from the lodge (private recreational anglers and artisanal charters – i.e. non-lodge fishery), total effort was estimated using visual counts (location, number of boats, number of rods and fishing method per boat) that were performed at regular intervals by lodge skippers during fishing outings during 2016 and 2017 only. This was performed separately for private vessels and for artisanal charters.

In 2016, observations of fishing effort were made as regularly as possible with a minimum of eight weekday counts and eight weekend counts performed each month (four counts per week). In order to understand whether the use of less observation days in 2017 would significantly affect results, four observations were randomly selected for each calendar week (two weekdays and both weekend days) and a mean daily effort was calculated per weekday and per weekend in 2016. Thereafter, two observations were randomly selected per week (one weekday and one weekend day) from the same dataset and an unpaired student's t-test was utilised to assess for difference between the mean daily effort during the week and during the weekend between the

2-day sampling and the 4-day sampling technique. Based on the result ($t = -0.31$, d.f. = 28, $p = 0.76$), fishing effort in 2017 was assessed using a reduced sampling methodology where a minimum of four weekday counts and four weekend counts were performed each month (two counts per week).

Species-specific catch was estimated for the non-lodge fishery using the fishing method-specific effort data collected for the non-lodge fishery and the fishing method-specific CPUE from the lodge fishery.

### *6.2.3 Economic assessment*

Since the focus of this chapter is to ascertain the direct economic contribution of the fishery for *P. quadrifilis* on the Kwanza Estuary and estimate the percentage of value retained within the local community, a number of typical methodological considerations need to be made and accounted for. Income and economic activity generated through the lodge is only partly the result of recreational fishermen. A large component of lodge income is derived from casual tourists who are not visiting the area for the purposes of fishing. However, the lodge would not exist if it were not for its establishment as a fishing lodge and thereby, revenue generated through casual tourist spending may not have taken place without its establishment (or at least not within this location). There are arguments for both the inclusion and exclusion of casual spending within this study (Frechtling, 2006). Therefore, economic impact within this chapter will be presented both with and without the inclusion of casual spending at the lodge.

#### *Definition of the local, regional, national and international scale*

Tourist and lodge spending was recorded and estimated at the local, regional, national and international scale (Figure 6.1b and 6.2). For the purpose of this study, the international scale incorporated spending outside of the country (Figure 6.2a). The national scale constituted anywhere outside of the province and included payments to national government (Figure 6.2b).

The regional scale included expenditure in the nearest two towns of Ramiros (39 km by road) and Benfica (65 km by road) and the capital city, Luanda (80 km by road) (Figure 6.2c). The local scale included the local village, commonly referred to by locals as the ‘comuna’, and the immediate surrounding area (within an approximately 15 km radius of the lodge – Figure 6.2d). All expenses were converted to a value in United States Dollars (US$) using an exchange rate of 165 Angolan Kwanza to the Dollar and 15 South African Rand to the Dollar, which was appropriate during the study period (XE currency charts, 2019).

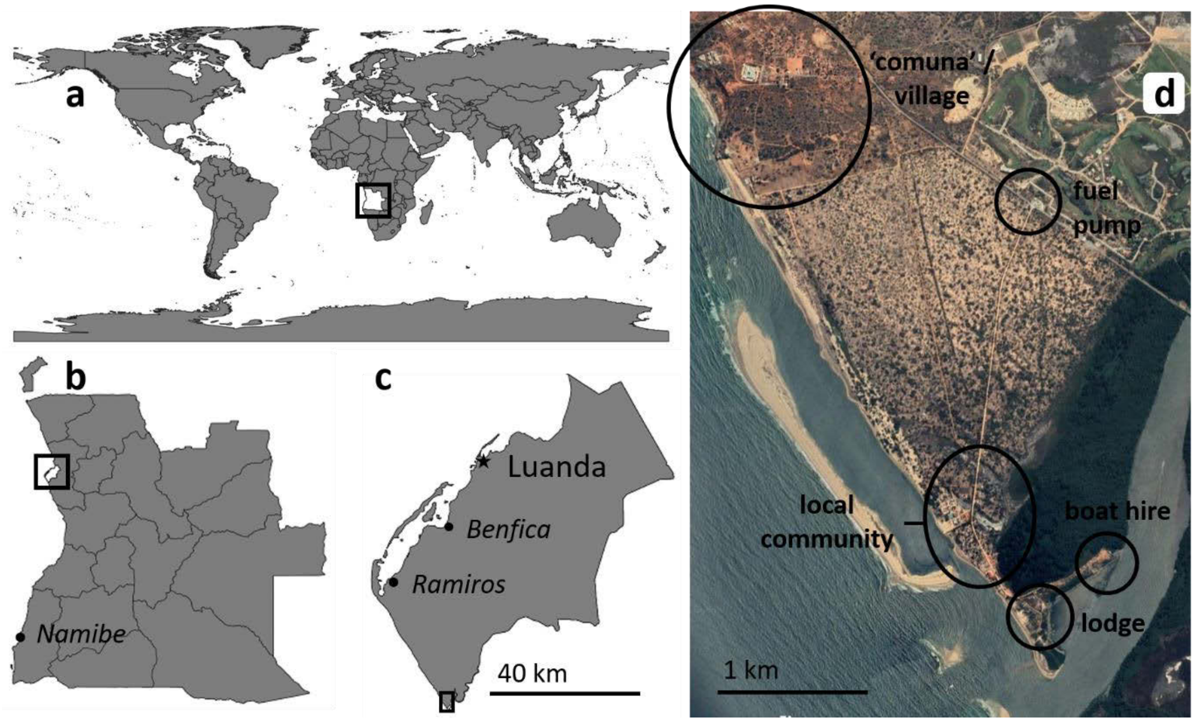


**Figure 6.2:** A visual representation of the international (a), national (b), regional (c) and local (d) scales as defined within this chapter. All fishing tourist spending within the various scales was considered within total revenue (TR). The satellite image (Google Earth, Google Inc.) displaying the local area at the Kwanza Estuary mouth (d) indicates the locations where local fishing tourist spending took place (including at the lodge, fuel pump and village and for artisanal boat hire) and contributed to local total revenue (LTR).

*Economic terminology and definitions*

In order to gain an understanding of the retention of value accruing from recreational fishing for *P. quadrifilis* on the Kwanza Estuary, it was necessary to calculate total revenue (TR), local total revenue (LTR) and leaked revenue (LR) generated through tourism (Sandbrook, 2010b). Within this chapter, TR is defined as the money spent by tourists that visited the lodge (lodge fishery) or visited the study site for the purposes of recreational fishing (non-lodge fishery). A component of TR is spent locally (within an approximately 15km radius of the lodge – Figure 6.1b and 6.2d) and is referred to as LTR. For example, money spent on guest flights to Angola was considered within TR but not within LTR, whereas money spent at the lodge was considered within both TR and LTR (Figure 6.1b). Leaked revenue is defined as LTR that does not accrue to a local person, either through payment or profit, even though the initial spending occurred locally (Figure 6.1b).

*Total revenue (TR) and local total revenue (LTR)*

Total revenue and LTR were recorded from 1 June to 30 September 2016 and 2017 only and were calculated separately for the lodge fishery and the non-lodge fishery. All tourist spending was considered within TR, while tourist spending at the lodge, at the local fuel pump, within the local village and community and with local artisanal fishermen was considered LTR (Figure 6.2). The average daily spend per tourist per day was calculated according to the number of tourists and was presented in terms of TR and LTR (by dividing the value by the number of tourists). This was calculated separately for day tourists and overnight tourists in each sector.

*Lodge fishery (foreign, domestic and lodge casuals)*

Total revenue within the foreign lodge fishery was calculated by summing the spending of each foreign fishing tourist. Foreign tourists were transported to and from the airport in Luanda by lodge staff and they paid a fixed daily rate during their stay which included their meals, accommodation and boat fees. These tourists did not spend extra money in the local economy and all spending within the country took place and was recorded at the lodge (except perhaps for some ‘out of pocket' regional spending at the airport which was disregarded). However, some spending took place outside of the country and was recorded. A record was kept of their country of origin, duration of stay and flight details (airline and cost of return ticket). The cost of a tourist visa was calculated per guest according to their country of origin.

For the domestic lodge fishery, expenses at the lodge were recorded. Fishing tourist spend on food, beverages and transport were recorded per group. Transport information that was recorded included their area of origin (in Angola), number of vehicles used during transport and the size of the travelling party. Transport expense was calculated per travelling party using the calculated distance of travel, the fuel price of 160 Kz/l (which remained constant over the sampling period) and an assumed fuel consumption of 10 km/l.

Total revenue accrued from lodge casuals was also recorded according to expenditure at the lodge only. This included spending on accommodation, meals, drinks and river cruises. However, casual's spending outside of the lodge (including private transport to and from the lodge) was not considered based on the fact that they did not travel to the area for the purposes of fishing and information was not available to estimate other 'out of pocket' spending within the area, although it was assumed to be minimal.

*Non-lodge fishery*

The direct economic contribution of the domestic recreational fishery operating separately from the lodge was estimated using the simple equation: *direct economic contribution of fishermen spending = number of fishermen * average spending per fisherman* (Stynes, 1999; Stynes & Sun, 2003).

Estimates of the number of domestic recreational fishermen fishing privately or with the use of artisanal charters were gained from the fishing effort data collected and described earlier.

Since estimates of the number of domestic recreational anglers were only available during the week and weekends in 2016 and 2017, the economic estimates were only made for those years.

Tourist spending was estimated per travelling party instead of per angler since the cost of travel and boat usage was shared amongst anglers (see Stynes, 1999). Average spending estimates for the non-lodge fishery were collected via interviews with 19 recreational anglers (Chapter 7) and included their daily spending on food and beverage ($45.76), travel to the study area ($24.00), accommodation ($212.12) (when applicable) and the cost of the day's fishing (fuel for the boat ($46.71) or boat hire).

*Leaked revenue (LR)*

Leaked revenue was determined from 1 June to 30 September 2016 and 2017 and was calculated separately for the lodge fishery and the non-lodge fishery. Leaked revenue was considered as LTR that was not retained locally through lodge spending at locally-owned businesses or directly with artisanal fishermen, lodge spending on salaries for local staff and profit accrued by local artisanal fishermen for the hiring of their boats (Figure 6.1, Table 6.1). Retained revenue was defined as the money that was retained within the local community following estimated leakage. It was calculated by subtracting estimated LR from the LTR and was calculated for each of the fishery sectors. Both LR and retained revenue were expressed in USD and as the percentage of the LTR.

*Lodge fishery (foreign, domestic and lodge casuals)*

For the lodge fishery, all LTR accrued to the lodge as all tourist spending (locally) occurred at the lodge. Therefore, an analysis of leakage was estimated using lodge expenditure – i.e. tracing guest spending one-step further from spending at the lodge to spending by the lodge on supplies and operational costs.

**Table 6.1:** Components of local tourist spending considered retained or leaked for the *Polydactylus quadrifilis* recreational fishery on the Kwanza Estuary. Only local tourist spending / local total revenue (LTR) was considered. Leaked revenue (LR) was further defined as LTR leaked to the regional, national and international scales (see Figure 6.1b).

| Local total revenue (LTR) considered retained | LTR considered leaked to the regional scale | LTR considered leaked to the national scale | LTR considered leaked to the international scale |
|---|---|---|---|
| All money spent by the lodge and tourists on goods and services from locally-owned businesses as well as directly with local fishermen | All money spent by the lodge on goods and services from businesses located outside of the local area but within the region / All money spent by the lodge and tourists at local businesses with regional owners. | All money spent by the lodge on goods and services from businesses located outside of the region but within the country / All money spent by the lodge and tourists at local businesses with national owners | All money spent by the lodge on goods and services outside of the country / All money spent by the lodge and tourists at local businesses with international owners |
| All salaries paid by the lodge to local staff | All salaries paid by the lodge to non-local staff living outside of the local area but within the region | All salaries paid by the lodge to non-local staff living outside of the region but within the country | All salaries paid by the lodge to foreign staff |
| Profit accrued by local artisanal fishermen for the rental of boats to recreational fishermen | All lodge vehicle permitting and fines | All staff flights on the Angolan airline - TAAG | All staff flights on foreign airlines |
| | All lodge boat/vessel permitting | Personal income tax paid on lodge employee salaries varying between 9% and 17% | The cost of work visas for foreign staff |
| | | Lodge permitting | Lodge profit |
| | | Lodge communications costs | |

Total spending by the lodge was assessed and leakage was estimated using the guidelines outlined in Table 6.1. The retained revenue was calculated by subtracting the LR from the LTR. Retained revenue was presented as a percentage of LTR for the lodge fishery. This percentage was then utilised to calculate the retained revenue and LR from the LTR separately for the foreign lodge fishery, the domestic lodge fishery and lodge casuals.

*Non-lodge fishery*

Leakage here was estimated by tracing the spending of domestic fishing tourists using private vessels and artisanal charters. Any money spent locally (LTR) by domestic fishing tourists outside of the lodge was assumed to be spent in either one of two locations – at the local fuel pump, or directly to artisanal fishermen for boat hire (Figure 6.2). Money spent at the fuel pump was considered leaked because the business was owned by a non-local who did not live in the area. Some fuel pump employees were local but would not disclose their salaries. However, domestic fishing tourists likely contributed relatively little towards the overall income at the fuel pump and therefore contributed little towards local employee salaries. A percentage of the money paid directly to local fishermen for boat hire was considered retained. This percentage was dictated by the cost of daily boat hire ($151.52) minus the daily fuel cost of a charter, which was estimated to be $47.78 by artisanal boat owners during interviews (see Chapter 7).

*Direct economic contribution in terms of fish and per kg of fish*

The economic contributions were converted to a monetary value in terms of fish and per kg of fish for all species and for *P. quadrifilis* only. Catch values, in terms of fish and kg of fish, were calculated from the CPUE data. Values were expressed in terms of TR, LTR and retained revenue for each fishery sector and during each season according to the following formulae:

$$Economic\ value\ per\ fish\ (\$) = \frac{TR\ or\ LTR\ or\ retained\ revenue}{Catch(no.of\ fish)}$$

$$Economic\ value\ per\ kg\ (\$) = \frac{TR\ or\ LTR\ or\ retained\ revenue}{Catch(kg)}$$

The calculated values were then compared to the market value of fish in the artisanal sector to present a recreational-to-commercial ratio (RCR) of economic value (Belhabib et al., 2016).

The market value of artisanal catch was provided by artisanal fishermen during interviews (approximately \$7.44 for all recreational species and \$8.38 per kg for *P. quadrifilis* - Chapter 7).

## 6.3 Results

### *6.3.1 Catch-per-unit-effort (CPUE)*

#### *CPUE – lodge fishery*

Catch and effort data were collected for lodge clients for a total of 210 days over the three-year period with 85 data-collection days in 2016, 77 days in 2017 and 64 days in 2018. Total angling effort for the three years was 6 014 angler-hours with 1 977 angler-hours recorded in 2016 (23.3 angler-hours per day), 2 075 in 2017 (27.0 angler-hours per day) and 1 962 in 2018 (30.7 angler-hours per day). Fishing effort was dominated by artificial lure fishing (87%), followed by bait fishing (7%) and trolling (6%).

A total of 847 fish were captured during the three periods (CPUE = 0.14 ± 0.24 fish per angler-hour) with a cumulative mass of 7 721 kg (mean = 9.2 kg, CPUE = 1.28 ± 2.51 kg per angler-hour) although it varied drastically between years. The best catches were achieved in 2018 with 380 fish (CPUE = 0.19 ± 0.30 fish per angler-hour) caught with a mass of 3 252 kg (CPUE = 1.66 ± 2.84 kg per angler-hour). In contrast, 2017 produced poor catches totalling 156 fish (CPUE = 0.08 ± 0.15 fish per angler-hour) with a total mass of 1 526 kg (CPUE = 0.74 kg ± 1.67 per angler-hour) (Figure 6.3). Bait fishing produced the highest mean CPUE in terms of both fish number (0.18 ± 0.29 fish per angler-hour) and weight (2.06 ± 4.20 kg per angler-hour) followed by artificial lure angling (0.14 ± 0.25 fish per angler-hour; 1.23 ± 2.48 kg per angler-hour) and trolling (0.07 ± 0.15 fish per angler-hour; 1.14 ± 2.42 kg per angler-hour). In terms of average fish size, trolling produced the biggest fish (mean = 15.46 kg) followed by bait fishing (mean = 11.79 kg) and artificial lure angling (mean = 8.74 kg).

*Polydactylus quadrifilis* (50%), *C. hippos* (23%) and *S. afra* (5%) were the dominant species while members of the genus *Lutjanus* (9%) and *Pseudotolithus* (6%) were also commonly caught. In terms of cumulative numbers, *P. quadrifilis* had the highest CPUE (0.07 fish per angler-hour) followed by *C. hippos* (0.03 fish per angler-hour) and *Lutjanus* spp. (0.01 fish per angler-hour). In terms of cumulative mass, *P. quadrifilis* also had the highest CPUE (0.64 kg per angler-hour) followed again by *C. hippos* (0.29 kg per angler-hour) and *Lutjanus* spp. (0.14 kg per angler-hour).

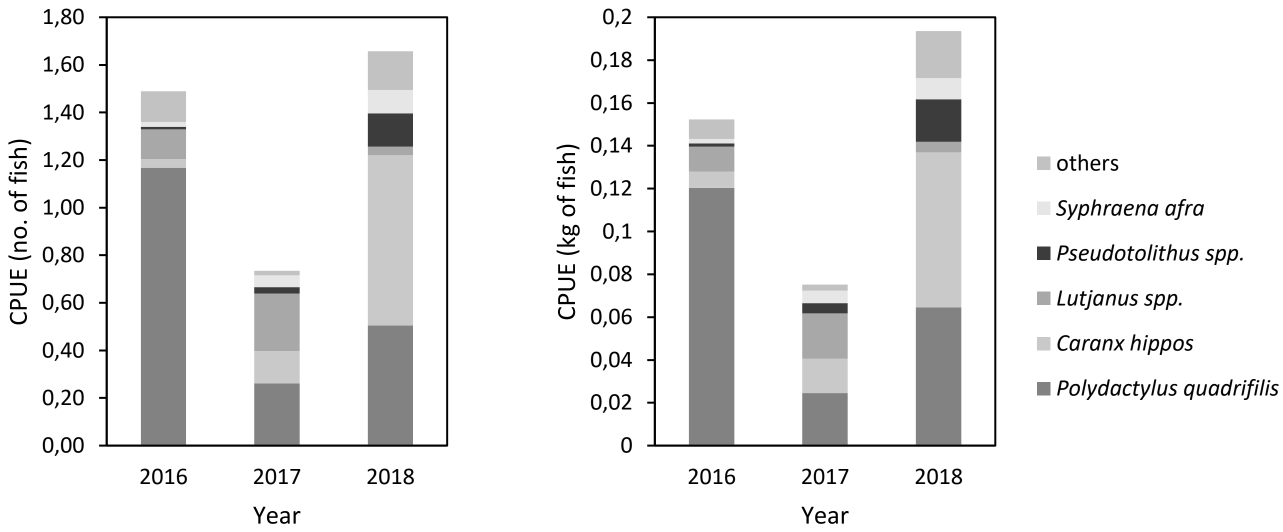


**Figure 6.3:** Catch-per-unit-effort (CPUE) of the dominant species caught by the recreational fishery on the Kwanza Estuary in Angola between June and September in 2016, 2017 and 2018.

The species composition varied dramatically between years with *P. quadrifilis* dominating catches in 2016 (238 individuals, 79%) before large reductions in 2017 (51 individuals, 33%) and 2018 (127 individuals, 33%) (Figure 6.3). In contrast, *C. hippos* did not contribute strongly to the fishery in 2016 (15 individuals, 5%) while they formed a large percentage of catches in 2017 (44 individuals, 28%) and were the most prolific species in 2018 (142 individuals, 37%). Likewise, *Lutjanus* species were scarce in 2016 (23 individuals, 8%) and 2018 (10 individuals, 3%) but were dominant in 2017 (44 individuals, 28%) (Figure 6.3) where they were heavily targeted with the use of live-bait (increase of effort from 98 angler-hours (5% of total effort) in 2016 to 205 angler-hours (10% of total effort) in 2017).

The majority of fish captured during the sampling period were large (mean, 9.22 kg). Mean weights for *P. quadrifilis*, *C. hippos*, *S. afra*, *Lutjanus* spp. and *Pseudotolithus* spp. were 9.2, 9.3, 9.5, 10.7 and 6.8 kg respectively.

*CPUE – non-lodge fishery*

Domestic fishing effort within the non-lodge fishery was recorded most frequently during the 2016 season with 61 days of direct observation. During this season, based on four days of observation per week (2 weekdays, 2 weekend days), average effort was estimated to be 35.5 angler-hours per day during weekdays and 94.8 angler-hours per day during weekends. This was not significantly different for weekdays (unpaired student's t-test: $t = -0.21$, d.f. = 31, $p = 0.83$) or weekends ($t = -0.31$, d.f. = 28, $p = 0.76$) from the estimates (33.1 angler-hours per day during weekdays and 89.6 angler-hours per day) based on two days of observation (1 weekday, 1 weekend day). Based on these findings, fishing effort for the non-lodge fishery during the 2017 season was assessed using two days of observation per week.

In 2017, daily local effort was calculated as 64.3 angler-hours per day during weekdays and 79.4 angler-hours per day during weekends. In terms of fishing method across both seasons, trolling was the most popular technique utilised (81.9%) followed by artificial lure fishing (17.5%). Based on the CPUE calculated for each method in the lodge fishery, the total catch of the non-lodge fishery was estimated as 483 fish with a weight of 7 612 kg in 2016 and 242 fish with a weight of 3 058 kg in 2017. In terms of *P. quadrifilis*, a total catch of 160 fish with a weight of 1 554 kg was estimated for 2016 and 91 fish with a weight of 973 kg for 2017.

*6.3.2 Economic assessment*

*Total revenue (TR) and local total revenue (LTR)*

Total revenue, which consists of spending that takes place locally (LTR) or outside of the local scale (regionally, nationally or internationally) is presented in Table 6.2. The TR generated from fishing tourism (both the lodge fishery and non-lodge fishery) at the Kwanza Estuary (including lodge casuals) was estimated as \$295 638 in 2016 and \$268 469 in 2017 (mean of \$282 054 per fishing season) (Table 6.2). Of this, a mean of \$236 826 (83.9%) was spent locally and a mean of \$33 010 was retained (13.9% of LTR) per season. With the exclusion of lodge casual tourist spending, TR was reduced to \$158 259 per season of which \$113 031 (71.4%) was spent locally and \$24 670 was retained (21.8% of LTR).

*Lodge fishery (foreign, domestic and lodge casuals)*

An average of 36 foreign fishing tourists visited the lodge and spent an average of 219 bed nights there per season (Table 6.2). The average total cost for foreign tourists was estimated at \$288.24 per person per day and contributed, on average, \$62 981 per season (Table 6.2). The local contribution of each foreign fishing tourist was estimated at \$201.28 per person per day during the study period and contributed an amount of \$43 981 towards LTR per season (69.8% of TR). This came in the form of foreign guest spending at the lodge on accommodation (mean per season = \$27 850), drinks (\$1 994) and fishing days (\$14 087). Non-local spending included the cost of guest visas (mean per season = \$3 200) and flights (\$15 800) and amounted to an average of \$19 000 each season (Table 6.2)

**Table 6.2:** The mean spending per fishing tourist (USD), estimated total revenue (TR), local total revenue (LTR), estimated leaked revenue (LR) and retained revenue per tourist category for the recreational fishery for *Polydactylus quadrifilis* at the Kwanza Estuary, Angola. Values present the means per season across two fishing seasons (1 June to 30 September) in 2016 and 2017. Bold text represents the cumulative total values.

| Sector | Number of tourists | Number of bed nights | Mean total and [local] spending pppd for overnight guests | Mean total and [local] spending pppd for day visitors | TR | LTR | Non-local spending (TR less LTR) | LR (% of LTR) | Retained revenue (% of LTR) |
|---|---|---|---|---|---|---|---|---|---|
| **Lodge Fishery** | | | | | | | | | |
| **Foreign lodge fishery** | 36 | 219 | 288.24 [201.28] | - | 62 981 | 43 981 | 19 000 | 40 858.35 (92.9%) | 3 122.65 (7.1%) |
| **Domestic lodge fishery** | 102 | 41 | 355.58 [291.41] | 217.70 [153.53] | 28 126 | 21 646 | 6 480 | 20 109.13 (92.9%) | 1 536.87 (7.1%) |
| **Casuals** | 1 700 | 408 | [175.68] | [58.99] | 123 795 | 123 795 | - | 115 005.55 (92.9%) | 8 789.45 (7.1%) |
| **Lodge fishery excl. casuals** | | | | | **91 107** | **65 627** | **25 480** | **60 967.48 (92.9%)** | **4 659.52 (7.1%)** |
| **Lodge fishery incl. casuals** | | | | | **214 902** | **189 422** | **25 480** | **175 972.77 (92.9%)** | **13 448.50 (7.1%)** |
| **Non-lodge fishery** | 963 | 48 | 196.44 [175.92] | 63.10 [42.58] | 67 152 | 47 404 | 19 748 | 27 842.72 (58.7%) | 19 561.84 (41.3%) |
| **Lodge and non-lodge fishery excl. casuals** | | | | | **158 259** | **113 031** | **45 228** | **88 360.35 (78.2%)** | **24 670.20 (21.8%)** |
| **Lodge and non-lodge fishery incl. casuals** | | | | | **282 054** | **236 826** | **45 228** | **203 815.80 (86.1%)** | **33 009.51 (13.9%)** |

An average of 102 domestic fishing guests visited the lodge, spending an average of 41 bed nights there and generating a mean TR of $28 126 per season (Table 6.2). The direct total contributions of domestic lodge fishing tourists to LTR were estimated at $355.58 per person per night for overnight guests and $217.70 per person per day for day guests. Local TR averaged $21 646 (77% of total TR) per season and was spent at the lodge on accommodation (mean per season = $6 094), drinks ($1 214), meals ($811) and boat hire ($13 528). Local contributions were estimated at $291.41 per person per night for overnight guests and $153.53 per person per day for day visitors in 2016 and 2017 (Table 6.2). Non-local spending included guest expenditure on transport to and from the lodge (mean per season = $1 360) and on food and beverages ($5 120).

*Non-lodge fishery*

A total of 1 925 fishing days (one day's fishing for one fishing tourist) were estimated for 2016 and 2017. Of those, a total of 1 099 fishing days were estimated for local charters, while 826 fishing days were attributed to private vessels. The total estimated contribution per person per night was $196.44 for overnight guests and $63.10 per person per day for day visitors (Table 6.2). The TR generated averaged $67 152 per season and included local spending on accommodation (mean per season = $6 417), boat fuel for private vessels ($13 223) and boat hire from artisanal fishers ($27 764) averaging $47 404 (70.6% of TR) per season (Table 6.2). Local contributions were estimated at $175.92 per person per night for overnight guests and $42.58 per person per day for day visitors. Non-local revenue included spending on food and beverages (mean per season = $12 954) and transportation ($6 794).

*Leaked Revenue (LR)*

*Lodge fishery (foreign, domestic and lodge casuals)*

Expenses incurred by the lodge amounted to $159 437 in 2016 and $151 107 in 2017 (mean per season = $155 272). Of this, only a small percentage (7.1% of LTR- $13 449 per season including casuals or $4 660 per season excluding casuals) was considered retained within the local economy (Table 6.2 and 5.3). This came in the form of salaries to local staff (mean per season = $9 151), expenditure on locally sourced fish and seafood ($2 966) and miscellaneous items ($1 322) (Table 6.3). The lodge employed 17 full-time Angolan staff in both 2016 and 2017 including two boat captains, two cooks, four security guards, three cleaners, three gardeners, one handyman, one carpenter and one driver. However, only seven staff members were from the local community, while three were from Luanda and seven were from the town of Namibe in the south of Angola. Of the 17 Angolan staff, only the driver and the handyman could speak basic English.

The majority of lodge supplies were sourced in and around Luanda and therefore direct leakage into the regional economy was high (77.1% of lodge spending / LTR - $119 745) (Table 6.3). This was mostly comprised of operational costs (food, beverages, fuel for electricity generation, general maintenance etc.) averaging $101 494 per season. Other direct leakages to the regional economy included lodge transportation costs (fuel and vehicle maintenance) at $13 407 per season and lodge employee salaries at $4 845 per season (Table 6.3). Leakages of LTR directly to the national economy averaged $20 200 per season and were mostly in the form of leakages via the salaries of non-local Angolan staff and personal income tax paid on employee salaries (Table 6.3). Direct leakages of LTR out of the country came in the form of salaries paid to foreign staff (mean per season = $7 684) and via the repatriation of lodge profit (calculated as $40 309 and $27 990 before tax in 2016 and 2017 respectively – Table 6.3).

**Table 6.3*:*** Detailed total spending of a recreational fishing lodge during the winter fishing season (June 1 – September 30) of 2016 and 2017. Lodge expenditure originated as local total revenue (LTR) generated from foreign and domestic fishing as well as casual tourists and is further allocated as money retained within the local economy (retained revenue) or leaked (leaked revenue - LR) to either the regional or national economies. Money leaked out of the country is not indicated in the table but can be identified by subtracting all values from LTR.

| | **2016** | | | | **2017** | | | | **mean (2016 & 2017)** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **LTR (US$)** | **Retained revenue (US$)** | **Leaked to regional economy (US$)** | **Leaked to national economy (US$)** | **LTR (US$)** | **Retained revenue (US$)** | **Leaked to regional economy (US$)** | **Leaked to national economy (US$)** | **LTR (US$)** | **Retained revenue (US$)** | **Leaked to regional economy (US$)** | **Leaked to national economy (US$)** |
| **Lodge Transport costs** | | | | | | | | | | | | |
| Petrol and Diesel | 8 502 | | 8 502 | | 6 012 | | 6 012 | | 7 257 | | 7 257 | |
| Car maintenance | 4 054 | | 4 054 | | 2 067 | | 2 067 | | 3 060 | | 3 060 | |
| S&T | 2 517 | | 2 517 | | 2 970 | | 2 970 | | 2 744 | | 2 744 | |
| Staff flights | 426 | | | 426 | 473 | | | 473 | 450 | | | 450 |
| Vehicle permits and fines | 570 | | 570 | | 121 | | 121 | | 345 | | 345 | |
| Total | 16 069 | 0 | 15 643 | 426 | 11 643 | 0 | 11 170 | 473 | 13 856 | | 13 407 | 450 |
| **Lodge Operational costs** | | | | | | | | | | | | |
| **Boats** | | | | | | | | | | | | |
| Fuel | 1 614 | | 1 614 | | 1 729 | | 1 729 | | 1 672 | | 1 672 | |
| Maintenance | 1 043 | | 1 043 | | 2 445 | | 2 445 | | 1 744 | | 1 744 | |
| Permits | 1 030 | | 1 030 | | 1 030 | | 1 030 | | 1 030 | | 1 030 | |
| **Lodge** | | | | | | | | | | | | |
| Diesel (electricity) | 19 988 | | 19 988 | | 17 673 | | 17 673 | | 18 831 | | 18 831 | |
| Food | 55 750 | 3 184 | 52 566 | | 47 832 | 2 748 | 45 084 | | 51 791 | 2 966 | 48 825 | |
| Drinking water | 3 811 | | 3 811 | | 2 752 | | 2 752 | | 3 281 | | 3 281 | |
| Beverages | 10 667 | | 10 667 | | 8 202 | | 8 202 | | 9 435 | | 9 435 | |
| Permits | 606 | | 606 | | 606 | | 606 | | 606 | | 606 | |
| Communication | 1 342 | | | 1 342 | 1 555 | | | 1 555 | 1 448 | | 0 | 1 448 |
| Maintenance (building material and tools) | 9 871 | | 9 871 | | 12 326 | | 12 326 | | 11 098 | | 11 098 | |
| Cleaning supplies | 3 340 | | 3 340 | | 4 151 | | 4 151 | | 3 745 | | 3 745 | |
| Gas | 964 | | 964 | | 594 | | 594 | | 779 | | 779 | |
| Miscellaneous | 2 144 | 1 765 | 379 | | 1 414 | 899 | 515 | | 1 779 | 1 332 | 447 | |
| Total | 112 171 | 4 949 | 105 880 | 1 342 | 102 309 | 3 647 | 97 107 | 1 555 | 107 240 | 4 298 | 101 494 | 1 448 |
| **Lodge Salaries and Visas** | | | | | | | | | | | | |
| Angolan staff | 21 597 | 8 025 | 4 249 | 9 323 | 27 655 | 10 276 | 5 440 | 11 939 | 24 626 | 9 151 | 4 845 | 10 631 |
| Foreign staff | 9 200 | | | 1 516 | 9 200 | | | 1 516 | 9 200 | | | 1 516 |
| Staff visas | 400 | | | 400 | 300 | | | 300 | 350 | | | 350 |
| Total | 31 197 | 8 025 | 4 249 | 11 239 | 37 155 | 10 276 | 5 440 | 13 755 | 34 176 | 9 151 | 4 845 | 12 497 |
| **Lodge Profit** | | | | | | | | | | | | |
| Total | 40 309 | | | 6 853 | 27 990 | | | 4 758 | 34 150 | 0 | 0 | 5 805 |
| **Total contribution** | **199 746** | **12 974** | **125 771** | **19 860** | **179 097** | **13 923** | **113 718** | **20 541** | **189 422** | **13 449** | **119 745** | **20 200** |

*Non-lodge fishery*

Local TR within the non-lodge fishery included spending on local accommodation, boat hire and boat fuel. Over the two-year period, an average of $19 562 (41.3% of LTR) per season was considered retained within the local community (Table 6.2). This came in the form of money paid directly to artisanal fishermen for boat hire (mean per season = $27 764) less estimated fuel cost ($8 755) averaging $19 009 per season and a percentage of the money spent on accommodation at the lodge at $553 per season. Money spent on boat fuel for private vessels ($13 223 per season) was considered leaked to the regional scale.

*Direct economic contribution in terms of fish and per kg of fish*

The estimated value of fish caught recreationally on the Kwanza Estuary varied between the lodge fishery and non-lodge fishery and between the fishing seasons in 2016 and 2017 (Figure 6.4, Table 6.4). Prices per fish and per kg of fish were considerably higher in 2017 based on reduced catches in that year (i.e. a lower 'supply' of fish). In terms of TR, the estimated prices per fish and per kg of fish for all species and for *P. quadrifilis* were generally higher within the lodge fishery (Figure 6.4, Table 6.4). Based on the TR accrued within the lodge fishery, with the inclusion (and exclusion) of casual spending, the total direct economic contribution in terms of fish (all spp.) was calculated as $560.96 ($231.22 excl. casual spending) per fish and $57.36 ($23.64) per kg in 2016 and $950.11 ($415.53) per fish and $97.15 ($42.49) per kg in 2017 (Table 6.4). However, when considering retained revenue alone, values dropped to $31.80 ($7.30) per fish and $3.25 ($0.75) (RCR < 1) per kg in 2016 and to $65.84 ($15.45) per fish and $6.73 ($1.58) (RCR < 1) per kg in 2017 (Figure 6.4, Table 6.4).

In terms of the primary target species, *P. quadrifilis*, the total economic contribution for the lodge fishery was estimated as $709.46 ($292.42 excl. casual spending) per fish and $73.19

**Table 6.4:** The estimated values of recreationally-caught fishes and *Polydactylus quadrifilis* from the Kwanza Estuary, Angola in 2016 and 2017 displayed in dollar terms (US$ - A) and in terms of recreational to commercial ratio (RCR - B) using a commercial market value of $7.44 per kg for all species and $8.38 per kg for *P. quadrifilis*. Values are given using estimates of total revenue (TR), local total revenue (LTR) and retained revenue.

| | 2016 | | | | 2017 | | | |
|---|---|---|---|---|---|---|---|---|
| **A** – US$ | **All species** | | ***P. quadrifilis*** | | **All species** | | ***P. quadrifilis*** | |
| | **per fish** | **per kg** | **per fish** | **per kg** | **per fish** | **per kg** | **per fish** | **per kg** |
| **Lodge Fishery** | | | | | | | | |
| **Including casual spending** | | | | | | | | |
| TR | 560.96 | 57.36 | 709.46 | 73.19 | 950.11 | 97.15 | 2 906.22 | 273.46 |
| LTR | 489.55 | 50.06 | 619.13 | 63.87 | 846.93 | 86.60 | 2 590.60 | 243.77 |
| Retained revenue | 31.80 | 3.25 | 40.21 | 4.15 | 65.84 | 6.73 | 201.40 | 18.95 |
| **Excluding casual spending** | | | | | | | | |
| TR | 231.22 | 23.64 | 292.42 | 30.17 | 415.53 | 42.49 | 1 271.04 | 119.60 |
| LTR | 159.80 | 16.34 | 202.10 | 20.85 | 312.35 | 31.94 | 955.41 | 89.90 |
| Retained revenue | 7.30 | 0.75 | 9.23 | 0.95 | 15.45 | 1.58 | 47.25 | 4.45 |
| **Non-lodge fishery** | | | | | | | | |
| TR | 99.11 | 6.29 | 299.19 | 30.81 | 197.81 | 15.65 | 526.06 | 49.20 |
| LTR | 69.56 | 4.41 | 209.99 | 21.62 | 138.83 | 10.99 | 369.21 | 34.53 |
| Retained revenue | 27.50 | 1.75 | 83.03 | 8.55 | 54.90 | 4.34 | 145.98 | 13.65 |
| **B** - RCR | | | | | | | | |
| **Lodge Fishery** | | | | | | | | |
| **Including casual spending** | | | | | | | | |
| TR | | 7.71 | | 8.73 | | 13.06 | | 32.63 |
| LTR | | 6.73 | | 7.62 | | 11.64 | | 29.09 |
| Retained revenue | | 0.44 | | 0.50 | | 0.91 | | 2.26 |
| **Excluding casual spending** | | | | | | | | |
| TR | | 3.18 | | 3.60 | | 5.71 | | 14.27 |
| LTR | | 2.20 | | 2.49 | | 4.29 | | 10.73 |
| Retained revenue | | 0.10 | | 0.11 | | 0.21 | | 0.53 |
| **Non-lodge fishery** | | | | | | | | |
| TR | | 0.85 | | 3.68 | | 2.10 | | 5.87 |
| LTR | | 0.59 | | 2.58 | | 1.48 | | 4.12 |
| Retained revenue | | 0.24 | | 1.02 | | 0.58 | | 1.63 |

($30.17) per kg in 2016 and $2 906.22 ($1 271.04) per fish and $273.46 ($119.60) per kg in 2017 (Table 6.4). However, in terms of retained value, the estimated value of *P. quadrifilis* caught in the lodge fishery was drastically reduced and fell below that of artisanally caught fish in 2016 ($7.98 per kg – RCR < 1 – Table 6.4), being valued at $40.21 ($9.23) per fish and $4.15 ($0.95) per kg (Figure 6.4, Table 6.4). Due to reduced catches in 2017, the estimated

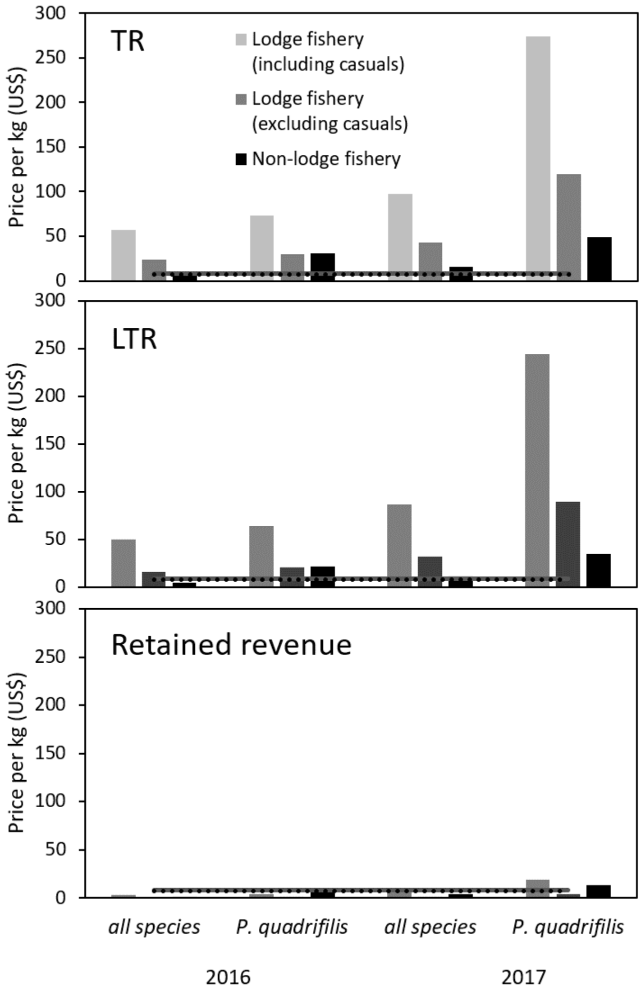


**Figure 6.4:** Estimated recreational values of fish (all species) and of *Polydactylus quadrifilis* caught within the lodge and non-lodge recreational fisheries present on the Kwanza Estuary, Angola in 2016 and 2017. Values are estimated in terms of total revenue (TR), local TR and locally retained LTR. Grey solid lines represent the price per kg of *P. quadrifilis* (\$8.38) and black dotted lines represent the price per kg of all species (\$7.44) in the artisanal fishery.

value of recreationally caught *P. quadrifilis* remained moderately high, at \$201.40 (\$47.25) per fish and \$18.95 (\$4.45) per kg (RCR including casual spending = 2.26, RCR excluding casual spending = 0.53).

Based on increased total catch and lower per person spending within the non-lodge fishery, the estimated value of fish in terms of TR and LTR was lower than what was observed within the lodge fishery (Figure 6.4, Table 6.4). However, the value of fish in terms of retained revenue was relatively higher, due to lower rates of leakage (Figure 6.4, Table 6.4). Based on TR, fish (all spp.) were estimated to be worth \$99.11 per fish and \$6.29 per kg in 2016 and \$197.82 per fish and \$15.65 per kg in 2017. When considering retained revenue alone, fish value was estimated at \$27.50 per fish and \$1.75 per kg in 2016 and \$54.90 per fish and \$4.34 per kg in 2017. For *P. quadrifilis,* the estimated fish value based on TR was \$299.20 per fish and \$30.81 per kg in 2016 and \$526.06 per fish and \$49.20 per kg in 2017. The estimated retained value of recreationally caught *P. quadrifilis* remained above that of artisanally caught fish (RCR > 1) in both 2016 (\$83.03 per fish and \$8.55 per kg) and 2017 (\$145.99 per fish and \$13.65 per kg) (Figure 6.4, Table 6.4).

## 6.4 Discussion

The recreational fishery for *P. quadrifilis* generated significant economic activity in an area that would otherwise likely receive little input from external sources. However, rates of economic leakage from the study area were found to be high (up to 92.9% in the lodge fishery) and may inhibit the achievement of potential ecotourism goals. It was found that the main sources of economic leakage were via the sourcing of lodge supplies, services and staff outside of the local area and through the repatriation of profit by foreign business owners (at the lodge and the local fuel pump). Capacity building within the local community is likely required in order to reduce leakages and to create 'linkages' between the local community and the recreational fishery (Meyer, 2007; Sandbrook, 2010b). Greater community involvement within the fishery, including the provision of business shares and greater communication and control, is suggested in order to achieve sustainability and provide incentive for the protection of recreationally important fishery species and their associated ecosystems (Scheyvens, 1999).

In terms of the total and local total revenue generated through the winter recreational fishery at the Kwanza Estuary, recreationally-caught fishes were considerably more valuable than the same species caught within the artisanal fishery (Figure 6.4). For example, *P. quadrifilis* consistently fetched the equivalent of \$8.38 per kg within the artisanal fishery during the study period (Chapter 7). However, the estimated value of *P. quadrifilis* captured within the recreational fishery ranged between three and 32 times higher depending on the fishery sector and the fishing season (Figure 6.4, Table 6.4b). This suggests that recreational fisheries can potentially raise the value of landed catch, thus incentivising their development and the protection of recreationally important species within other sectors. This scenario represents what has been suggested by a number of authors when evaluating the recreational value of fish species (Potts et al., 2009; Belhabib et al., 2016) and what has been used to demonstrate the potential of recreational fisheries for ecotourism (Wood et al., 2013).

Despite the economic potential of recreational fisheries, few studies take into consideration the concept of economic leakage and the value of recreational species to other specific fishery stakeholders. For example, a recreational species may generate 100 times more economic activity than the same fish caught within the artisanal fishery. However, if that economic activity is not appreciated by artisanal fishers or their families, there will be no incentive for them to protect that species. Additionally, in this instance, there are few enforced laws governing artisanal or recreational fisheries and therefore ecotourism would need to be achieved through voluntary cooperation between the two fishery sectors and thus mutual beneficiation would seemingly play an important role. When economic leakage was considered, the value of recreationally caught fish dropped considerably and largely fell below the market price of artisanally-caught fish (Figure 6.4, Table 6.4b). This suggests that although recreational fishing has the potential to raise the value of landed catch, currently, the local benefit is not likely to be large enough to meet ecotourism standards or incentivise a shift for local artisanal fishermen away from targeting recreationally important species or towards involvement within the recreational fishing sector. Therefore, it is imperative that solutions are explored to limit leakage.

The concept of creating 'linkages' between the local community and the recreational fishery may provide one solution towards combatting leakage (Meyer, 2007; Sandbrook, 2010b). The area at the Kwanza Estuary mouth is underdeveloped and currently the lodge sources all food supplies (except for fresh fish and seafood) from outside of the local area. However, there are certain supplies which could, theoretically, be locally sourced. These would, for example, include fresh produce and vegetables. It is suggested that where possible, capacity building and the training of local community members may allow for the provision of local resources. For example, the local community could be approached and offered the opportunity to provide fresh produce on a contractual basis. It is likely that some training may be required and should be facilitated by the lodge.

Another major area of leakage within the lodge fishery was via the employment of non-local staff. This is common in ecotourism primarily because most operations are situated in remote rural wilderness areas where the levels of education are low and where local communities are often unable to meet skilled labour requirements (Ankomah, 1991). Here, local employment is ordinarily limited to low-skilled positions including cleaners, bartenders, waiters and general labour (Ankomah, 1991). This is identical to what was found in the lodge fishery whereby the higher paying jobs, including the managerial position and position of fishing guide, were occupied by foreigners. Furthermore, other higher paying positions including the head of maintenance (handyman) and the driver were occupied by non-local Angolans. This further limits local economic benefit by reducing the potential for multiplier effects within the local economy, as local staff are earning smaller salaries (Ankomah, 1991).

The issues surrounding the provision of skilled local staff are more complicated because they are governed by larger socio-political, economic and cultural structures (Tosun, 2000). For example, a very basic yet important barrier that was identified within the lodge fishery was the inability of most local staff to speak English. The majority of foreign clientele are English speaking and therefore non-English speaking staff cannot occupy high paying jobs within management or as guides. Additionally, where staff could speak English, cultural differences may prevent the appropriate levels of communication expected, for example, from a fishing guide.

In order to break down barriers to local employment, the development of local, skilled staff needs to be prioritised, although it will take time. In many sub-Saharan countries, tourism training 'institutes' and 'academies' exist which are aimed at addressing this need and are funded through national government with technical assistance from the developed world (Ankomah, 1991). However, Angola has only recently opened its doors to tourism and does not currently have similar facilities, despite the likely growth of tourism. In the interim, the training of local people to fulfil higher positions could be facilitated outside of Angola (Ankomah, 1991) and basic English language lessons could be arranged for willing local staff members at the expense of lodges and businesses involved in the tourism industry. Additionally, opportunities or 'ladders' should be provided for local employees to upgrade themselves to higher positions or at least increase their skill-set and employability across other employment categories and within other employment sectors (Meyer, 2007).

In the short-term, the reduction of leakages may be better addressed through greater community shares and involvement in the fishery (Barnett et al., 2016). Local community involvement within the recreational fishery is imperative and the community should maintain some share in profits if it is to successfully meet ecotourism goals. A community-based approach which aims to simultaneously promote the quality of life of local people and the conservation of resources (Scheyvens, 1999) is recommended in this case. This has been achieved elsewhere through a compensatory approach to the restricted access of local people to natural resources (Sindiga, 1995). However, in this case, local fishermen are unlikely to be lawfully 'restricted' in their access to fishing rights as would be the case for local people living within national parks for example. A compensatory approach may be appropriate (see Barnett et al., 2016) but may require a higher level of regulation and governance of the fishery, which is not present. Therefore, the reduced harvesting of recreationally important species by local people is reliant on self-governance and mutual agreements between all stakeholders.

One strategy that may help to shift pressure away from artisanal fishing for recreational species may be to maintain a higher level of communication and cooperation between the lodge and non-lodge charter fishery in order to facilitate direct local benefits from the recreational sector. For example, prices for fishing charters should be negotiated and maintained between the two charter providers (the lodge and artisanal fishers). The lodge could then help develop the non-lodge charter fishery through the facilitation of adequate training of artisanal fishers as skippers and guides and by aiding with the marketing of chartered trips on the artisanal boats. Additionally, the non-lodge fishery is likely hamstrung via a lack of access to credit or capital funds to set-up appropriate recreational fishing businesses. If they were supported in their endeavours to join the industry, they would seemingly be more likely to succeed. However, the current involvement of many artisanal fishermen within the recreational sector via the chartering of their fishing vessels provides a good starting point and, with adequate support, could offset artisanal fishing effort in the future.

The market for domestic fishing tourism was evident within this study and it was illustrated that the non-lodge fishery ($134 304 over both seasons) generated similar revenue to foreign fishing tourism ($125 962). Furthermore, a higher percentage of revenue from the non-lodge fishery was retained locally due to the direct hiring of boats from local artisanal fishermen (41.3% compared with 7.1% in the lodge fishery). Therefore, it may be wise to shift domestic fishing tourism towards charters with local artisanal fishermen. This will not only reduce the overall leakage but will create a local vested interest in the recreational sector. This potential solution is interesting because few authors have approached or appreciated domestic fishing tourism in the developing world and in West Africa specifically (Potts et al., 2009; Wood et al., 2013; Barnett et al., 2016; Belhabib et al., 2016). However, the sector appears to be lucrative and may provide an opportunity for higher rates of local job creation because domestic tourists are culturally and linguistically more similar. The single drawback is that the incentive for the domestic recreational fishery to practice C&R fishing is lower, particularly when compared with the foreign recreational fishery, and therefore sustainability goals may be negatively impacted. Ultimately, a regulatory framework which sets and enforces catch limits (including bag and size restrictions) may be appropriate. Hopefully, through appropriate devolution of authority by national government, this could be driven and managed by the local community with direct funding through access fees for domestic and foreign recreational anglers (Bower, 2017).

It was evident, based on the CPUE data, that recreational fishing effort for different species shifted between years depending on their relative abundance. For example, in 2017 where the catches of *P. quadrifilis* were poor, the lodge fishery shifted effort towards fishing with live-bait more frequently in order to target *Lutjanus* species. Similarly, *C. hippos* were extremely abundant in 2018 and became a common target species in the lodge fishery comprising the highest percentage of catch by number (37%). Therefore, although the recreational fishery revolves around *P. quadrifilis*, other species also play an important role in maintaining the quality of the fishery. Similarly, if the recreational fishery is to provide a source of livelihoods to artisanal fishers, it is important that recreational fishing takes place on a year-round basis. Therefore, the other species which become more recreationally important in the summer months, such as *M. atlanticus*, require research and management consideration. Thus, the co-management of recreational angling species should extend beyond *P. quadrifilis*. For this, education programs with local communities, and particularly artisanal fishers, may aid in opening the lines of communication between the sectors and facilitating cooperation to achieve mutually beneficial goals.

All in all, a fisheries management strategy that aims to address local community benefit is likely to be the best solution going forward. The potential value of the recreational fishery should be communicated to and realised by the local community in order to build environmental stewardship and conservation mindedness within the community (Barnett et al., 2016), while strategies to reduce leakage through the creation of linkages should be implemented. However, economic benefit alone may not be enough to incentivise sustainability and environmental stewardship (Barnett et al., 2016). A deeper understanding of the social-ecological system in which the recreational fishery is nested would provide invaluable information for fisheries management and information should be gathered from a range of other social and environmental fields. Overall community involvement within the fishery is necessary to negotiate and facilitate mutually beneficial goals which can be incorporated into a holistic management framework.

# Chapter 7

## The preferences, behaviours, socio-economic traits and local ecological knowledge of local artisanal and domestic recreational fishers targeting *Polydactylus quadrifilis* on the Kwanza Estuary

### 7.1 Introduction

Common pool resources, such as fisheries, are prone to overexploitation, particularly when they are open-access in nature (Dietz et al., 2003). This is commonly the result of human greed and where there are no usage rights or restricted access to a resource, there is no incentive for users to conserve it for the benefit of others (Basurto, 2005). Additionally, in poor areas, poverty can contribute towards overexploitation due to a larger reliance on the resource for food (Bene et al, 2010). Therefore, adequate resource management is required to control the inputs to and outputs from the system. Management can take a variety of forms and ranges from highly formative top-down control, characterised by enforced regulations and monitoring, to community-based self-regulation (Allison, 2001). Variable approaches are likely more or less suitable based on the characteristics of the resource user groups. Therefore, it is critical that there is an understanding of the human dimensions within a resource system so that the correct choice of management strategy can be facilitated in order to build towards a resilient social-ecological system (SES) (Ostrom, 2009).

In recreational fisheries, important human dimensions research can provide information about system users and “their behaviours, preferences, perceptions, attitudes and well-being in support of fisheries management efforts” (Hunt et al., 2013). Additionally, understanding the socio-economics traits within the system can give managers an indication of the value of the fishery to users and, in conjunction with an understanding of fisher local ecological knowledge (LEK) (Johannes et al., 2008), can guide potential research and management (FAO, 2012).

Fisheries are an important source of food globally and the demand for fish is expected to grow in line with global annual human population growth (Mora et al., 2009). Currently, world fisheries are in a crisis and overall production has been in decline since 1996 with 31.4% of global fish stocks overexploited, 58.1% fully exploited and a mere 10.5% underutilised (FAO, 2016). In coastal developing countries, there is often a large reliance on fisheries as they have been shown to support large groups of people through the provision of jobs and often contribute towards regional and national economies and towards localised food security and poverty alleviation (Allison, 2001; Jacquet & Pauly, 2008). Here, small-scale fisheries (SSFs), which include artisanal fisheries, have the potential for the low-impact and efficient exploitation of fisheries resources because of their smaller ecological-footprint, lower reliance on government subsidies and their direct involvement of larger numbers of people (Jacquet & Pauly, 2008), when compared with industrialised commercial sectors. Despite these obvious benefits, the fish stocks targeted by small-scale fisheries are also subject to overexploitation, primarily due to their open-access nature and lack of management, leading to an exacerbation of poverty (Allison & Ellis, 2001).

One of the greatest hurdles for fisheries management, particularly for rural developing regions, is the lack of historical fisheries data (Andrew et al., 2007). This undermines the implementation of fisheries strategies and is illustrated, in numerous cases, by the unsuccessful application of traditional management in the developing world (Johannes et al., 2008). In cases where no historical data are available, the use of fisher LEK can provide a useful alternative (Johannes et al., 2008). Although not rigorous, this information can be used to form hypotheses, evaluate the status of the fishery and guide management decisions. In certain cases, a disregard for this 'unscientific data' by fisheries scientists' has led to the mismanagement of fisheries, leading to an underutilisation of the resource and potentially putting the welfare of users at risk (Johannes et al., 2008).

More recently, the roles of recreational and small-scale fisheries are gaining recognition as increasingly important contributors to both human welfare and the exploitation of fisheries resources (Cooke & Cowx, 2004; Mora et al., 2009; Belhabib et al., 2015; Cooke et al., 2018). Although these fisheries are not as intensive as commercial fisheries, they tend to have extensive spatial coverage and high rates of participation (Post et al., 2002; Mora et al., 2009). Additionally, recreational fisheries are growing rapidly in the developing world, and in Angola, where they provide an alternative use of natural resources, which may be able to increase the local economic value and sustainability of the resource (Wood et al., 2013; Belhabib et al., 2016) (Chapter 6). However, it is critical that the development of recreational fisheries does not infringe on the ability of local resource users, such as artisanal and small-scale fishers, to derive a livelihood from the resource (FAO, 2012) and competition and conflict between resource users needs to be identified and managed (Arlinghaus, 2017).

Artisanal fisheries are critically important in Angola, comprising more than half of the fishing participation within the country (FAO, 2019). Furthermore, there is a high reliance on fish and fish products which comprises 25% of the average annual protein intake and stood at 14.7 kg per person in 2010 (FAO, 2019). Angola is one of the world's poorest countries with 68% of the population estimated to be living below the poverty line and 15% living in extreme poverty (IFAD, 2014). In 2016, the human development index (HDI) of Angola ranked 150$^{th}$ out of 188 countries and fell into the lowest bracket (UNDP, 2016). Fish protein consumption is estimated to rise at the rate of current annual population growth of 3.6% per annum and artisanal fisheries have expanded in recent years to accommodate for this growth (FAO, 2019) (see Chapter 2).

The Kwanza Estuary mouth is located close to the capital city of Luanda and is therefore subject to the effects of urban sprawl. Anecdotal evidence suggests there has been a large increase in artisanal fishing pressure in the area, which has not been monitored or acknowledged due to a general lack of management (see Chapter 2). Additionally, there is no historical fisheries data for the resource system (catch and effort data), which would be highly useful for potential management (see Chapter 2). There is also a growing domestic recreational fishery made up of a diverse group of Angolan nationals and expatriates living and working in the country (see Chapters 2 and 6). The open-access nature of the fishery is likely to lead to high rates of consumptive recreational fishing and the practice of catch-and-release (C&R) angling currently requires voluntary action (see Chapter 2). Therefore, it is important to understand the attitudes, behaviours and perspectives of the anglers in the domestic recreational fishery to assess the potential impact they may have on fish stocks and to guide future management.

The aim of this chapter was to gain information regarding the human dimensions of the local artisanal and domestic recreational fisheries for *Polydactylus quadrifilis* present on the Kwanza Estuary. Specifically, the objectives were to identify the basic demographic traits of both user groups, to understand the gears and methods that they use, to identify normative user behaviours, to investigate the basic economic cost-benefit of fishing to the different user groups, to understand fisher perceptions about the state and management of the fishery and, lastly, to assess fisher LEK.

## 7.2 Methods

Two separate surveys were designed to gain information from members of the local artisanal and domestic recreational fisheries for *P. quadrifilis* on the Kwanza Estuary and were approved by the Rhodes University ethics council (Ethics approval 2019-0178-820, Rhodes University, Grahamstown, South Africa).

Survey questions (see Appendix A and B) were designed to identify basic demographic traits, fisher preferences, behaviours and socio-economics, fisher perceptions of the state and management of the fishery and interrogate fisher LEK. Participants responses were presented separately for artisanal fishers and domestic recreational anglers for all categories except fisher LEK. However, the responses for questions regarding fisher LEK were pooled for artisanal and recreational respondents in order to increase the number of responses and, in certain cases, compare the perceptions of the two user groups.

### *7.2.1 Artisanal survey*

Artisanal surveys were completed at the Kwanza Estuary between 3 and 24 July 2017 and targeted local community members that were directly involved in the artisanal fishery on the Kwanza Estuary. Participants included artisanal fishers who consistently fished using gill-nets, baited handlines, baited longlines and rod-and-reel in the Kwanza Estuary targeting *P. quadrifilis*, either intentionally or incidentally. Gill-nets were further categorised as “big gill-nets” or “small gill-nets” by artisanal fishers (pers. comm.) based on their mesh size and were therefore classified as such in the survey questions. Another necessary trait for participant selection was the use of artisanal fishing as their main or only source of livelihood. Artisanal fishers who resided within the community but fished out at sea (i.e. not in the Kwanza Estuary) were not interviewed as they did not regularly capture *P. quadrifilis* (pers. obs.) or utilise the same fishing environment as the recreational fishery. Artisanal fishers were approached within the community and asked to participate in the study following written consent. The community of potential participants was therefore small and was conservatively estimated as 35–50 fishers.

In order to obtain the most realistic results, surveys were conducted in person, with the use of a Portuguese translator. Questions were mostly informal and open-ended so as not to lead respondents to specific answers and to necessitate specific thought about the questions posed. Questions regarding the current state of the fishery were in a 3-point likert-style scale, ranging from “disagree” to “agree” with a neutral option available. Applicants were provided with the option to complete written surveys themselves, or with aid from a researcher and translator/transcriber in cases where they were unable to. A note was made of the ability of applicants to read and write and was used to estimate the literacy rate of the sample group. All surveys were completed privately from other members of the artisanal community and anonymity was assured following written consent.

Artisanal fishers were classed as either local (originally from the area) or non-local (moved there as an adult), based on their survey responses. In order to understand whether all artisanal fisher responses could be pooled, non-parametric Mann-Whitney tests were performed to assess for statistical difference in the experience levels of local and non-local artisanal fishers (Rstudio version 1.1.463).

### *7.2.2 Recreational survey*

The recreational fishery survey was available to applicants from 1 June to 1 September 2019 and was aimed at collecting information from the domestic recreational fishing community that regularly targets *P. quadrifilis* on the Kwanza Estuary (anglers from the non-lodge fishery and domestic lodge fishery – see Chapter 6). Any person residing in Angola during the study period that fished regularly for *P. quadrifilis* on the Kwanza Estuary (twice or more per year) was considered for the survey. Although anyone that was willing to participate and whom fitted the target criteria was encouraged to complete a survey, anglers with a long history of angling experience in this fishery were specifically targeted via email. The size of the recreational fishing community from which responses were drawn was small and was conservatively estimated at approximately 40–50 anglers (pers. obs. – catch per unit effort observations, Chapter 6).

It is acknowledged that the survey may be subject to avidity bias as it largely targets anglers with a substantial interest in the fishery. Therefore, it is acknowledged that the recreational community as a whole may demonstrate different perspectives (Chipman & Helfrich, 1988). However, the anglers targeted with the survey were likely responsible for a large proportion of the fishing effort within the domestic recreational fishery and were likely better equipped to provide an educated perspective on the fishery based on their experience. Responses were considered as the 'best case scenario' in many cases based on the relationships that have been noted between angler experience and conservation ethic (Fedler & Ditton, 1986; Aas & Kaltenborn, 1995; Kyle et al., 2007)

The survey contained 38 non-compulsory questions and an optional section containing 13 questions. This additional section was suggested for anglers who considered themselves "experts" and was targeted at understanding fisher LEK. The survey was primarily conducted online using Google Forms (Google Inc.). Three types of questions were included. Questions regarding the current state of the fishery were in a 5-point likert-style scale, ranging from "strongly disagree" to "strongly agree" with a neutral option available. All other questions allowed for either one only or numerous responses to be selected from a prescribed list of options. In certain cases, where relevant, the option to select "other" was provided with the opportunity to provide a description. The domestic recreational fishing community was multicultural and made up of a mixture of expatriate workers (who mostly spoke English) and

Angolan Portuguese-speaking nationals. Therefore, the survey was offered in either English or Portuguese.

Recreational anglers were classed as either nationals or expatriates, based on their survey responses. In order to understand whether all recreational angler responses could be pooled, non-parametric Mann-Whitney tests were performed to assess for statistical difference in the experience levels of nationals and expatriates (Rstudio version 1.1.463). Additionally, from an economic perspective, it was important to interrogate the sourcing of fishing equipment within the sample group. Expatriate workers would seemingly have a higher accessibility to foreign sourced equipment, due to regular travel back to their home country. Therefore, Chi-squared tests were used to understand whether there was a difference in the ratio of local versus non-local sourcing of equipment between Angolan and expatriate recreational anglers

### *7.2.3 Fisher local ecological knowledge (LEK) – artisanal and domestic recreational survey responses*

Thirteen questions pertaining to fisher LEK were applied to both the artisanal and recreational survey participants (see Appendix A and B). The questions were designed to interrogate fisher LEK and provide important information about the potential biology and ecology of *P. quadrifilis*. Other questions were designed to test whether the perceptions of participants, about the biology of *P. quadrifilis*, aligned with the findings of the research undertaken during this study (Chapter 3 and 4), with the aim of understanding the potential reliability of using fisher LEK as a source of dependable information. Chi-squared tests were then used to understand whether there was a difference between the perceptions of artisanal fishers and domestic recreational anglers.

## 7.3 Results

### *7.3.1 Artisanal survey*

*Demographics*

A total of 23 artisanal fishermen took part in the artisanal survey. This is estimated to correlate with approximately 46.0–65.7% of the targeted group of artisanal fishers at the Kwanza Estuary. All but one of the respondents were male and ranged in age from 20 to 75 years with a mean (± S.D.) of 35.7 ± 12.8 years. Based on the observed capability of respondents to read and write, the literacy rate of the sample group was estimated at 78.3%.

Approximately half (47.8%) of the respondents were originally from the local area (as defined in Chapter 6), while the remainder (52.2%) relocated to the area as adults. The majority of respondents (52.2%) had been involved in the artisanal fishery for more than 15 years. The average experience reported by respondents was 16.8 ± 13.0 years (range: 0–65 years). There was no significant difference between the levels of experience shown by artisanal anglers originally from the area (mean = 21 years) and those that had relocated to the area as adults (mean = 13 years, $W = 44.5$, $p = 0.20$).

Respondents had an average of 6.8 ± 5.3 dependants each (range: 0–23). Half of the respondents reported that they were the sole ‘breadwinner’ for their dependents while 35% reported that they were one of two ‘breadwinners’. When questioned about what other job opportunities were available to fishers, the most popular response was that fishing was the only employment option (30.4% of respondents), while many respondents listed a wide variety of other options including low- to medium-skilled trades ranging from farming and peddling to computing and plumbing (Figure 7.1).

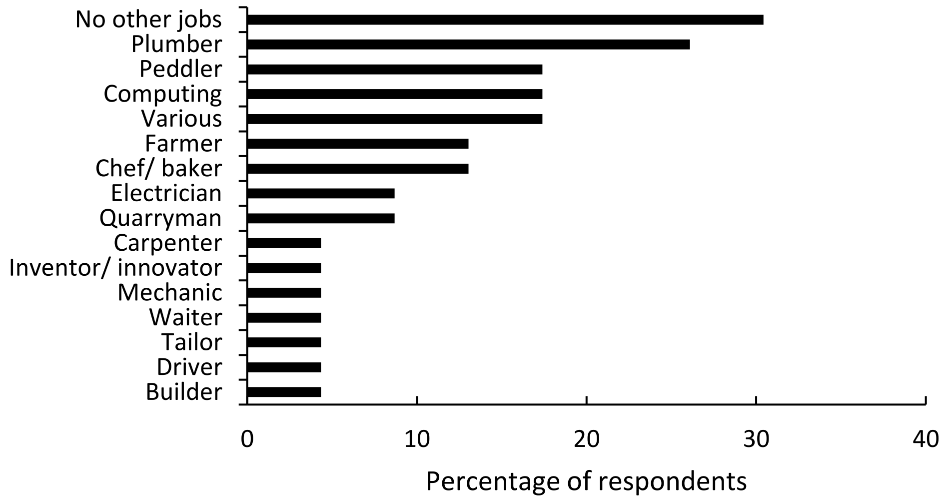


**Figure 7.1:** Twenty-three artisanal fishers were asked to list job opportunities that were available to them as an alternative to fishing on the Kwanza Estuary.

*Artisanal fisher preferences, behaviour and economics*

A number of fishing gears were listed by respondents with gill-nets being the most popular (Figure 7.2). Respondents were questioned regarding the qualities of their specific fishing gear (Questions 20–40, Appendix A). Large-mesh gill-nets were either 100 m (four responses) or 200 m (two responses) in length and only one respondent listed the depth of nets to be 3 m. Stretched mesh sizes were most commonly 457 mm (four responses) while one respondent listed sizes of 355–406 mm. Small-mesh gill-nets were 100 m in length, 3 m in depth and had a stretched mesh size of 102–152 mm. Respondents stated that longlines ranged between 100 m and 300 m in length (four stated 100 m, three stated 200 m and two stated 300 m) with one hook every metre (three responses) or every two metres (five responses). Hook sizes were large ranging from 7/0 to 9/0.

In terms of catch, respondents were questioned about the average numbers of fish and *P. quadrifilis* they caught per gear per day. In terms of number of all species, longlines were thought to produce the highest catch by number (20.4 fish) followed by large-mesh gill-nets

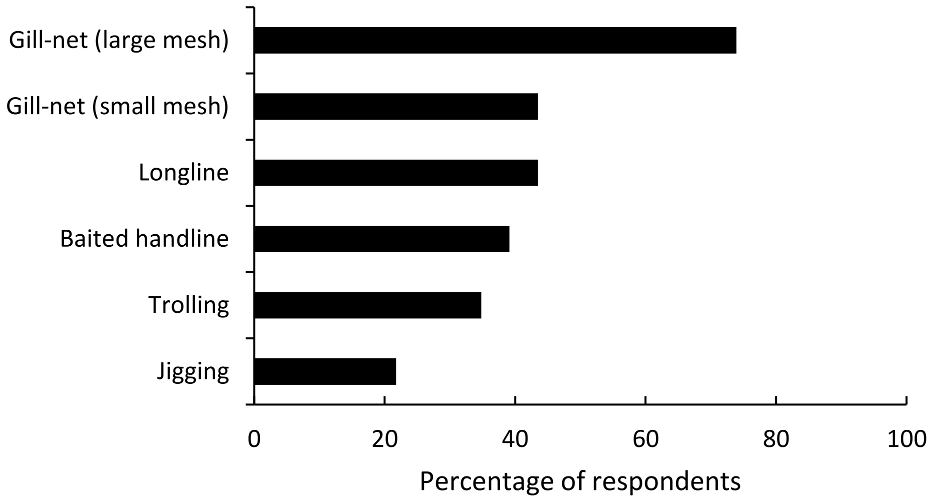


**Figure 7.2:** Fishing gears used by 23 artisanal fishers on the Kwanza Estuary. The large mesh gill-nets had a hanging mesh size ranging from 355 to 547 mm while small mesh gill-nets ranged from 102 to 152 mm.

(14.8 fish) (Table 7.1a). In terms of *P. quadrifilis* catch, jigs and plastics were thought to produce the highest catches by number (11.8 fish) followed by large-mesh gill-nets (8.0 fish) (Table 7.1b).

**Table 7.1:** Estimated numbers of fishes (a) and *Polydactylus quadrifilis* (b) captured per day using the various gear types found in the artisanal fishery on the Kwanza Estuary.

| | Gill-net large mesh | Gill-net (small mesh) | Jigs and plastics | Trolling lipped crankbaits | Longline | Baited handline |
|---|---|---|---|---|---|---|
| a - All fish | | | | | | |
| Mean | 14.8 | 6.5 | 10.0 | 6.0 | 20.4 | 3.5 |
| Mode | 10.0 | 2.5 | 6.0 | 10.0 | 15.0 | 2.0 |
| SD | 17.4 | 4.0 | 6.4 | 4.2 | 18.1 | 2.1 |
| Min | 4.0 | 2.5 | 3.0 | 1.0 | 1.5 | 2.0 |
| Max | 50.0 | 15.0 | 20.0 | 10.0 | 50.0 | 7.0 |
| b - *P. quadrifilis* | | | | | | |
| Mean | 8.0 | 4.1 | 11.8 | 4.5 | 3.4 | 1.9 |
| Mode | 2.0 | 2.5 | - | 2.0 | 1.0 | 2.0 |
| SD | 10.4 | 2.6 | 7.1 | 4.3 | 3.8 | 0.7 |
| Min | 2.0 | 2.0 | 4.0 | 1.0 | 1.0 | 1.0 |
| Max | 20.0 | 10.0 | 20.0 | 10.0 | 10.0 | 3.0 |

Fishing gears appeared to be easily obtained with options to purchase equipment available within the region, in the capital city of Luanda. Some services, such as boat and gill-net repair, were available locally. Artisanal fishers were asked to estimate specific running costs including the repair of gear, licencing costs and fuel costs. Answers varied greatly between respondents (Table 7.2) and it is likely that the questions were not adequately understood in many cases or that the answering relied on an understanding of mathematics. Therefore, costs were estimated based on the subjective choosing of the most realistic answers (i.e. after removal of statistical outliers) although the means calculated according to all data submitted are also presented (Table 7.2).

Artisanal fishers received prices ranging from \$3.64 to \$9.70 per kg for their catch (Table 7.3). Of the recreationally important species, *Lutjanus* spp. and *P. quadrifilis* were the most valuable

**Table 7.2:** Operational costs estimated by artisanal fishers on the Kwanza Estuary.

| | Licencing | Boat repair | Fuel (non-chartering) | Net repair | Other equipment |
|---|---|---|---|---|---|
| | Annual | Annual | Monthly | Monthly | Monthly |
| Mean (all data) | 199.40 | 1 041.08 | 169.56 | 632.17 | 687.88 |
| Mode | 212.12 | 606.06 | 96.97 | 18.18 | 1 212.12 |
| Minimum | 30.30 | 484.85 | 72.73 | 18.18 | 109.09 |
| Maximum | 403.18 | 3 030.30 | 303.03 | 4 848.49 | 1 212.12 |
| Standard deviation | 86.88 | 792.49 | 89.07 | 1 305.72 | 563.74 |
| Mean (revised) | 210.61 | 792.42 | 133.16 | 26.26 | 687.88 |

on the artisanal market, while *Caranx hippos* received the lowest value (Table 7.3). *Megalops atlanticus* were not commonly observed in artisanal catches. Respondents tended to keep some fish for personal consumption and estimated the percentage of fish eaten (as opposed to being sold) to be between 5% and 50% (mean percentage sold ± S.D: 73.5 ± 25.7%). One respondent provided additional information stating that he kept the first fish caught each day to eat and thereafter attempted to sell the rest. The majority of fishers (92.3%) salted and dried some proportion of their catch for preservation purposes. Most fishers (61.5%) provided a simple ratio of dried to fresh fish although some respondents provided additional information. Some respondents stated that they ‘dry everything except what they keep fresh for personal consumption’ (15.4%), others dried what they could not sell fresh (15.4%) and some chose to dry or sell fish fresh based on the type of fish caught (7.7%). Two respondents (15.4%) mentioned that fresh fish received higher market price compared with dried catch.

**Table 7.3:** The mean artisanal market price per kg (US$, whole weight) estimated for fish species that are also targetted by the recreational fishery on the Kwanza Estuary.

| | *Polydactylus quadrifilis* | *Caranx ignoblis* | *Sphyraena afra* | *Pseudotolithus* spp. | *Lutjanus* spp. |
|---|---|---|---|---|---|
| Mean | $8.38 | $5.69 | $6.93 | $7.46 | $8.74 |
| Standard deviation | $0.81 | $0.99 | $1.12 | $1.36 | $0.84 |
| Minimum | $6.06 | $3.64 | $4.85 | $6.06 | $6.06 |
| Maximum | $9.09 | $7.27 | $8.06 | $9.09 | $9.70 |

Twelve of the 22 (54.5%) respondents reported that they personally owned, or partially owned, boats. Of these, six (27.3%) owned one boat, five (22.7%) owned two boats and one (4.6%) owned four boats. Of those that owned boats, all respondents reported that they offer fishing charters to recreational anglers for $151.52 per day (i.e. it was a fixed rate) and estimated their fuel cost for these charters to be $47.78 ± $28.67 (S.D).

*Artisanal fisher perceptions of the state and management of the fishery*

The perceptions of artisanal fishers regarding changes to *P. quadrifilis* catch were negative (Figure 7.3). The majority of respondents (86.4%) thought that overall catches had decreased over the past ten years while 77.3% felt that the catch of large fish (> 30 kg) had declined. In terms of predicted changes moving forward, many respondents (40.1%) stated that catches would remain stable over the next 10 years. However, the remaining 50.9% of respondents predicted further decreases and no respondents predicted any sort of recovery (Figure 7.3).

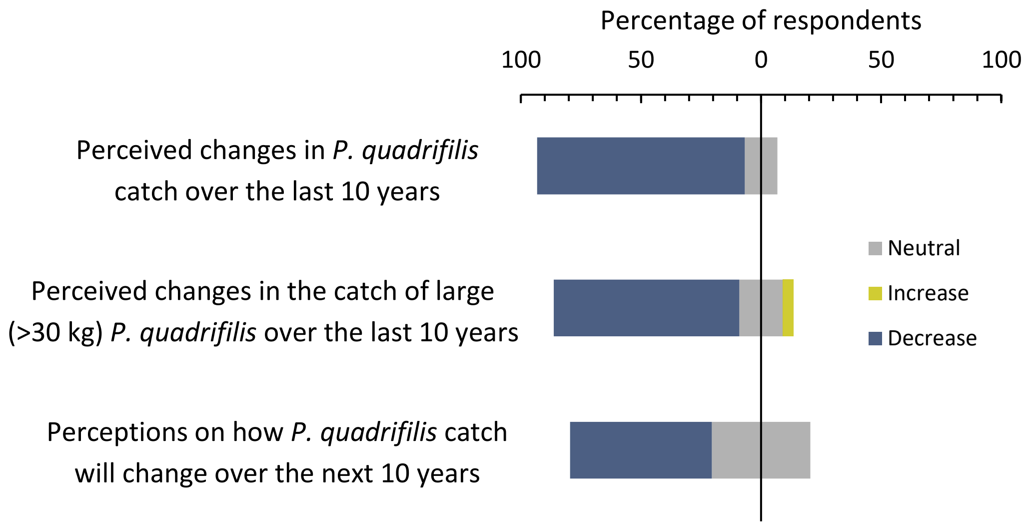


**Figure 7.3:** Artisanal fisher perceptions about the changes in *Polydactylus quadrifilis* catch over the last ten years and predicted changes in catch for the next ten years.

*7.3.2 Recreational survey*

*Demographics*

A total of 19 responses were gained from the recreational survey which is estimated to correlate with approximately 38–48% of the regular domestic recreational angling community at the Kwanza Estuary. Thirteen (68%) respondents chose to answer in Portuguese while six (32%) chose to answer in English. The majority of respondents had extensive experience fishing for *P. quadrifilis* on the Kwanza Estuary (Figure 7.4). The average experience listed by the respondents was 18.9 ± 10.4 (S.D.) years (range: 3–35 years), while 56% listed more than 20 years of experience and only one angler (6.3%) listed less than five years of experience. Three respondents chose not to disclose their levels of experience.

Twelve respondents (63%) were Angolan nationals while seven (37%) were expatriates working and residing in Angola. Experience levels were similar between expatriates and Angolan nationals ($W = 26$, $p = 0.60$) (Figure 7.4). All respondents were male and the average age of respondents was 44 ± 11.5 (S.D.) years (range: 23–63 years), while the majority (73%)

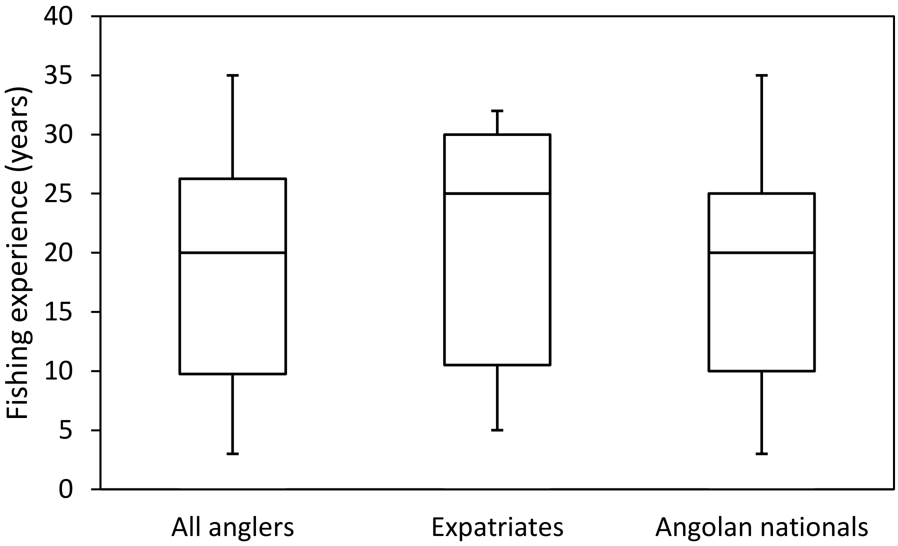


**Figure 7.4:** Experience levels of 19 domestic recreational anglers on the Kwanza Estuary.

of anglers were over the age of 40 years and 33% were over the age of 50 years (four respondents chose not to disclose their age).

*Recreational angler preferences, behaviour and economics*

The majority of respondents (16, 84.2%) estimated that they made between one and ten fishing trips to the Kwanza Estuary to target *P. quadrifilis* per year. Five respondents (26.3%) reported that they made 1–2 trips per year, six (31.6%) reported 3–5 trips per year, five (26.3%) reported 6–10 trips per year, one (5.3%) reported 11–20 trips per year and two (10.5%) reported more than 20 trips per year. Respondents reported that they usually fished in a group of between two and five anglers with the average number of anglers per fishing group being 3.4 ± 0.84.

The most popular months for recreational fishing for *P. quadrifilis* on the Kwanza Estuary were from June to September (Figure 7.5). However, recreational fishing in the Kwanza Estuary took place year-round, with at least two respondents (10.5%) listing that they fished for *P. quadrifilis* in each calendar month (Figure 7.5).

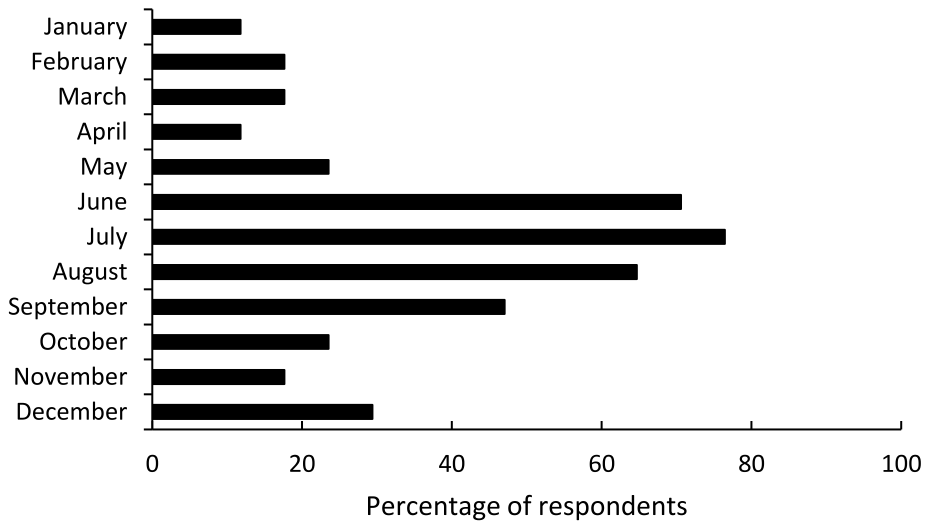


**Figure 7.5:** Year-round effort of domestic recreational anglers fishing for *Polydactylus quadrifilis* on the Kwanza Estuary

When fishing for *P. quadrifilis,* most respondents (13, 68.4%) used private boats. Nine of the respondents (47.3%) indicated that they commonly fished from the river bank, five (26.3%) from chartered boats owned by artisanal fishers and one (5.3%) from chartered boats owned by the Kwanza Lodge. In terms of fishing method, the trolling of lipped crankbait lures (12, 63.2%) and the use of jigs and plastics (12, 63.2%) were the most favoured while the use of dead-bait was listed four times (21.1%) and the use of live-bait once (5.3%). When asked how anglers chose to land *P. quadrifilis,* ten (52.6%) indicated that they used a gaff, six (31.6%) used a landing net and three (15.8%) used their hands.

In terms of gear ownership, the majority of respondents (10, 52.6%) owned one private boat which they used to fish recreationally for *P. quadrifilis*. One respondent (5.3%) owned two boats and eight (42.1%) did not own a boat. In terms of fishing rods used to target *P. quadrifilis*, eight respondents (42.1%) owned 3–4 rods, five (26.3%) owned 1–2 rods and three (15.8%) owned more than ten rods. One respondent (5.4%) each owned 5–6 rods, 7–8 rods and 9–10 rods respectively.

Respondents most commonly sourced fishing boats abroad in either Europe, Asia or the Americas (5 of 10 respondents, 50.0%). Four respondents (40%) said that they sourced fishing boats in Angola and three respondents (30.0%) sourced boats in South Africa. In terms of fishing tackle (fishing rods, reels, line, lures and hooks), 13 of 19 respondents (68.4%) said that they source tackle in Angola, 12 (63.2%) said that they source tackle in Europe, Asia and the Americas, seven (36.8%) said that they source tackle in South Africa and three (15.8%) in Namibia. There was no significant difference found for the local (inside the country) and non-local sourcing of fishing equipment between Angolan nationals and expatriates (d.f. = 1, n = 19, $X^2 = 3.35$, $p = 0.07$)

Anglers were asked what their average daily spend was on fuel for transport, fuel for fishing, food and beverages and accommodation per fishing trip. Respondents estimated that they spend an average of \$24.00 ± \$12.64 (range: \$6.06–\$48.49) on fuel for transport and \$46.71 ± \$34.74 (range: \$6.06–\$96.97) on fuel for fishing boats per fishing trip. Respondents estimated average food and beverage costs to be \$45.76 ± \$28.15 (range: \$12.12–\$121.21) per trip. Only one respondent listed spending money on accommodation at the lodge at \$212.12 per night. Three of the 19 respondents (15.8%) reported that they chartered their private boats to other recreational anglers for an average of \$212.12 ± \$42.86 (range: \$181.82–\$242.42) per day. These respondents each reported that they undertook 1–2 charters per month.

All 19 respondents reported that they usually retain fish that they catch to eat. Of these, eight anglers (42.1%) reported that they only retain one or two fish per fishing trip, seven (36.8%) reported that they retain the majority of their fish to eat and four respondents (21.1%) reported that they retained all fish that they capture. Respondents reported that they retained an average of 2.7 ± 1.2 (range: 1–5) *P. quadrifilis* per fishing trip. When asked if respondents ever sold or bartered their catch, 18 (94.7%) reported that they never sold nor bartered their catch while one respondent (5.3%) said that he sold his catch to his friends.

*Recreational angler perceptions of the state and management of the fishery*

Respondent's answers regarding the changes in recreational *P. quadrifilis* catches over time were negative (Figure 7.6). When asked whether or not respondents had noticed a change in the number of *P. quadrifilis* caught at the Kwanza Estuary since they began fishing there, the vast majority (14 of 17 responses, 82.4%) reported a strong decrease in catch (Figure 7.6). Of the remaining three respondents, two (11.8%) reported a weak decline and one respondent (with three years of experience in the fishery) thought that the population had remained the same. Two respondents selected not to answer. Similarly, when posed the same question specific to large *P. quadrifilis* (over 30 kg), 14 respondents (82.4%) reported a strong decrease in numbers and three (17.6%) reported weak decreases. Again, two respondents chose not to answer. In terms of angler perceptions of stock status moving forward, 10 out of 18 (55.5%) respondents anticipated strong decreases in *P. quadrifilis* catch over the next ten years (Figure 7.6). The remaining eight respondents (44.5%) anticipated weak decreases in catch and no respondents selected that catches would remain the same or increase. One respondent chose not to answer.

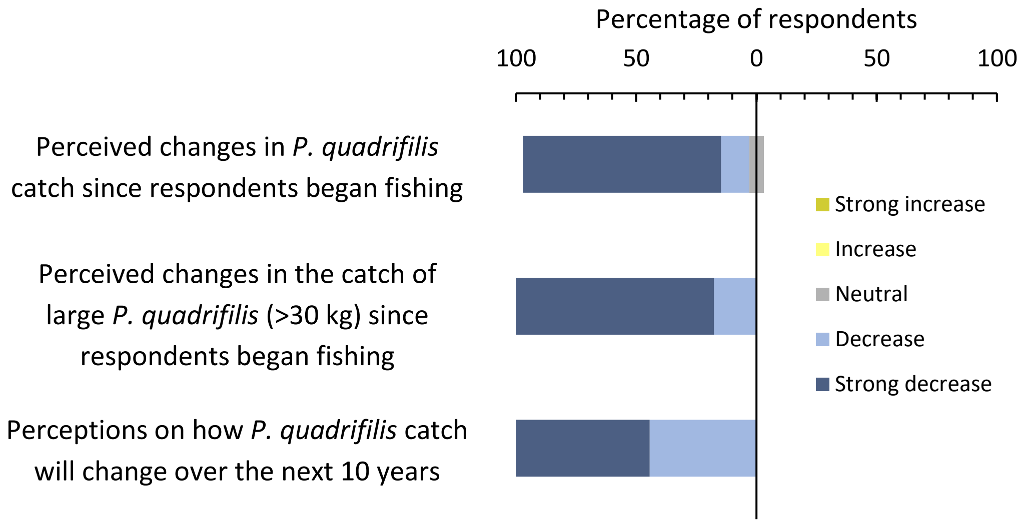


**Figure 7.6:** Domestic recreational angler perceptions about the historical changes in *Polydactylus quadrifilis* catch and predicted changes in catch for the next ten years.

When asked what the potential reasons were for declines in current and future *P. quadrifilis* catch, all respondents thought that overfishing by the artisanal gill-net fishery was an important factor (Figure 7.7). This was followed by changes in water flow, as a result of water abstraction (38.9%), overfishing with the use of rod-and-reel (33.3%), environmental changes (22.2%), pollution (22.2%) and overfishing by the artisanal longline sector (16.7%) (Figure 7.7). No respondents chose to add any further factors.

When asked about potential management strategies, all 19 respondents indicated that there should be some enforced laws regarding *P. quadrifilis* in the recreational fishery. Of these, four (21.1%) thought that there should be enforced bag limits, four (21.1%) thought that there should be enforced size limits and 11 (57.9%) thought that there should be both enforced bag limits and size limits.

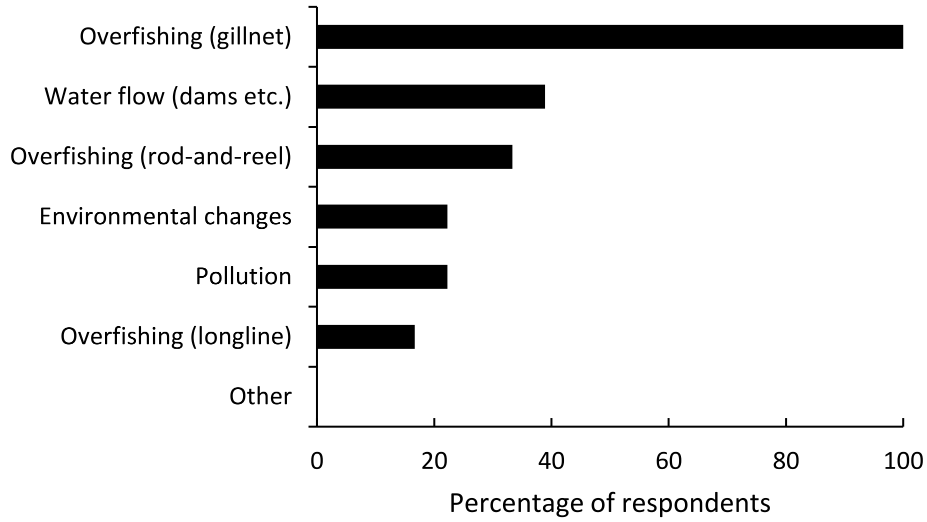


**Figure 7.7:** The perceived factors influencing declining catches by recreational anglers of *Polydactylus quadrifilis* on the Kwanza Estuary.

*7.3.3 Fisher local ecological knowledge (LEK) – artisanal and domestic recreational survey responses*

All 23 respondents of the artisanal survey answered questions pertaining to fisher LEK (although some did not answer certain questions), while ten of the 19 respondents of the recreational survey answered the additional section involving LEK.

Respondents (artisanal and recreational) felt that adult *P. quadrifilis* individuals arrived at the Kwanza Estuary from January to July with the most reporting their arrival in the months of May (28%) and June (44%) (Figure 7.8). Respondents thought that *P. quadrifilis* then left the Kwanza Estuary from July to December with a strong peak in September (68%) (Figure 7.8). When questioned about large *P. quadrifilis* (> 30 kg), respondents suggested their presence in the Kwanza Estuary between May and September with many respondents listing the months of July (59%) and August (59%) (Figure 7.8).

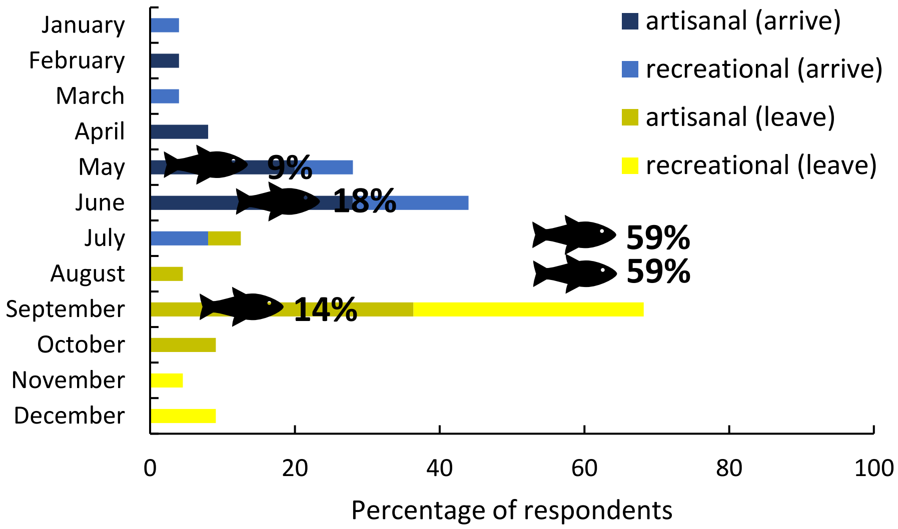


**Figure 7.8:** Twenty-five survey respondents (15 artisanal fishers and 10 recreational anglers) were asked to indicate which month they thought *Polydactylus quadrifilis* arrived (blue) and left (yellow) the Kwanza Estuary each year. Additionally, respondents indicated which months (option to select multiple months) they perceived to be the best for catching large (>30 kg) *P. quadrifilis* – indicated by fish symbols.

Respondents (recreational and artisanal fishers) were asked why they thought *P. quadrifilis* came to and spent time in the Kwanza Estuary and respondents largely listed reproduction as a factor (81%). Other reasons included resting (6%) and avoiding salt water (6%) while two respondents (6%) were unsure why they came to the Kwanza Estuary. When questioned about where *P. quadrifilis* spawn, all artisanal fishers (21) suggested that they spawn inside the estuary/river while a further eight (38%) suggested that they spawn upriver in lagoon systems. Of the six recreational respondents, four (67%) suggested that they spawn at sea while two (33%) suggested they spawn in the estuary/river. Respondents were questioned about where small (<1 kg) *P. quadrifilis* could be located. Of the recreational respondents (six), 33% thought that small *P. quadrifilis* could be found in the river while 67% thought that could be found in the sea. Of the artisanal respondents (20), all thought that small *P. quadrifilis* could be found in the river and 45% went further to state that they occur in large lagoon systems upriver.

When questioned about the perceived sex of large *P. quadrifilis* (>30 kg), 'female only' was the most common answer (41% of grouped responses) followed by 'either male or female'

(38%), ‘unsure’ (19%) and ‘male only’ (3%) (Figure 7.9). When disregarding ‘unsure’ answers, respondents’ answers differed between artisanal fishers and recreational anglers (d.f. = 6, n = 26, $X^2 = 42.9$, $p < 0.01$). All recreational anglers, and only 35% of artisanal fishers, suggested large *P. quadrifilis* were ‘female only’. Of the remaining artisanal fisher responses, 5% thought large *P. quadrifilis* were ‘male only’ and 60% thought they were ‘either male or female’. Of the respondents that provided reasons for their answers, five stated that they always observed eggs in large *P. quadrifilis* (two recreational, three artisanal), three stated that it was because *P. quadrifilis* changes sex from male to female (three artisanal) and two stated that someone had told them that (two recreational).

When respondents were questioned about the sex of small *P. quadrifilis*, 53% thought they were ‘either male or female’, 22% thought they were ‘male only’, 6% thought they were ‘female only’ and 19% were ‘unsure’ (Figure 7.9). Again, when disregarding ‘unsure’ answers, there was a difference between the answers of recreational and artisanal fishers (d.f. = 6, n = 26, $X^2 = 49.1$, $p < 0.01$). Five recreational anglers (83%) thought small *P. quadrifilis* were ‘male only’ while only one angler (17%) thought that they were ‘either male or female’. Conversely, 16 artisanal anglers (80%) thought small *P. quadrifilis* were ‘either male or female’ while two (10%) thought they were ‘male only’ or ‘female only’, respectively. Of the nine respondents who provided answers, five stated that small *P. quadrifilis* rarely or never had eggs (three artisanal, two recreational), two stated that it was because *P. quadrifilis* changes sex from male to female (two artisanal) and two stated that someone had told them that (two recreational).

Respondents were asked about the furthest upriver that they had witnessed or heard of people observing *P. quadrifilis*. Many recreational anglers were unsure (64%) while three (36%) stated the town of Culumbo (48 km upriver from the ocean). Of the 20 artisanal respondents, two (10%) were unsure, one (5%) suggested Culumbo (48 km upriver from the ocean), seven (35%)

suggested Bom Jesus (68 km upriver from the ocean), eight (40%) suggested Massangano (135 km upriver from the ocean) and two (10%) suggested Muxima (180 km upriver from the ocean). Lastly, respondents were asked how many different types (species) of threadfin they knew of from the Kwanza Estuary and Angola in general. Nine out of ten recreational respondents stated that they knew of two species while one stated that they only knew of *P. quadrifilis*. Most artisanal respondents said that they knew of two species (65%), while 26% said that they only knew of *P. quadrifilis* and 9% stated that they knew of three species.

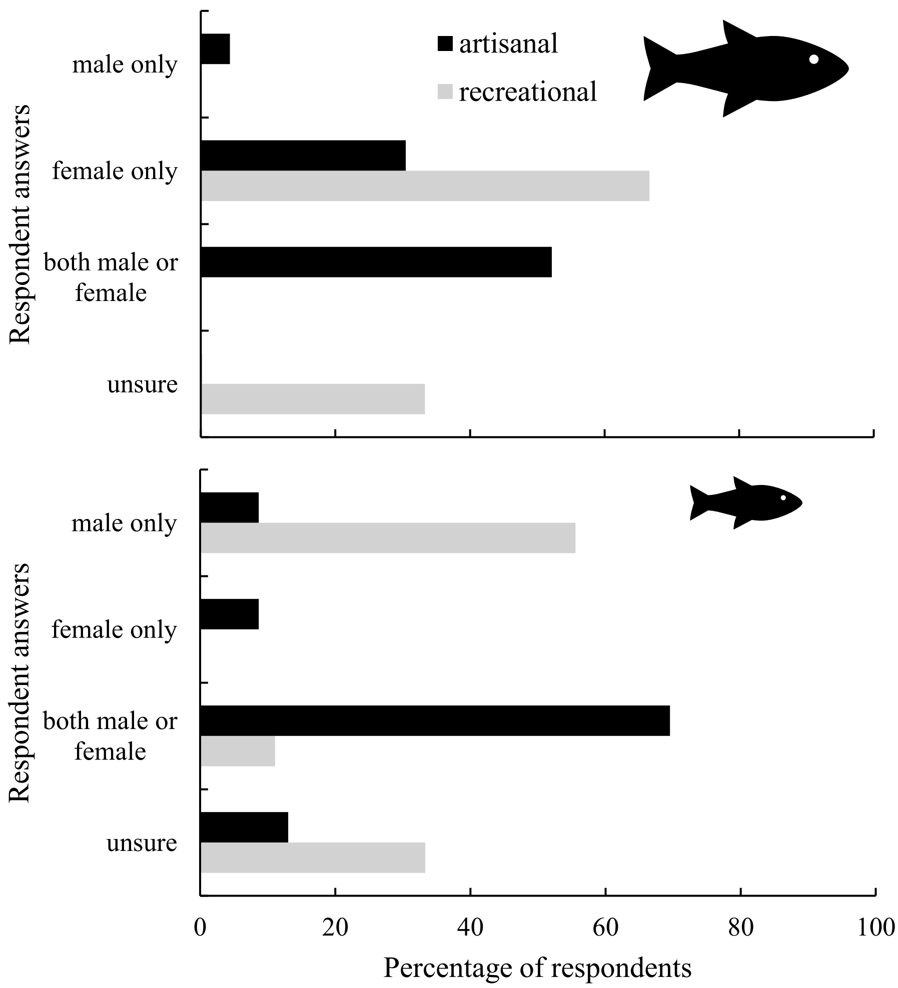


**Figure 7.9:** Artisanal fisher and domestic recreational angler perceptions about the gender of large (>30 kg) (top) and small (bottom) *Polydactylus quadrifilis* caught on the Kwanza Estuary, Angola.

### 7.4 Discussion

Both the artisanal and recreational fisheries for *P. quadrifilis* on the Kwanza Estuary are well-established and are characterised by users with a long history of participation. The artisanal fishery appears to hold high value as a source of livelihoods for the local community and has further supported non-local Angolans following their migration to the area as adults. Artisanal fishers whom have the capacity to provide recreational fishing charters appear willing and eager to be involved in the recreational sector due to the prospect of extra earnings. While this is promising, both recreational and artisanal fishers reported decreases in *P. quadrifilis* catch over the recent past and predicted further declines moving forward. It is likely that enforced catch and effort restrictions may be required to limit consumptive fishing within the artisanal and domestic recreational line-fishery. Potential conflict was identified whereby recreational anglers perceive the artisanal gill-net fishery to be a threat towards the sustainability of *P. quadrifilis* stocks. This may affect the behaviour of recreational anglers and it is likely that, in order to promote compliance in the recreational fishery, a greater deal of management and monitoring presence is required for the artisanal gill-net sector so that recreational anglers perceive the fishery to be well-managed and sustainable.

The artisanal community demonstrated a high dependence on fishing as a means of livelihood, with approximately a third of respondents listing fishing to be their only available source of income (Figure 7.1). However, in reality, this figure is likely to be far higher as the majority of the numerous other job opportunities mentioned by respondents were either arbitrary positions (e.g. as inventors or innovators) or seemingly high-paying positions (e.g. as mechanics, electricians or plumbers). If these jobs were available to fishers, one would expect that they would acquire them. It is likely that this question was misinterpreted by the respondents as “what jobs are you capable of fulfilling” rather than “which jobs are available to you”. The artisanal fishery also appeared to support informal local job creation in the form of boat and net repair, but the purchase of equipment largely took place outside of the local community. Irrespective, artisanal fishing seems to play an important role within the local community as a source of food and income as is commonly the case across Angola, West Africa (Belhabib et al., 2015) and much of the developing world (Béné et al., 2010).

The artisanal fishery primarily utilises gill-nets to capture *P. quadrifilis* and other species (Figure 7.2). However, longlines, baited handlines, the trolling of crankbait lures and jigging plastics were also important methods. Although less than a quarter of artisanal fishers reported the use of jigs and plastics, it was apparent that this technique was becoming more common within the sector (pers. obs.). This is likely driven by the high rate of success of this method for the capture of *P. quadrifilis* (Table 7.1) and the high market value of the species (Table 7.3). Additionally, it is likely that artisanal fishers have been exposed to and learnt the technique through their observations of recreational fishing activities and their involvement in that sector. The development of the recreational fishery has also resulted in lures becoming more freely available within the region and artisanal fishers reported that they were available for purchase in Luanda. Recreational fisheries have been known to influence the behaviour of local resource users (Arlinghaus et al., 2016) and, in this case, it is likely that the development of the recreational sector has impacted the behaviour of artisanal fishers in terms of how they interact with *P. quadrifilis*.

Besides exposure to new fishing techniques and the availability of new fishing gears, a number of artisanal fishers received additional benefit from the recreational fishery through the chartering of their boats or via their employment as skippers for charters. Indeed, artisanal fishers appeared eager to reap benefit from the recreational sector. This was demonstrated by the willingness of those who owned vessels to provide chartered trips to recreational anglers as frequently as possible. There was also a potential for high returns with an estimated profit of $103.74 per charter (based on an income of $151.52 less fuel expense at $47.78).

From the economic assessment of the recreational fishery (Chapter 6), it was suggested that artisanal fishers should be supported in their involvement in the domestic recreational fishery so as to increase local economic benefit and shift fishing effort from the artisanal to the recreational sector. However, this management solution seemingly relies on the premise that the domestic recreational fishery is more sustainable and less environmentally impactful than the artisanal fishery, which may not be true. In terms of *P. quadrifilis*, the non-lodge recreational fishery produces moderately high catch, estimated as 126 *P. quadrifilis* with a weight of 1 264 kg per four-month winter fishing season. Furthermore, the non-lodge recreational fishery catches other recreationally important species, estimated at an additional 237 fishes with a weight of 4071 kg per winter season (Chapter 6), and, unlike the lodge fishery, fishing effort is year-round with a peak in winter (Figure 7.5). Therefore, it is likely that the non-lodge recreational fishery can make a considerable contribution to the mortality of *P. quadrifilis* as well as other recreational species via consumptive angling and C&R mortality. If there are high levels of fish mortality arising from consumptive angling and C&R in the domestic recreational fishery, the recommendations made in Chapter 6 would likely be inappropriate.

From the survey responses, it appeared that C&R angling was not prevalent in the domestic recreational fishery with many anglers retaining the majority of their daily catch. The respondents estimated that they retained an average of 2.7 *P. quadrifilis* per person per day. This figure may appear low and, therefore, perhaps suggest that some *P. quadrifilis* are released on most outings. However, it is likely that the number of *P. quadrifilis* caught during most fishing outings does not reach the point at which anglers would begin releasing fish. For example, if there are an average of 3.4 anglers per outing and they retain an average of 2.7 *P. quadrifilis* each, the number of fish retained (± 9 fish) is approximately similar to the number of fish caught (estimated by artisanal fishers as 11.8 fish per day for jigging plastics and 4.8

fish per day for trolling). Furthermore, less than ten *P. quadrifilis* were observed being released by domestic recreational anglers in the non-lodge fishery during three consecutive winter fishing seasons and none were observed being released by the local charter vessels (pers. obs.). It appeared that recreational anglers who chartered artisanal fishing vessels retained the right to keep any fish captured, while the excess was often given to the artisanal boat owner or skipper. Therefore, it is likely that most, if not all, *P. quadrifilis* are retained by the non-lodge recreational fishing sector.

High rates of consumptive fishing are common in domestic developing world recreational fisheries (Belhabib et al., 2016) and have even resulted in the collapse of certain fish stocks (e.g. Namibia's West coast steenbras, *Lithognathus aureti,* Holtzhausen et al., 2001). Additionally, some authors have suggested that there is a large overlap between the traits of domestic recreational anglers and subsistence fishers in West Africa, suggesting a broad food-fun nexus (Cooke et al., 2018) and that domestic recreational anglers are motivated by outcomes other than recreation (i.e. subsistence or trade) (Belhabib et al., 2014, 2016). This was evident in the preferences and behaviours of recreational anglers whereby the majority responded that they land fish using a gaff, as opposed to a landing net. This behaviour is not typical of a fishery which practices voluntary C&R and further supports the notion that there are high rates of consumptive fishing within the domestic sector. Interestingly, however, it appeared from this survey, that trade was not a major motive for recreational anglers, with only one angler suggesting that he sometimes sold his catch to friends.

It is important to consider the recreational sample group in this study as anglers have been shown to be heterogenous in terms of their attitudes, perspectives, motives and behaviour (Kyle et al., 2007). Chipman and Helfrich (1988) demonstrated that recreational anglers with higher levels of experience were more likely to suggest non-consumptive motives for fishing, such as trophy fishing, to rely on skill more than luck, to practice C&R more frequently and to favour enforced restrictions. Similar trends have been noted by a number of other authors (Fedler & Ditton, 1986; Aas & Kaltenborn, 1995; Kyle et al., 2007) and, therefore, it is likely that respondents in this study represented the most conservation-minded and least consumptive anglers within the domestic recreational angling community. This is because the respondents largely demonstrated long-term involvement in the fishery, were pro-management and willingly participated in the survey. These attributes suggest that they have relatively high investment in the fishery (Chipman & Helfrich, 1988) and it is therefore possible that the perspectives of those that did not take part in the survey may be less conservation oriented, they may be less agreeable to the implementation of restrictions and may be more likely to have sale- or trade-related motives for retaining catch.

There was a perception (by both the artisanal and domestic recreational respondents) that the catch of *P. quadrifilis* had declined and that this was likely to continue. Fisher knowledge has been advocated as a means of collecting realistic historical fisheries data in situations where formal data is lacking (Johannes et al., 2008). Therefore, this result likely indicates some level of overfishing. Interestingly, when questioned about the major problems facing the fishery, domestic recreational anglers specifically blamed gill-netting while rod-and-reel fishing was only thought to be an issue for some (Figure 7.7). Therefore, it is likely that many recreational anglers do not view their consumption of *P. quadrifilis* to be a major contributing factor to perceived population declines. This is fairly common and people have been shown to be more likely to perceive other users as a threat to a common resource as their social proximity decreases (Nguyen et al., 2016). In other words, it seems that recreational anglers are currently more likely to blame gill-netting for decreases in catch before looking at their own actions or those of others within their own community. This is important as the consumptive behaviour of domestic recreational anglers is likely to be increased by the perception that the artisanal gill-net fishers are over-fishing. Furthermore, this perception is likely to negatively affect compliance behaviour if fisheries regulations are to be implemented (Bova et al., 2017).

It is likely that gill-netting may contribute significantly to the high levels of mortality in the system, but it is not possible to validate the viewpoint of recreational anglers without formalised monitoring of the artisanal sector. However, based on the findings of this study, it appears that the catch of *P. quadrifilis* in the artisanal gill-net fishery is approximately equal to or less than that of the non-lodge recreational fishery. This is because of the high effort observed in the non-lodge recreational fishery (between 35.5 and 94.8 angler-hours per day, Chapter 6) and because recreational fishing uses techniques, such as jigging plastics and trolling crankbait lures, which are more effective for the capture of *P. quadrifilis* (pers. obs., Table 7.1). Furthermore, although *P. quadrifilis* were common in artisanal gill-net catches, they were never captured in large numbers (approximately 0–10 fish per day between all fishers, pers. obs.).

Other aspects of fisher LEK provided by the surveys revealed some interesting perspectives on the biology and ecology of *P. quadrifilis* which may provide additional information for current (Chapter 3 and 4) and future biological investigations. It is well-understood that there is a general perception amongst resource users that *P. quadrifilis* have a predominantly seasonal presence at the Kwanza Estuary. This has, understandably, prompted the notion that they migrate to the area from elsewhere. From respondents' answers, it appears that *P. quadrifilis* 'arrive' at the Kwanza Estuary in May and June before 'leaving' the system in September (Figure 7.8). However, it was interesting to note that the time at which respondents anticipated the highest number of large (>30 kg) *P. quadrifilis* overlapped with the time at which they were thought to stop arriving and start diminishing from the system (July, August; see Figure 7.8). If they are arriving at the Kwanza Estuary for a specific purpose, it would seem that the large (female) fish are the last to arrive.

When questioned about the purpose of this perceived migration to the Kwanza Estuary, many respondents listed reproduction as the cause (81% of respondents). This is unsurprising, as adult *P. quadrifilis* are reproductively-mature at this time (Chapter 3) and fishers likely notice this when cleaning harvested fish. However, it was interesting to note that many respondents, particularly artisanal fishers (100% of respondents), thought that spawning took place inside the estuary or river. This is important as the factors which influence sex change in sequential hermaphrodites are often linked to reproductive behaviour (Todd et al., 2016) and, therefore, understanding where and how *P. quadrifilis* spawn may provide insights into their life-history (see Chapter 4). Spawning in *P. quadrifilis* has not been documented, however nearshore spawning aggregations of large adults were reported in Gabon (Loubens, 1964). The likelihood of spawning taking place inside the estuary or river is low on two counts. Firstly, if one considers the high flow rate of the Kwanza River, it is likely that eggs would be rapidly swept out to sea. Secondly, it is most likely that spawning aggregations would have been observed due to the heavy use of the river by the different fishery sectors. Nevertheless, it is not possible to disprove the assertions of the artisanal fishers without an appropriate scientific investigation.

Another interesting finding of the LEK survey was the perceptions of respondents about how far upriver *P. quadrifilis* occur. From artisanal fisher responses, it appeared that *P. quadrifilis* may occur up to 180 km from the mouth of the Kwanza River, suggesting a high tolerance to fresh water. It is possible that this may be true as other authors reported this species 250 km upriver from the sea (Laë et al., 2004; Simier et al., 2004). If *P. quadrifilis* do persist that far upriver, it would be interesting to understand what purpose the upstream environment has for the species. Certain artisanal fishers (eight) suggested that *P. quadrifilis* not only spawn in the river but in large lagoon systems that occur far upstream. However, through conversations with local fishers, it seems that this notion is not driven by the presence of large adult fish upstream or by observations of spawning taking place, but rather via the presence of high numbers of small juvenile *P. quadrifilis* within these lagoon systems (pers. comm.). While working on a Gabonese estuarine system, Loubens (1966) reported the presence of large adult and small juvenile *P. quadrifilis* (less than 20 cm standard length) in close proximity to the mouth of the estuary. Thereafter, he noticed increasingly larger size classes as he sampled further upstream and concluded that juvenile *P. quadrifilis* likely undertake a vertical ontogenetic migration with the purpose of migrating into upstream nursery environments, from a marine origin. This theory largely aligns with the observations of artisanal fishers, with large numbers of juvenile individuals upstream, and is likely the case for the Kwanza population of *P. quadrifilis* as well.

Despite the reports of *P. quadrifilis* juveniles upstream, it is possible that the threadfin observed here belong to a separate species as there are two other polynemids which occur in Angola and both commonly frequent estuaries and rivers (Longhurst, 1957; Laë et al., 2004; Motomura, 2004; Simier et al., 2004). When questioned about the number of threadfin species in the Kwanza system, only a few respondents knew of all three species (*P. quadrifilis*, *Galeoides decadactylus* and *Pentanemus quinquarius*). For the recreational fishery, this is unsurprising as it is unlikely that anglers come into contact with *P. quinquarius* via recreational angling due to their small size (Motomura, 2004). However, since all three species are common in artisanal gill-net catches (pers. obs.), it was surprising that only 9% of artisanal fishers thought that there were three separate species. Thus, it is possible that artisanal fishers may misidentify other polynemids as juvenile *P. quadrifilis* in upstream lagoon systems. However, the two respondents which correctly identified that there were three species, also stated that *P. quadrifilis* spawn in these lagoon systems and confirmed the presence of many small individuals there. This suggests that *P. quadrifilis* may indeed occupy the upper reaches of the Kwanza River.

It was interesting to note that respondents were often unaware of the largely male-dominated gender of smaller *P. quadrifilis* individuals and the near exclusive female gender of larger fish

(>30 kg) (see Chapter 3). This was particularly true for artisanal fishers as only 9% of respondents thought that smaller individuals were 'male only' and only 30% thought large fish were 'female only' with many thinking that small (70%) and large fish (52%) could be male or female. In contrast, 55% and 66% of recreational anglers felt that small fish were only male and large fish were only female, respectively. This difference may suggest that recreational anglers have a better understanding of the biology of the resource they utilise, when compared to the artisanal fishers, and suggests that artisanal fisher LEK may be less reliable for incorporating into management processes.

It is likely that the reliability of information gathered from fisher LEK may depend on the specific relevance of that information to the users that it was collected from. For example, an understanding of the reproductive style of *P. quadrifilis* has no real value or consequence for artisanal fishers in terms of their benefit gained from the fishery and, therefore, if they were to identify this trend, it would be purely driven by a general interest in what was going on. Simply put, noticing that big fish are female and small fish are male may be interesting, but it does not directly impact the basic livelihood function of the fishery for artisanal fishers and, therefore, they may not take note of it. Maslow (1943) posited that every human has the same basic needs and that these needs are hierarchical. In his revised work (Maslow, 1970a; 1970b), he suggested that there are eight levels within this hierarchy. At the bottom, there are basic needs, which are most likely to align with those of artisanal fishers, such as physiological needs (air, water, food, shelter etc.), safety needs (personal security, employment, health etc.) and social needs (belongingness, family, relationships etc.). On the other hand, cognitive needs (which includes the need to understand and question things) only appears at a moderately high level. In other words, if the basic needs of artisanal fishers are not sufficiently met, it is unlikely that the needs at higher levels (such as cognitive needs) will be important to them. As a result, artisanal fishers may only provide reliable information about things that directly affect their current needs, like catch rates over time, but weak information about other less direct factors, like the number of polynemid species within the system or the genders of small or large *P. quadrifilis*.

Recreational anglers, on the other hand, will likely occupy higher positions on Maslow's hierarchy. Therefore, they may have a higher degree of interest, enquiry and subsequent understanding. When this is coupled with higher levels of education and access to information (via the internet and literature for example), it is likely that recreational anglers may be more knowledgeable on certain components of LEK. For example, it is likely that recreational anglers may have heard, interpreted and accepted the outcomes of the current research on *P. quadrifilis* which diagnosed the species as a protandrous hermaphrodite. Indeed, two of the recreational anglers mentioned that they were told about the sex-changing nature of *P. quadrifilis* by someone else. In contrast, many artisanal fishers who were told about the sex changing nature of the species, at the conclusion of the survey, refused to accept this information.

It is important to acknowledge that the reliability of survey data depends on respondents' recollection of events and thus estimates of catch and historical trends are prone to a level of error. Therefore, the figures produced should be used with caution. However, surveys still provide a cost- and time-effective means of collecting basic data and the findings of this study have provided much needed information about the human dimensions within the fishery which can be incorporated into Ostrom's (2009) adapted SES framework. Numerous authors have highlighted the increased need to acknowledge and attend to the human dimensions within recreational fisheries (Hunt et al., 2013; Arlinghaus, 2017). However, by applying a SES approach, it was possible to simultaneously acknowledge and appreciate the human dimensions within other larger SESs, which directly affect the recreational fishery, such as those within the artisanal sector. The incorporation of this information into the SES framework, and its translation into a more balanced and adaptive governance system which aims to result in positive system outcomes which maximise both social and ecological performance (Ostrom, 2009), is now necessary and will be the focus of the final chapter.

# Chapter 8

## General discussion

The general aim of this thesis was to apply a social-ecological systems (SESs) approach to the investigation of the recreational tourist fishery for *Polydactylus quadrifilis* on the Kwanza Estuary. This involved simultaneously analysing data from a variety of sources to build a holistic understanding of the recreational fishery (Arlinghaus, 2017). More specifically, it involved engaging Ostrom's (2007, 2009) general framework and investigating the characteristics and traits of the four core subsystems - the resource system (Chapter 2, 4, 7 and 8), it's resource units (Chapter 2, 3, 4, 5, 6, 7 and 8), the users groups involved (Chapter 2, 5, 6, 7 and 8) and governance (Chapters 2 and 8) (Figure 8.1). Additionally, it explored the interactions and 'linkages' between these subsystems (Chapters 5, 6, 7 and 8) as well as external linkages to other larger SESs by incorporating other resource users, the ecosystem and society in general, in order to build a social-ecological understanding of the fishery and to predict potential outcomes and future directions that promote sustainability (Chapter 8) (Figure 8.1). This approach provides insight on how scientists and managers should perceive and deal with recreational fisheries in the developing world and in Africa in particular.

Adaptive governance systems are critical components of SESs and are required for the achievement of desirable outcomes such as sustainability, resilience and stability (Ostrom, 2007, 2009; Arlinghaus, 2017). Therefore, it is important to point out that there are currently few governance systems that apply to the recreational SES at the Kwanza Estuary (see Chapter 2). Further to that, there are few governance systems which apply to *P. quadrifilis* within the

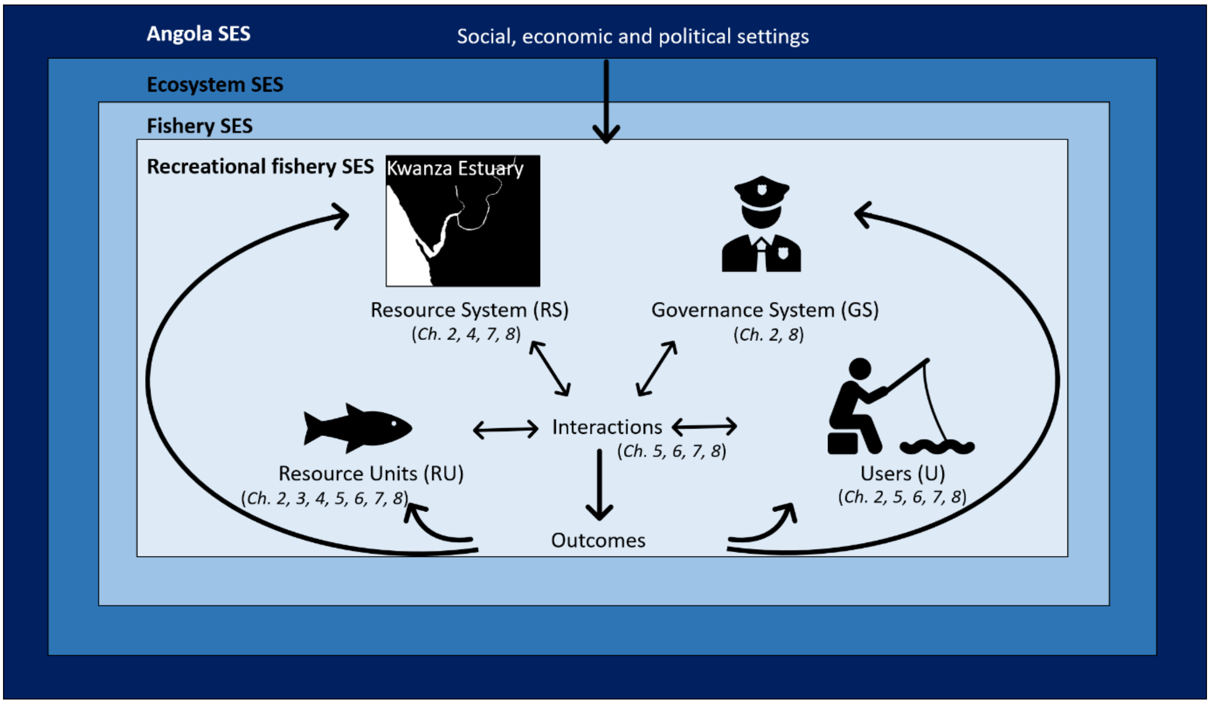


**Figure 8.1:** The social-ecological system (SES) in which the recreational fishery for *Polydactylus quadrifilis* is nested, adapted from Ostrom (2009). The SES involves four core subsystems including the resource units (*P. quadrifilis*), the resource system (Kwanza Estuary), governance system and the users (recreational anglers). Interactions between the core subsystems result in outcomes which feed back into the system. Additionally, the SES is influenced and impacted by external social, economic and political settings and via linkages to larger SESs. The relevant chapter that deal with each of the core subsystems and their interactions are outlined in brackets.

larger SESs in which the recreational fishery is nested (Figure 8.1 and 8.2). Currently, the only aspects of governance that are present within the fishery SES (the SES incorporating all fishery sectors, recreational and artisanal) are via rules relating to catch-and-release (C&R) enforced within the lodge recreational fishery and through social pressures and the resultant normative behaviours of the users (see strong link between governance and lodge anglers and weak link between governance and non-lodge domestic recreational anglers - Figure 8.2). Additionally, the artisanal fishery is subject to a small number of 'paper-laws' which are not implemented or enforced by the officials present within the system and do not, therefore, act as part of the current governance system (see weak links between governance and artisanal fishers - Figure 8.2).

It is commonly understood that where resource systems remain open-access, they are likely to experience overuse, resulting in degradation and the loss of ecosystem benefits to users (Basurto, 2005). This appears to be the case at the Kwanza Estuary and the survey responses from the recreational and artisanal users suggested a decline in *P. quadrifilis* stocks (Chapter 7). Therefore, in order to alter the current outcomes of the SES (overexploitation of the resource), it is seemingly important that management actions are taken in order to effect change in the way that users are currently interacting with the resource system. The focal point of this final chapter will largely be centred around the development of an adaptive governance system based on the qualities of the SES as a whole.

In order to gain an understanding of any SES, it is critical that there is an appropriate understanding of the resource units as they are the commodity which drive the common pool resource (Ostrom et al., 1994; Arlinghaus, 2017). This is similar to what is suggested in traditional fisheries management whereby an understanding of the biology of fishery species is thought to be a critical first step towards appropriate management (Beverton & Holt, 1954; King & McFarlane, 2003). Key areas of investigation include the growth, reproductive and life-history traits of fishery species as they provide insights into ecologically important areas and times for the population and allude to the overall sensitivity of the population towards potential impacts. *Polydactylus quadrifilis* were found to be protandrous hermaphrodites with moderate growth rates and multiple developmental pathways (partial protandry) (Chapters 3 and 4). From this, it was noted that they are likely at increased risk of overexploitation, especially via rod and line fishing, as it selectively targets large, fecund females from the population and may result in recruitment overfishing.

The protection of large *P. quadrifilis* is also likely to align with the management objectives of the foreign recreational fishery, whereby large 'trophy' fish are desirable to anglers. This is important as the foreign recreational fishery, like other recreational fisheries in the developing world (FAO, 2012; Wood et al., 2013; Belhabib et al., 2016), has ecotourism potential (Chapter 6). In other words, if managed appropriately, the tourism fishery can simultaneously contribute to the creation of local jobs and limit the environmental impact on the resource. While ecotourism has been promoted as the panacea for rural development in many parts of the developing world, the results of this (Chapter 6) and other studies (Sandbrook, 2010b, 2010a; Barnett et al., 2016) have shown that this is only likely if economic leakages are reduced and local benefits are maximised.

It is uncommon, and therefore fortunate, that the management objectives of the recreational and artisanal fisheries, in terms of prioritising the protection of large *P. quadrifilis*, align. This is because the objectives of artisanal fisheries management align with maintaining food security and maximising physical yield (FAO, 2012). However, it is not commonly possible to simultaneously maximise physical yield and the number of trophy fish (García-Asorey et al., 2011). Yet, in this case, due to the critical role that large females play in population sustainability, their protection is advantageous to both sectors. Therefore, it is important that the protection of large female *P. quadrifilis* individuals is prioritised in potential management strategies.

Due to the seasonal presence of large female *P. quadrifilis*, a seasonal closure of the fishery seemingly provides a logical and potentially effective management control. However, the implications this may have on the recreational and artisanal sectors needs consideration. The foreign recreational fishery for *P. quadrifilis* primarily operates during this period due to the attraction of catching extremely large fish. Therefore, a seasonal closure during this time would likely collapse the foreign recreational sector. Additionally, the artisanal sector primarily operates using gill-nets which are not species-selective. Therefore, a closure would require a cessation of most artisanal fishing effort and may infringe on numerous livelihoods. Thus, seasonal closure of the fishery is likely inappropriate as a viable management solution and the use of slot limits may present a more appropriate output control.

Gill-nets have been shown to be highly size-selective in their capture of fishes (He, 2006). Therefore, within the artisanal gill-net fishery, enforced mesh-size restrictions can provide a simple yet appropriate means of avoiding the capture of large *P. quadrifilis*. Additionally, based on the mesh sizes currently used by the artisanal fishery (Chapter 7), the capture of very large *P. quadrifilis* (>30 kg) is unlikely and large individuals were seldom observed in artisanal gill-net catches (pers. obs.). However, in the line-fisheries present within the system (artisanal, domestic and foreign recreational), avoiding the capture of larger individuals is impossible. Therefore, if the protection of large females is to take place within these sectors of the fishery, the implementation of mandatory and voluntary C&R needs to be promoted (Figure 8.2). As it stands currently, only voluntary C&R angling is practiced and this is only common in the lodge fishery (Chapter 7). Therefore, the promotion of the C&R of large female *P. quadrifilis* in the other sectors (and particularly the non-lodge recreational fishery) is believed to be critical for the long-term sustainability of the fishery.

A number of governance systems are available to promote C&R angling and range from formative top-down regulation and monitoring of the fishery to collaborative co-management (Pinkerton, 2007) and community-based self-control (Allison, 2001). However, regardless of the management approach, it is important to maximise the health and minimise the mortality of *P. quadrifilis* after their release. From Chapter 5, it was evident that *P. quadrifilis* demonstrated both physiological and physical impairment following C&R in the foreign recreational sector and long air exposure and, to a lesser extent, fight times appeared to have a major impact on fish health. This was particularly true for larger individuals as air exposure

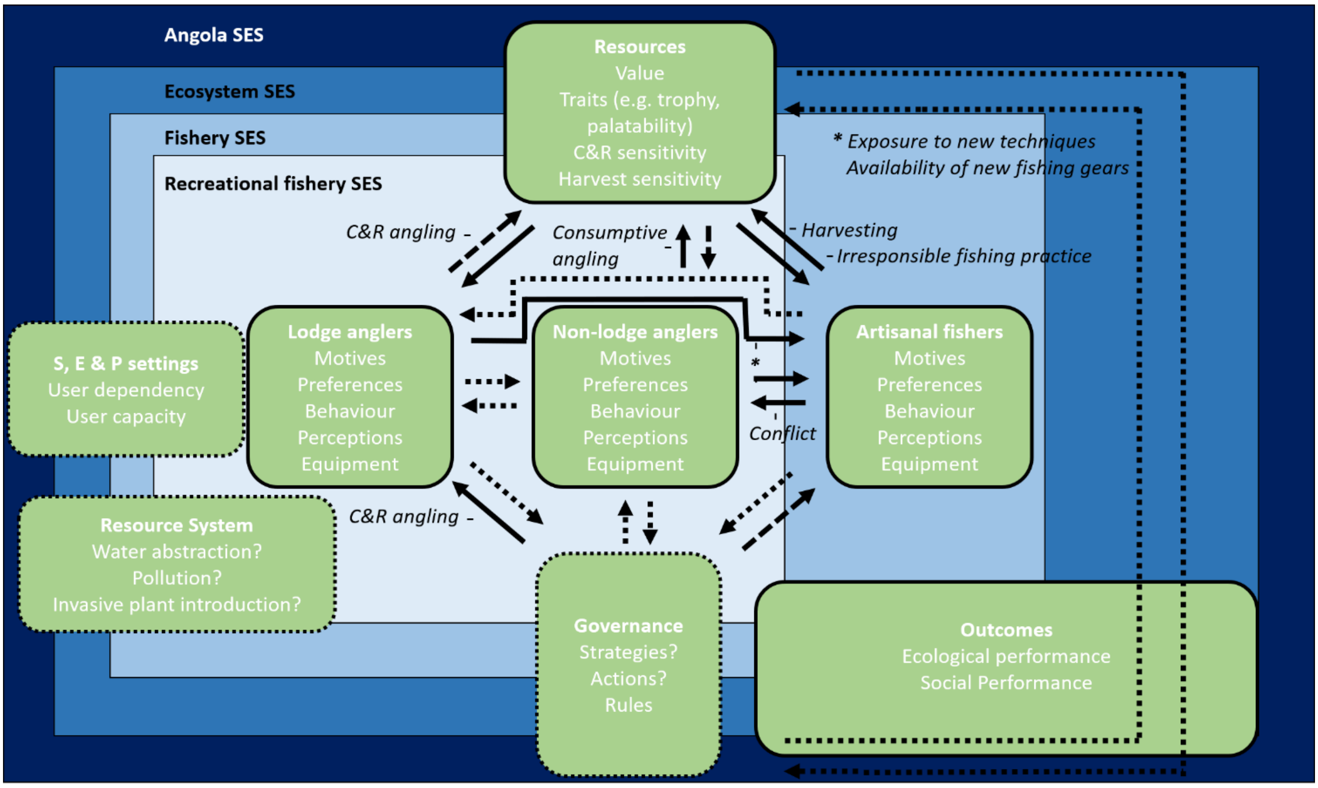


**Figure 8.2:** An illustration of the *Polydactylus quadrifilis* recreational fishery social-ecological system (SES) on the Kwanza Estuary, Angola. The recreational fishery SES is nested within the fishery SES (incorporating other sectors on the Kwanza Estuary – e.g. the artisanal sector), which is nested within the ecosystem SES (including other aquatic ecosystem components and users, such as tourists) which, in turn, is nested within the Angola SES which largely drives the social (S), economic (E) and political (P) settings of the system. Embedded boxes represent influential components within the respective SESs and the text within represents important second- or third-tier variables. Key linkages between the core subsystems are illustrated by arrows. Solid arrows suggest a strong directional linkage, while dashed and dotted arrows suggest progressively weaker or less influential linkages. For example, there were obvious links between resource users and the resource units. Lodge recreational anglers maintained a weak linkage to the resource system through the reduced impacts (dashed arrow) they had on fish stocks via catch-and-release (C&R) angling. However, the resource system had a large effect (solid arrow) on lodge anglers whereby the perception of healthy stocks and trophy fish was a driving factor influencing foreign angler involvement in the fishery. Critical interactions that were identified during this study are illustrated in italicized text. The dotted boxes surrounding governance, the resource system and the social (S), economic (E) and political (P) settings illustrate their minor influence (governance) or the poor understanding that we have of these subsystems (resource system, S, E and P settings). The various interactions have the potential to result in outcomes which affect larger SESs. For example, interactions such as the highly consumptive fishing of domestic recreational anglers may have a negative impact on ecological performance via the reduction of fish stocks which will feed back to have an effect on artisanal fishers via a reduction in the shared resource which may then lead to conflict and so on.

and fight times were positively correlated with fish size (Chapter 5). Therefore, it is critical that these fish are fought and handled appropriately if they are to survive and reproduce after release.

There is already some emphasis placed on appropriate fish handling at the Kwanza Lodge. However, this is often driven by individual guides and their turnover rate is relatively high. Therefore, it is recommended that the lodge adopts a clear C&R policy that will guide the behaviour of angling guides and guests. For this policy, it is recommended that the guides should monitor and control fish handling by ensuring that predetermined air exposure times are not exceeded. In addition, the use of floating holding nets for handling, unhooking and reviving fish is recommended (see Figure 5.1, Chapter 5). Additionally, in an ideal scenario, very large fish (>15 kg) should be handled in the water where possible and should not be removed unnecessarily (Brownscombe et al., 2015). This can be facilitated by slowly driving the boat to a sand bank or shallow area while the fish is allowed to recover in the holding net. Once there, these individuals can be handled and photographed in the water to minimise air exposure.

While these guidelines are appropriate and are likely to be implemented in the lodge fishery (see strong link between lodge anglers and governance - Figure 8.2), reducing the C&R stress and mortality of *P. quadrifilis* in the non-lodge domestic recreational fishery will likely be more complicated. This is because it will first require a shift in the behavioural norm (from catch-and-kill to C&R) and then voluntary adherence to recommendations for improving the health and survival of released fishes. Shifting behavioural norms around C&R is a major challenge. However, recent research (Mannheim et al 2018) has suggested that it may be possible through extensive engagements, that gain the trust of anglers, and the implementation of a range of interventions. These could include education drives which aim to promote a conservation ethic amongst anglers and thereafter illustrate the importance of good handling when practicing C&R. Alternatively, the development of C&R-only competitive angling is thought to promote the adoption of C&R outside of competitions and may improve angler handling practices (Dellacasa & Braccini, 2016; Mannheim et al., 2018). This could be driven by the major stakeholders in the recreational fishery, such as the Kwanza Lodge, and participation encouraged with sponsored prizes for winning teams. Other alternatives that address the normative paradigm to shift angler behaviour and promote C&R include a social norms approach (see Bova et al., 2017) and the use of 'nudges', which apply indirect suggestion to alter angler behaviour and promote desired behaviours (see Mackay et al., 2018).

Fishermen C&R behaviour is influenced by their attitudes about the fishery, fishing preferences, motives for fishing and other social pressures from inside and outside of their community (Arlinghaus et al., 2007). Therefore, the current fish handling practices in the non-lodge domestic recreational and artisanal fisheries are likely to be far worse, for fish health and survival, than what was observed in the foreign recreational sector (Chapter 5). This is based on the motives, preferences and normative behaviours of the fishers and because anglers within these sectors are presumably less accustomed to prioritising fish health during angling (Chapter 7). For example, the foreign recreational fishery largely uses fishing techniques and equipment that minimise damage to fish via hooking injury, including the use of single J-hooks (instead of treble hooks) on lures and jigs and the use of circle hooks when bait fishing (Chapter 5) (Figure 8.2). In contrast, trolling lipped crankbait lures with two large treble hooks is popular in the non-lodge domestic recreational fishery (81.9% of effort – Chapter 6) and is considered to be a method associated with severe hooking injuries (Burkholder, 1992; Muoneke & Childress, 1994) and, potentially, higher rates of hooking-related mortality (Nuhfer & Alexander, 1992). In addition, the use of dual treble hooks has been found to increase unhooking time and, therefore, increase air exposure (Diggles & Ernst, 1997; O'Toole et al., 2010).

It is also unlikely that fishermen in the artisanal and domestic recreational fisheries are currently equipped to handle fish sufficiently well to ensure low rates of mortality post-release, particularly when dealing with large fish. For example, domestic recreational anglers seldom landed fish with landing nets and largely stowed a gaff on board their boats (Chapter 7). This behaviour is likely related to the motives and preferences of the users within each fishery sector. Artisanal fishers do not typically release any fish and therefore it is not unusual that they only utilise a gaff. Similarly, the domestic recreational user group appears to be highly consumptive and therefore the use of a gaff is common (Chapter 7). When extremely large female *P. quadrifilis* are captured, it is difficult to safely remove the fish from the water by hand and the use of a gaff is not a viable option if the fish is to be released. Hence, it is likely that angler behaviour will need to be manipulated in these fishery sectors if C&R mortality is to be minimised.

Bearing this in mind, the issues surrounding how fish are landed are only problematic if the fish needs to be landed (removed from the water). The fishers in the different sectors find different values and traits of the resource units appealing and this affects their behaviour. For example, the characteristics of *P. quadrifilis* which class it as a 'bucket-list' or 'trophy' fish are appealing to foreign sport-fishermen (Figure 8.2). Therefore, the behaviour whereby fish are removed from the water for photographs is common within the foreign recreational sector based on the motives and preferences of the anglers. Here, anglers' motives for fishing are aligned with sport and they, therefore, often want a photo of their catch to maintain as a souvenir or 'trophy' (Brownscombe et al., 2015). However, the motives of anglers in the artisanal and domestic recreational fisheries may differ and this is likely to affect their behaviour if C&R is required. For example, it is unlikely that artisanal fishers will want to remove fish for a photo before releasing it, based on their motivation to fish as a livelihood. Therefore, if C&R is necessitated (e.g. if slot limits were implemented as a control), it is possible that they may handle, unhook and release fish in the water alongside the boat, thus keeping air exposure to a minimum.

In contrast to the artisanal fishers, the motives for domestic recreational anglers may be more aligned with sport and they may, therefore, behave similarly to foreign recreational anglers. However, it has been noted that domestic recreational anglers in the developing world (Cooke et al., 2018) and in West Africa (Belhabib et al., 2016) may have different motives for fishing compared to anglers in developed countries. Indeed, many of the domestic recreational anglers did appear to have motives centred around fishing for food (Chapter 7) and, therefore, they may practice different C&R methods. Therefore, it is recommended that a more detailed understanding of the 'expectations, preferences and behaviours' of domestic recreational anglers will be needed to develop appropriate governance systems for this fishery.

Alternatively, angler C&R behaviour can be manipulated using enforced regulations. For example, it is illegal to remove recreationally caught *Megalops atlanticus* of over 40 inches fork-length from the water in some American states (Florida Fish and Wildlife Conservation Commission, Rule 68B-32). Therefore, it may be possible to protect large *P. quadrifilis* by lawfully prohibiting certain behaviours, such as removing them from the water during C&R. This strategy may tie in well if slot-limits are enforced as an output control, with the upper size limit corresponding with the size at which fish must remain in the water during handling. However, these approaches require consistent monitoring and enforcement which is not present for the recreational fishery on the Kwanza Estuary. Furthermore, recreational fisheries management is likely to have low socio-political priority in Angola, as is the case in other developing countries (Arlinghaus, 2017). As a result, government is unlikely to take action. Hence, if regulations are to be put in place and function properly, it is likely that self-governance will have to play an important role and lobbying by the recreational angler group may be required to incite government involvement or devolution of appropriate control.

In order to build self-governance within the fishery, it is critical that appropriate information from this research is communicated to users, to improve their knowledge and encourage appropriate decision making processes for governance (Townsend, 1995; Dietz et al., 2003). If users are involved in management decisions, they will be more likely to comply with restrictions based on the fact that they agree with their necessity (Pinkerton, 2007) and because they will be more likely to comprehend and understand them (Cooke et al., 2013b). This process should perhaps be driven by the lodge due to their reliance on the health of the resource and their strong presence and constant involvement in the fishery. User involvement in the co-management of resource systems can also lead to the creation of more robust and adaptive management solutions because they are informed by local user knowledge (Pinkerton, 2007). This is particularly relevant and important for data-poor systems such as this fishery.

It is possible that the communication of information about the fishery, including information regarding best-practice for C&R, will facilitate the development of a conservation ethic amongst the resource users (Cooke et al., 2013b). It is hoped that this may lead to a conservation-minded decision-making process that goes beyond what is lawfully required. For example, following dialogue between user groups, potential officials and scientists, decisions to implement size and bag-limits may be chosen as a management strategy. However, based on insights gained from the process of dialogue, some users may choose to go further and release all *P. quadrifilis* caught based on a conservation ethic which was developed as a result of the process (Cooke et al., 2013b).

If management strategies aim to develop self-governance through building cohesion between user groups, it is important that there is equity between users, or at least the perception of equity (Ostrom & Cox, 2010; Arlinghaus, 2017). There are strong linkages between the recreational fishery SES and the fishery SES driven by shared resource use (Figure 8.2). Therefore, it was important to investigate and understand the differences in resource value between the different user groups. The results of Chapter 6 demonstrated that recreationally angled fishes were far more valuable in terms of the total revenue generated for their capture (and release), thus suggesting that the fishery could be classed as ecotourism and incentivising the development of the recreational sector and potential enforcement of stricter management of the artisanal sector. However, the same resource is critically important for the artisanal fishery and facilitates the provision of jobs and livelihoods for locals (Chapter 7). In terms of benefit to the local community alone, the values for recreationally caught *P. quadrifilis* and other fishes largely dropped below the market value of fishes in the artisanal sector due to high rates of economic leakage. Therefore, currently, there is little incentive for artisanal fishers to be involved in the development of the recreational sector as this fishery does not provide them or their families many tangible benefits.

It may be possible to raise the locally-retained value of recreationally caught fishes if the local community receives a higher rate of direct benefit from the recreational fishery via the reduction of economic leakage (Chapter 6). Potential solutions have been explored and included the creation of linkages between the local community and the recreational fishery (Meyer, 2007; Sandbrook, 2010b). In this study, a higher rate of community involvement in the recreational fishery was identified as a potential management solution (see Chapter 6), which will likely tie in well with governance systems if co-management is implemented. Therefore, it is important that the social, economic and political barriers to community involvement in the recreational fishery are broken down. For example, important barriers included the ability to speak English as a barrier to higher paying employment positions in the foreign fishing tourism industry. Additionally, there was a general lack of capacity within the local community, preventing community members from providing boat hire and skippering services to the domestic recreational fishery or potentially gaining employment in or supplying local goods and services to the lodge fishery (Chapter 6).

If barriers to community involvement in the recreational SES are to be broken down, it is critical that conflict between shared resource users is avoided (Nguyen et al., 2016) to circumvent system dysfunction (Arlinghaus, 2017). Currently, the domestic recreational fishery views the artisanal gill-net fishery as a threat to the sustainability of the resource (Chapter 7). This is likely to affect the behaviour of the users within the recreational sector as they perceive the resource to be overexploited. The intersectoral conflict is also likely to impact potential compliance if regulations are implemented (Bova et al., 2017). Therefore, the cohesion of resource users is required in order to achieve sustainability and promote the co-management of the SES to ensure beneficial system outcomes. The most likely route for reducing conflict between the recreational and artisanal sector would be the implementation of a government monitoring program. This will hopefully promote perceptions of better governance and sustainability (Chapter 7) of the fishery.

It is likely that the first step towards developing a governance system will involve limiting the open-access nature of the SES in order to incentivise its protection (Basurto, 2005; Ostrom & Cox, 2010). By creating a permit system, resource users may become leaseholders to the fishery. This can promote a co-managerial approach (Ostrom & Cox, 2010) and, in turn, the concept that anglers must pay for their consumption of public resources (Arlinghaus et al., 2019). By allowing resource users to purchase access rights, it may be possible to promote self-governance through creating a sense of ownership within the user group. Money collected from the purchasing of access rights could then be directed towards management and could potentially fund monitoring within the SES. Additionally, if the recreational fishery is to grow, which it likely will (FAO, 2012), funding will increase accordingly. This approach has been applied across much of the developed world where it has been demonstrated that lease-holding anglers often self-organise to fulfil management and conservation actions (Arlinghaus, 2017). However, it is critical that highly-dependant users are not restricted in their access to resources. The socio-political climate in the developing world and in Angola is dissimilar and, therefore, the outcomes of a similar approach may differ. Therefore, it is important that there is a development of a governance system which is adaptive in nature and can adjust and revise itself to potential pitfalls.

It is unlikely that a single 'silver bullet' management solution exists for the recreational fishery SES, or any other SES for that matter (Ostrom, 2007; Ostrom & Cox, 2010). Therefore, it is suggested that a combination of various adaptive solutions is the best option. However, it would appear that management intervention is likely required soon in order to alter current overexploitation and other harmful system outcomes. A number of management options are available, and have been outlined, and it is likely that the simultaneous application of several will aid in building an adaptive multi-level polycentric governance system (Ostrom & Cox, 2010). This will rely on the co-management of the fishery with representative involvement from all user groups and interplay between stakeholders and centralised governance structures (Ostrom & Cox, 2010). Stakeholders should be allowed to develop management solutions and rules which apply to the fishery. If the SES is to achieve desirable outcomes, it is critical that the user groups within the fishery SES are actively involved in 'defining problems, identifying management objectives, selecting appropriate options and implementing them' (Arlinghaus, 2017). If anglers are directly involved with decision-making, they are likely to be more accountable and responsible (Arlinghaus et al., 2019). The chosen management solutions which are implemented should be monitored over time, evaluated after an appropriate period and adjusted accordingly to facilitate system learning and adaptability (Arlinghaus, 2017).

## 8.1 Additional observations

During the course of this PhD, I spent a cumulative period of 12 months (spanning three years) in the recreational fishery SES targeting *P. quadrifilis* at the Kwanza Estuary. There were a number of additional anecdotal observations that were made which were not included in any of the five data chapters but are nevertheless relevant for the management and sustainability of the fishery. Chiefly among those were the presence of high rates of ghost fishing, evidence of irresponsible fishing practice, the development of an unregulated small-scale commercial rod and line fishery targeting a range of species and the presence of an invasive aquatic plant species, the water hyacinth (*Eichhornia crassipes*).

Evidence of ghost fishing was common on the Kwanza Estuary where old fishing net material was often observed along the estuary banks, entangled in the root systems of aquatic plants and trees (Figure 8.3a) and wrapped around other objects such as jetties and rocks. Where it was found, there were often signs of aquatic animals that had been killed or were in the process of dying in the nets (Figure 8.3b). A large variety of animal species were observed in ghost nets including fish, crustaceans and reptiles although it is likely that ghost nets also pose a threat to aquatic birds as well as certain mammals (Matsuoka et al., 2005), including the vulnerable West African manatee (*Trichechus senegalensis*).

It has been noted that the potential for ghost fishing by lost or discarded gill-nets is related to the qualities of the seabed or habitat in which the net is lost (Matsuoka et al., 2005). The most common area in which gill-nets were observed on the Kwanza Estuary was within the root systems of mangrove trees. This is likely highly problematic as it has been demonstrated that


**Figure 8.3:** Ghost fishing gear in the form of lost or discarded gill-nets on the Kwanza Estuary, Angola. Gill-nets were commonly found along the estuary banks where they became entangled in the roots of aquatic plants (a). Here they commonly entrapped and killed a variety of aquatic creatures (b) and their removal from these areas was labour intensive (c).

a number of aquatic and terrestrial animals utilise these areas for a variety of purposes including feeding and refuge (Kathiresan & Bingham, 2001) and mangroves have been shown to act as nursery areas for a multitude of species (Nagelkerken et al., 2008). Furthermore, animals have been shown to utilise the channels between mangrove roots and have high rates of movement amongst them (Kathiresan & Bingham, 2001). If ghost netting is present across these areas of high movement, it is likely to result in the entanglement of mobile animals. Therefore, ghost fishing may have largescale impacts on the ecosystem functions of the mangrove habitat.

Additional evidence for ghost fishing was observed whereby gill-net material was commonly found on angled fishes (Figure 8.4). The source of this gill-net material is unknown and may be a result of ghost fishing gear or the poor quality of many actively used gill-nets within the system. Older nets that have been lost or have been used for long periods are likely to be weathered and the material from which they are made is likely to have a reduced breaking strain (Thomas & Hridayanathan, 2006). Larger fish that are caught within the net material are likely able to break free but maintain pieces of the netting caught around them where it causes damage to fin structure and tissue (Figure 8.4a, b). In some cases, fish that had supposedly broken through gill-nets in the past had completely grown around the remaining nylon material,

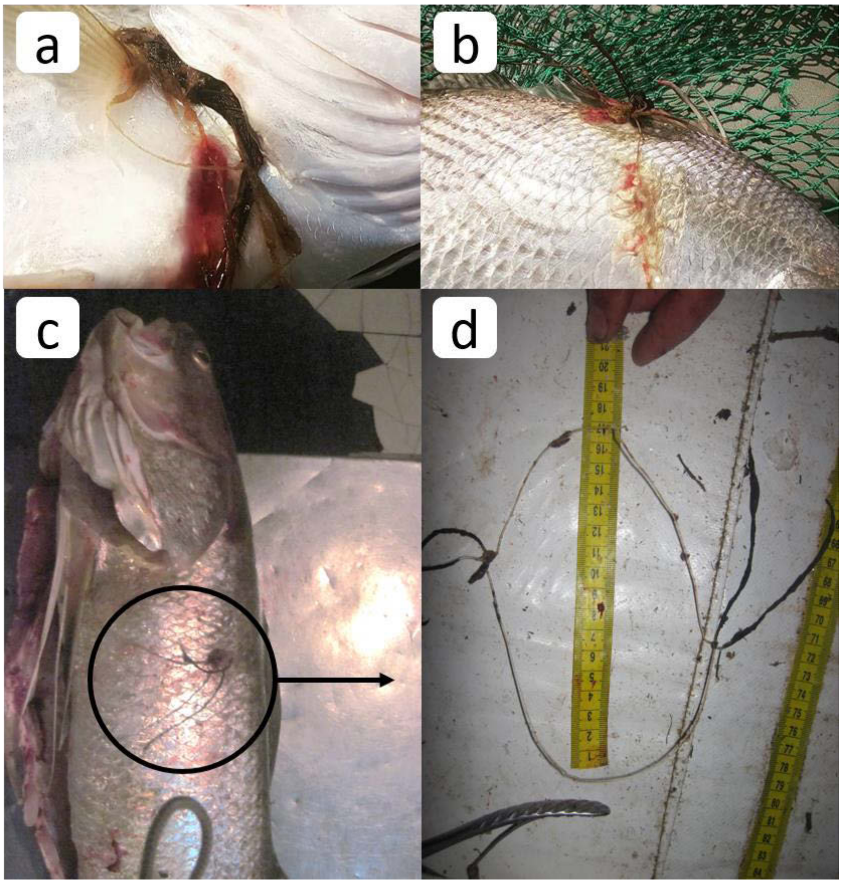


**Figure 8.4:** Damage to fishes caused by gill-net material on the Kwanza Estuary, Angola. In certain cases, where the net material inhibited somatic growth, it appeared that fish continued to grow around the material, incorporating it into their flesh (a, b – *Polydactylus quadrifilis*, approx. 900 mm fork-length). The net material caused damage to the skin, tissue (c) and fins (d) of observed fishes (c, d – *Pseudotolithus senegalensis*, approx. 1000 mm fork-length).

incorporating it into their flesh (Figure 8.4c, d). Furthermore, large angled *Lutjanus* species (primarily *L. agennes*) often (approximately more than 80% of angled *Lutjanus* spp. over 10 kg) had gill-net material in either one or both of their gill-sets resulting in a deformed, conglomerated mass of gill tissue (pers. obs.).

These deleterious by-products of the gill-net fishery are likely to have impacts on the sustainability and productivity of the ecosystem and should be addressed in management plans. A number of solutions exist to help curb the rates of ghost fishing (He, 2006) and it is likely that some form of management of the artisanal gill-net fishery is required. A number of new "de-ghosting" technologies exist which allow components of lost nets to degrade rapidly and thus reduce their potential to keep fishing (Matsuoka et al., 2005; He, 2006). However, these technologies are unlikely available to the artisanal fishery currently. In the shorter term, one potential solution would be via the allocation and distribution of identification tags for gill-nets. Each gill-net should be assessed and approved and thereafter allocated an identification tag which should be placed on the net at all times. If the net is lost at sea, then the tag will be lost with it and the fisherman will lose access to that gear. A replacement net will require a new tag and therefore management can keep track of lost nets and potentially penalise fishermen for losing gear. Additionally, tags should only last for a prescribed period before they require renewal following a re-evaluation of the gill-net. There is a strong presence of semi-regular government policing at the Kwanza Estuary whereby officials actively assess boats for licences and confiscate motors from unlicensed boats (pers. obs.). Therefore, the capacity for some form of policing of the artisanal gill-net fishery is in place and could be facilitated if identification tags were to be allocated to fishermen.

Another potential threat to the sustainability of the fishery at the Kwanza Estuary is the development of an unregulated small-scale commercial line-fishery targeting *P. quadrifilis* and other important fishery species. This activity was observed in 2017 and 2018 whereby a small number of artisanal anglers were observed regularly fishing off of two separate boats using weighted jigs. Through conversations with the local community and the fishermen themselves, it was discovered that these fishermen had been employed by non-local businessmen to fish professionally. In doing so, they were given access to boats and were provided with all necessary fishing tackle (including rods, reels and jigs and lures). Fishermen would fish every day and would contact someone to collect fish whenever they had caught sufficient numbers. The relative impact of this sector is heightened due to the increased efficacy of jig fishing (Chapter 7) and fishermen would often make large catches, exceeding 100 kg per day in some cases (pers. obs.). It is suggested that an investigation into the development of this sector is required in order to understand and monitor its impact. It is also likely that the resources are being extracted from the area by non-locals, thus potentially reducing the benefits of fisheries resources to locals.

Lastly, the invasive water hyacinth, *E. crassipes* has become established in the Kwanza River system and forms large mats in the estuary (Figure 8.5). Local fishers have suggested that the invasive plant boosts their fishing success as it provides structure for prey items, including crabs (primarily *Sesarma angolense* and other crab species) (pers. obs.), and inadvertently transports them downstream (Figure 8.5b). The *E. crassipes* mats become lodged on the banks of the river and then break away from the river margins, particularly during spring high tides. Once they reach the estuary mouth, wave action further breaks up the mats, knocking invertebrate prey into the water. This creates feeding opportunities for predatory fishes and anecdotal evidence from fishers suggest that catchability improves around these mats at the estuary mouth. *Eichhornia crassipes* has been found to alter macroinvertebrate communities and influence fish diets in other systems (see Schultz & Dibble, 2012) and therefore an understanding of its effect on the fishery SES on the Kwanza Estuary would provide useful information for management.


**Figure 8.5:** Invasive water hyacinth, *Eichhornia crassipes*, on the Kwanza Estuary, Angola. Plants are found along the length of the river (a) where they accumulate along the margins (b) and host macroinvertebrate communities. During period of high water, such as spring tides, masses of plants are dislodged and float downriver towards the ocean (c). Once here, it is suggested that wave-action dislodges macroinvertebrates, thus boosting the abundance of predatory fishes.

### 8.2 Future directions

Unfortunately, it was not possible to completely understand the recreational fishery for *P. quadrifilis* on the Kwanza Estuary from a SES perspective. This is largely due to the data-poor nature of the fishery and it is likely that significant further research is required before the application of predictive SES models can take place. However, the research undertaken here has provided a baseline for future SES research (Figure 8.2). It has also contributed important information towards the body of work incorporating SES science on recreational fisheries in the developing world (Bower, 2017).

In terms of further research, it is suggested that a greater focus is placed on the user groups within the fishery SES so as to better understand their motives, preferences and normative behaviours. This extends to all user groups including the artisanal fishers, domestic and foreign recreational anglers. Insights gained from artisanal and domestic recreational anglers will allow for the appropriate selection of governance systems and may also allow potential managers to anticipate fisher responses to management decisions. Additionally, it is important that there is a better understanding of the motives of domestic recreational anglers as it is possible that, in addition to the attraction of consumptive angling, they may be attracted by non-fishing related attributes of the system, such as beauty and tranquillity (Post et al., 2002). This may have important implications as domestic anglers may have the potential to continue fishing despite reductions in catch, based on the attractiveness of other attributes of the experience, and may therefore contribute significantly to overharvest (Post, 2013). Similarly, it is important to understand the motives of foreign recreational tourist anglers. Although their behaviour is largely governed by the guides and the lodges that they visit, an understanding of their motives will allow managers to decide on which attributes of the fishery are appealing to the sector and, therefore, which should be prioritised in management plans should the sector be developed and expanded.

Besides a focus on the human dimension, further biological and ecological research of the resource system would be highly beneficial. An understanding of the extent to which the Kwanza Estuary resource system connects with other systems will aid in understanding the extent to which fish are protected and managed in other areas. Suitable techniques may involve the use of acoustic telemetry or the implementation of a nation-wide tag-recapture program to gain an understanding of fish movement. Alternatively, the use of genetics may allow for an understanding of population connectivity across the species' range. Additionally, the biological characteristics of other important target species should be researched as they are a critical component of the resource system. The influence of invasive *E. crassipes* should be assessed to understand its potential effect on system biomass and productivity (Schultz & Dibble, 2012). It is also suggested that routes are explored and applied for the direct and indirect involvement of the local community within the recreational SES.

**8.3 Working with other recreational fisheries in the developing world and Africa**

Developing world recreational fisheries are largely data-poor in nature (Belhabib et al., 2016; Bower, 2017) making SES-related research difficult. Therefore, it is important that these fisheries are given greater recognition and research focus so that we can improve the reliability of data and build towards a significant body of work on the topic. Additionally, it was demonstrated throughout this thesis that there is a need for the greater recognition of domestic recreational sectors in the developed world and in Africa. Here, the focus of most investigations has primarily been on foreign tourism sectors (Potts et al., 2009; Wood et al., 2013; Belhabib et al., 2016), while domestic sectors receive little recognition and scientific attention (Arlinghaus et al., 2019). However, it was demonstrated during this study that the domestic recreational fishery operating separately from the Kwanza Lodge generated similar revenue to the foreign recreational fishery while simultaneously maintaining lower rates of economic leakage (Chapter 6). Furthermore, domestic recreational anglers in developing countries are likely to behave differently to those in the developed world based on differences in their motives and potentially due to a higher dependency on fish for food (FAO, 2012; Belhabib et al., 2016; Cooke et al., 2018). This, coupled with the fact that many developing world recreational fisheries are open-access, may lead to a significant impact on the resource.

In many cases, it is likely that the initial steps towards developing SES science in developing world recreational fisheries will involve basic inquiry about the biology and ecology of important recreational species, which is an important first step in understanding the system as a whole. This is particularly relevant for developing word fisheries, where little is known about the biology of fishery species. Therefore, important life-history traits of study species should be investigated, including fish size- and age-at-maturity and reproductive style, as their appropriate understanding is critical for management. In addition, it is suggested that applying a human or social dimension to the investigation of recreational fisheries will provide context for how the ecological and social components of the system interact (Bower, 2017). The use of surveys presents a highly cost- and time-effective means of collecting useful information. It is suggested that engagement with user groups should perhaps take place at the beginning of specific studies in order to question user perspectives, identify potential problems (e.g. overfishing) and formulate research objectives (Bower, 2017). Once research questions have been addressed, it may be possible to design more informed additional surveys that are aimed at understanding more specific user traits regarding recreational fishing and their interactions with the environment.

An important observation made within this study was the strong linkage between recreational anglers and other users (artisanal fishers) within larger SESs through shared resource use. This is likely to be similar for other developing world recreational fisheries due to the high dependence of people on fish as a food source (FAO, 2012). Therefore, it is important to identify how recreational fisheries interact and influence these communities. In doing so, it is important to understand how recreational fisheries impact the resources on which other communities rely, via consumptive or C&R angling. It is also equally important that there is an understanding of how other resource users influence the resources on which the recreational community relies, to promote transparency and avoid conflict. Interactions between resource users should also be investigated to identify potential for conflict. An understanding of the cultural and human traits of local fisheries is also important as potential governance may contradict local beliefs and value systems (Bower, 2017). For example, the promotion of C&R angling, which is common in many tourist fisheries such as the lodge fishery at the Kwanza

Estuary, may oppose local artisanal fisher perspectives and cultural viewpoints regarding the 'correct' use of fish (FAO, 2012).

In order for effective fisheries management, it is likely that funding will be required to facilitate the establishment of a management framework that supports the sustainable use of fisheries resources. A number of potential sources exist and should be explored across Africa in order to promote the sustainable development of recreational fisheries.

The application of tourism economics proved highly relevant for the investigation of the recreational tourist fishery and, more specifically, the local benefit derived from it (Chapter 6). It is suggested that the same methodology can be applied to other developing world tourist fisheries with the specific aim of identifying means in which economic leakage can be reduced, local benefit maximised, and ecotourism promoted. If realistic and effective solutions are found for the inclusion of consumptive fisheries users (such as artisanal or subsistence fishermen) within C&R recreational tourist fisheries, it may be possible to achieve ecotourism standards, thus diversifying the livelihoods of community members and creating economic incentives for the protection of recreationally important species and their associated ecosystems. However, it must be stated that the promotion of tourism fisheries, due to the perception that recreationally caught fish hold higher economic value (when compared to fish caught in other sectors), should not be used without an acknowledgment of the process of economic leakage and detailed assessment of local benefit.

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## Appendix A

**RHODES UNIVERSITY**

**DEPARTMENT OF ICHTHYOLOGY & FISHERIES SCIENCE (DIFS), RHODES UNIVERSITY**

***PO Box 94 • Grahamstown 6140 • South Africa***

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**PORTUGUESE**

Título do projeto: Entendendo uma pesca recreativa na África Ocidental como um complexo sistema socioecológico

Verbal: Você foi convidado por Ed Butler, do Departamento de Ictiologia e Ciências Pesqueiras, da Universidade de Rhodes, para participar de pesquisas sobre a pesca artesanal de barbatana gigante africana ou barbudo. A razão pela qual você foi escolhido é porque você é um pescador que ataca o threadfin (barbudo) no Kwanza. Sua participação nesta pesquisa é voluntária e você pode decidir a qualquer momento que não estiver disposto a participar. As informações coletadas farão parte de uma tese de doutorado e poderão ser publicadas no futuro, inclusive em periódicos científicos.

No entanto, este processo NÃO exige que você forneça seu nome e, portanto, as respostas que você fornecer serão armazenadas ANONYMOUSLY. Além disso, os dados coletados serão armazenados de forma segura e com total confidencialidade. Portanto, não há risco pessoal envolvido na conclusão desta pesquisa. Além disso, se você se sentir desconfortável com qualquer uma das questões encontradas nesta pesquisa, você não é obrigado a responder e pode pular perguntas à vontade. Esta pesquisa foi aprovada pelo comitê de ética da Universidade Rhodes, com ética no. xyz… e você pode pedir para ver este certificado à sua vontade. Ao concluir esta pesquisa, você NÃO renuncia a quaisquer reivindicações, direitos ou recursos legais.

Esta pesquisa contém 110 perguntas, que são a opção MUITO MÚLTIPLA, e essa entrevista não deve demorar mais do que 20 a 25 minutos para ser concluída. O objectivo destas questões é obter uma melhor compreensão da pesca artesanal no rio Kwanza, como opera e quais as percepções dos pescadores sobre a biologia e sustentabilidade do gigante africano, o threadfin / barbudo, historicamente e actualmente.

Todas as questões da pesquisa referem-se apenas às actividades de pesca artesanal no rio Kwanza e não em qualquer outro lugar.

Você tem alguma pergunta?
Seção de Consentimento
Estou ciente de que:

1. O objectivo do projecto de investigação é investigar a pesca artesanal de threadfin / barbudo no rio Kwanza.

2. A Universidade de Rhodes deu autorização ética para este projeto de pesquisa (Número de Ética ………) E eu posso pedir para ver o certificado de liberação.

3. Ao participar deste projeto de pesquisa, estarei contribuindo para o desenvolvimento de uma base de conhecimento que ajudará a melhorar a sustentabilidade da pesca.

4. Eu participarei do projeto participando e respondendo às perguntas da pesquisa com o melhor de minha capacidade.

5. A minha participação é totalmente voluntária e, se em algum momento eu quiser desistir de participar, posso fazê-lo sem quaisquer consequências negativas.

6. Seus pontos de vista e conhecimento não serão associados a você como um indivíduo e, portanto, não deve haver riscos ou retornos previsíveis para você como indivíduo.

7. O pesquisador pretende publicar os resultados da pesquisa na forma de teses de PhD / apresentações em conferências / artigos revisados por especialistas. No entanto, a confidencialidade e o anonimato dos registros serão mantidos e meu nome e identidade não serão revelados a ninguém.

8. Quaisquer outras perguntas que eu possa ter sobre a pesquisa ou a minha participação foram respondidas.

9. Ao assinar esta declaração de consentimento livre e esclarecido, não renuncio a quaisquer reivindicações, direitos ou recursos legais.

10. Uma cópia desta declaração de consentimento informado será entregue a mim, e o original será mantido em registro

Eu, ………………………………………………………………………… .. li as informações acima / confirmo que as informações acima foram explicadas para mim em um linguagem que eu entendo e estou ciente do conteúdo deste documento. Eu fiz todas as perguntas que gostaria de fazer e estas foram respondidas para minha satisfação. Eu entendo perfeitamente o que é esperado de mim durante a pesquisa.

Eu não fui pressionado de forma alguma e eu voluntariamente concordo em participar do projeto mencionado acima.

| | |
|---|---|
| …………………………………. | …………………………………. |
| **Assinatura do participante** | **Data** |

**ENGLISH**:

Project title: Understanding a West-African recreational fishery as a complex socio-ecological system

**Verbal:** You have been invited by Ed Butler from the Department of Ichthyology and Fisheries Science, Rhodes University to participate in research focusing on the artisanal fishery for giant African threadfin or barbudo. The reason you have been chosen is because you are a fisherman targeting threadfin (barbudo) on the Kwanza River. Your participation in this survey is voluntary and you may decide at any point that you are not willing to partake. The information collected will form part of a doctoral thesis and may be published in the future, including in scientific journals.

However, this process DOES NOT require you to provide your name and therefore the answers you give will be stored ANONYMOUSLY. Additionally, the data collected will be stored securely and with complete confidentiality. Therefore, there is no personal risk involved with completing this survey. Furthermore, if you feel uncomfortable with any of the questions found in this survey, you are not obliged to answer and may skip questions at will. This survey has been approved by the Rhodes University ethics committee with ethics no. xyz… and you are may request to see this certificate at your will. By completing this survey, you DO NOT waiver any legal claims, rights or remedies.

This survey contains 110 questions which are MOSTLY MULTIPLE CHOICE and this interview should take no-longer than 20-25 minutes to complete. The purpose of these questions is to gain a better understanding of the artisanal fishery on the Kwanza River, how it operates and what fishermen's perceptions on the biology and sustainability of the giant African threadfin / barbudo historically and currently.

All questions in the survey are pertaining to artisanal fishing activities in the Kwanza River only and not anywhere else.

Do you have any questions?

**Consent Section**

I am aware that:

1. The purpose of the research project is to investigate the artisanal fishery for threadfin / barbudo on the Kwanza River.

2. The Rhodes University has given ethical clearance to this research project (***Ethics number……….***) and I may request to see the clearance certificate.

3. By participating in this research project I will be contributing towards the development of a knowledge base, which will aid in improving the sustainability of the fishery.

4. I will participate in the project by taking part and answering the questions on the survey to the best of my ability.

5. My participation is entirely voluntary and should I at any stage wish to withdraw from participating further, I may do so without any negative consequences.

6. Your views and knowledge will not be associated with you as an individual and therefore there should be no foreseeable risks or comebacks to you as an individual.

7. The researcher intends publishing the research results in the form of a PhD thesis / conference presentations / peer-reviewed papers. However, confidentiality and anonymity of records will be maintained and my name and identity will not be revealed to anyone.

8. Any further questions that I might have concerning the research or my participation have been answered.

9. By signing this informed consent declaration I am not waiving any legal claims, rights or remedies.

10. A copy of this informed consent declaration will be given to me, and the original will be kept on record.

I, ………………………………………………………………………….. have read the above information / confirm that the above information has been explained to me in a language that I understand and I am aware of this document's contents. I have asked all questions that I wished to ask and these have been answered to my satisfaction. I fully understand what is expected of me during the research. I am older than 18 years of age.

I have not been pressurised in any way and I voluntarily agree to participate in the above-mentioned project.

………………………………….                                   ………………………………….

**Participant's signature**                                   **Date**

**Rhodes University Ethics Co-ordinator**

**T: +27 (0) 46 603 8055**

**E: ethics-committee@ru.ac.za**

# Artisanal Sector

1. **Nome? / Name?**

2. **Sexo: / Sex:**
   *Mark only one oval.*
   - Feminino / Female
   - Masculino / Male

3. **Idade: / Age:**

4. **Quantas pessoas existem na sua familia imediata? / How many people are there in your family?**

5. **Quantas pessoas da sua família imediata trabalham? / And how many have a job?**

6. **Há quanto tempo você pesca no rio Kwanza? / How long have you been fishing in the Kwanza River?**
   Por favor, forneça um valor em anos / years

7. **Que outros trabalhos estão disponíveis? / What other jobs are available?**

8. **Você cresceu em Barra do Kwanza? / Did you grow up in Barra do Kwanza?**
   *Mark only one oval.*
   - Sim / Yes
   - Não / No

## Perceptions about the state and management of the fishery

9. **Notou algum aumento ou diminuição do número de barbudo desde que começou a pescar no rio Kwanza? / Have you noticed an increase or decrease in the number of threadfin since you began fishing in the Kwanza River?**

   *Mark only one oval.*

   - diminuiu / decrease
   - aumentou / increase
   - permaneceu o mesmo / the same
   - Eu não sei / I am not sure
   - Eu não tenho pescado aqui tempo suficiente para dizer / I haven't fished here long enough to know

10. **Notou algum aumento ou diminuição no número de barbudos grandes (acima de 30 kg) desde que começou a pescar no rio Kwanza? / Have you noticed an increase or decrease in the number of large (over 30 kg) barbudo (threadfin) since you began fishing in the Kwanza River?**

    *Mark only one oval.*

    - diminuiu / decrease
    - aumentou / increase
    - permaneceu o mesmo / the same
    - Eu não sei / I am not sure
    - Eu não tenho pescado aqui o tempo suficiente para dizer / I haven't fished here long enough to know

11. **Pensa que vai pescar menos, mais ou a mesma quantidade de barbudo daqui a dez anos? / Do you think you will catch less, more or the same amount of barbudo (threadfin) in ten years time?**

    *Mark only one oval.*

    - mais / more
    - menos / less
    - o mesmo / the same

## Pesca / Fishing

12. **Quando você vem pescar barbudo no rio Kwanza, você… When you come fish at the Kwanza River for barbudo, you...**

    *Mark only one oval.*

    - Pesca da margem
    - Pesca usando o seu próprio barco
    - Pesca usando o barco de outra pessoa
    - outros

13. **Quem é dono do barco em que você trabalha? / Who owns the boat that you work on?**

14. **Quantos barcos você possui? / How many boats do you own?**
*Mark only one oval.*

- 0
- 1
- 2
- 3
- 4
- 5
- >5

15. **Como você pesca barbudo? / What gears do you use to fish for barbudo?**
pode selecionar mais de uma opção
*Check all that apply.*

- rede pequena / gill-net (small)
- rede grande / gill-net (big)
- linha de mao / bait (handline)
- dropshot
- rapala
- kimdamba / longline
- outros

## Untitled Page

## Quantos de cada um você possui? / How many of each gear do you own?

Apenas seleccione itens que você usa para pescar barbudo. Escreva 0 se você não possui nenhum.

16. **rede pequena / gill-net (small)**

17. **rede grande / gill-net (big)**

18. **cana de pesca / fishing rods**

19. **kimdamba / longlines**

## Untitled Page

## Qual é o comprimento, a profundidade e o tamanho de malha de suas redes PEQUENAS, do que elas são feitas e quanto voce usa em média? / What is the length, depth and mesh size of your small nets, what are they made of and how many do you use on average?

deixe em branco se você não usar / leave blank if you do not use

20. **comprimento / length**

21. **profundidade / depth**

22. **tamanho de malha / mesh size**

23. **tipo de material / material**

24. **Quantos você usa em média? / How many do you use on average?**

25. **Que tipos de peixes você pescar com redes pequenas? / Which fish do you catch with small nets?**
    escreva cinco tipos / write 5 types

## Qual é o comprimento, a profundidade e o tamanho de malha de suas redes GRANDES, do que elas são feitas e quanto voce usa em média? / What is the length, depth and mesh size of your big nets, what are they made of and how many do you use of average?

deixe em branco se você não usar / leave blank if you do not use

26. **comprimento / length**

27. **profundidade / depth**

28. **tamanho de malha / mesh size**

29. **tipo de material / material**

30. **Quantos você usa em média? / How many do you use on average?**

31. **Que tipos de peixes você pescar com redes pequenas? / Which fish do you catch with small nets?**
    escreva cinco tipos / write 5 types

## Quantos kimdambas você tem e quantos anzoís em cada um? Distancia entre anzol, tamanho do anzol e qual isca? / How many longlines do you have and how many hooks are there on each? What is the distance between the hooks, hook size and bait type?

deixe em branco se você não usar / leave blank if you do not use

32. **Quantos anzoís? / How many hooks are there on each longline?**

33. **Qual é o comprimento do kimdamba? / What is the length of the longline**

34. **Qual a distância entre anzoís? / What is the distance between hooks?**

35. **tamanho do anzol? / Hook size?**

36. **tipo de isca? / Bait type?**

37. **Que tipos de peixes você pescar com kimdamba? / Which fish do you catch with longlines?**
    deixe em branco se você não usar / leave blank if you do not use

38. **Que tipos de peixes você pescar com rapala? / Which fish do you catch with rapala?**
    deixe em branco se você não usar / leave blank if you do not use

39. **Que tipos de peixes você pescar com dropshot? / Which fish do you catch with dropshot?**
    deixe em branco se você não usar / leave blank if you do not use

40. **Quando você notou pela primeira vez pessoas pescando com dropshot no rio Kwanza?/ When did you learn about dropshot?**
    Qual ano

## Untitled Page

## Onde você compra seu... / Where do you buy your...

deixe em branco se você não usar / leave blank if you do not use

41. **redes pequenas / gill-nets (small)?**

42. **redes grandes / gill-nets (big)?**

43. **cana de pesca / fishing rods?**

44. **rapalas?**

45. **dropshot?**

46. **linha / line?**

47. **anzoís / hooks?**

48. **carretel de pesca / fishing reels?**

## Untitled Page

## Em media, quantos PEIXES você pescar por dia? / On average, how many fish do you catch per day per each method?

deixe em branco se você não usar / leave blank if you do not use

49. **redes pequenas / gill-nets (small)?**

50. **redes grandes / gill-nets (big)?**

51. **dropshot?**

52. **rapala?**

53. **kimdamba / longline?**

54. **linha de mao / bait?**

## Untitled Page

## Em media, quantos BARBUDOS você pescar por dia? / On average, how many barbudo (threadfin) do you catch per day per each method?

deixe em branco se você não usar / leave blank if you do not use

55. **redes pequenas / gill-net (small)**

56. **redes grandes / gill-net (big)**

57. **dropshot**

58. **rapala**

59. **kimdamba / longline**

60. **linha de mao / bait**

## Untitled Page

61. **Em média, qual proporçao de peixe você vende / mantém para comer? / On average, what proportion of the fish that you catch do you sell vs eat?**
    Se você pescar 10 peixes, quantos você venderia / comer? / If you caught 10 fish how many would you sell vs eat

62. **Onde estão os peixes vendidos? Where do the fish get sold?**
*Check all that apply.*

- [ ] marcado / market
- [ ] restaurante / restaurant
- [ ] Eu não sei / I don't know
- [ ] de outros / other

63. **E a que distância está? / And how far away is it?**

## Qual é o preço no rio Kwanza de... / What is the going price AT THE KWANZA RIVER for the following species...

Preço por quilograma em Kwanza Angolano / Price per kilogram in Angolan Kwanza

64. **barbudo (threadfin)**

65. **corvina**

66. **pargo / snapper**

67. **macoa / jack crevalle**

68. **baracuda**

69. **bagre de maré**

## Qual é o preço no mercado (Luanda) de... / What is the going price AT THE MARKET for the following species...

Preço por quilograma em Kwanza Angolano / Price per kilogram in Angolan Kwanza

70. **barbudo (threadfin)**

71. **corvina**

72. **pargo / snapper**

73. **macoa / jack crevalle**

74. **barracuda**

75. **bagre de maré**

76. **Qual proporçao de peixe você vende seca / fresco? / What proportion of the fish you catch do you dry vs sell fresh**
    Se você pescar 10 peixes, quantos você venderia seca / fresco? / If you caught 10 fish how many would you sell dry vs fresh

## Untitled Page

## Despesas / Expenses

Em media, quanto você paga por mês por: / On average, how much do you spend on the following each month...

77. **Licença / Licence**

78. **Combustível / Fuel (not chartering)**

79. **Reparação de barco / Boat repair**

80. **Reparo de rede / Net repair**

81. **Equipamento / Equipment**

82. **De outros / Other (state)**

## Untitled Page

## Aluguer de barcos / Chartering

83. **Você aluga o seu barco a outros pescadores recreativos? / Do you charter your boat to recreational fishermen?**
*Mark only one oval.*
- sim / yes
- não / no
- Eu não tenho barcos / I don't own a boat

84. **Quanto cobra para arrendar seu barco por um dia? / What does it cost to charter a boat for a day?**

85. **Em média, com que frequência você aluga o seu barco por mês? / On average, how often do you charter your boat per month?**

86. **Em média, quanto combustível você usa para o aluguer de um dia? / On average, how much fuel do you use for a day's charter?**

## Conhecimento local / fisher local ecological knowledge

87. **Quantos tipos de barbudo você conhece? (de Angola) / How many types of barbudo (threadfin) do you know of from Angola?**

*Mark only one oval.*

- 0
- 1
- 2
- 3
- 4
- 5
- mais de 5 / more than 5

88. **Quando você acha que o barbudo chega ao rio Kwanza em cada ano? / When do you think the barbudo (threadfin) arrive at the Kwanza River each year?**

*Mark only one oval.*

- Janeiro / January
- Fevereiro / February
- Março / March
- Abril / April
- Maio / May
- Junho / June
- Julho / July
- Agosto / August
- Setembro / September
- Outubro / October
- Novembro / November
- Dezembro / December

89. **Quando pensa que o barbudo deixa o rio Kwanza todos os anos? / When do you think the barbudo (threadfin) leave the Kwanza River each year?**

*Mark only one oval.*

- Janeiro
- Fevereiro
- Março
- Abril
- Maio
- Junho
- Julho
- Agosto
- Setembro
- Outubro
- Novembro
- Dezembro

90. **Por que você acha que eles vêm para o rio Kwanza? / Why do you think they come to the Kwanza River?**

91. **Onde estão os barbudos pequenos (menos de 1kg)? / Where are the very small barbudo (threadfin)? (Less than 1 kg)**

*Mark only one oval.*

- Option 1

92. **Quando é que o barbudos grande estão no rio? (mais de 30 kg)? / When are the big barbudo (threadfin) in the river? (more than 30 kg)**

selecione os meses (pode escolher mais do que uma opção)

*Check all that apply.*

- [ ] Janeiro
- [ ] Fevereiro
- [ ] Março
- [ ] Abril
- [ ] Maio
- [ ] Junho
- [ ] Julho
- [ ] Agosto
- [ ] Setembro
- [ ] Outubro
- [ ] Novembro
- [ ] Dezembro

93. **Os peixes pequenos são machos, fêmeas ou ambos? / Are the small fish male or female or both?**

*Mark only one oval.*

- ( ) macho
- ( ) fêmea
- ( ) ambos
- ( ) Eu não sei

94. **Porque você pensa isso? / Why do you think that?**

95. **Os peixes grandes (mais de 30 kg) são machos ou fêmeas ou ambos? / Are the big fish (more than 30 kg) male or female or both?**

*Mark only one oval.*

- ( ) macho
- ( ) fêmea
- ( ) ambos
- ( ) Eu não sei

96. **Porque você pensa isso? / Why do you think that?**

97. **Qual é o local mais acima no rio onde você ouviu falar que existe barbudo? / What is the furthest location up river that you have heard of there being barbudo?**

98. **Onde você acha que o barbudo se reproduz? / Where do you think the barbudo reproduce?**
    Escreva "inseguro" se você não sabe / write "unsure" if you do not know

99. **E quando você acha que eles se reproduzem? / And when do you think they reproduce?**
    Escreva "inseguro" se você não sabe

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## Appendix B

## RHODES UNIVERSITY


**DEPARTMENT OF ICHTHYOLOGY & FISHERIES SCIENCE (DIFS), RHODES UNIVERSITY**

***PO Box 94 • Grahamstown 6140 • South Africa***

**Telefax: +27 46 622 4827 • Telephone: +27 46 603 8415/6, 603 8824 • e-mail: ed.b@live.co.za**


**Consent:**

**Portuguese:**

Título do projeto: Entendendo uma pesca recreativa na África Ocidental como um complexo sistema socioecológico

Você foi convidado por Ed Butler, do Departamento de Ictiologia e Ciências Pesqueiras, da Universidade de Rhodes, para participar de pesquisas com foco no rosbife africano gigante ou barbudo. Sua participação nesta pesquisa é voluntária e você pode decidir a qualquer momento que não estiver disposto a participar. As informações coletadas farão parte de uma tese de doutorado e poderão ser publicadas no futuro, inclusive em periódicos científicos.

No entanto, este processo não requer que você forneça seu nome e, portanto, as respostas que você dá são completamente ANÔNIMAS. Além disso, os dados coletados serão armazenados de forma segura e com total confidencialidade. Portanto, não há risco pessoal envolvido na conclusão desta pesquisa. Além disso, se você se sentir desconfortável com qualquer uma das questões encontradas nesta pesquisa, você não é obrigado a responder e pode deixar as perguntas à vontade. Esta pesquisa foi aprovada pelo comitê de ética da Universidade Rhodes, com ética no. 2019-0178-820 e você pode pedir para ver este certificado à sua vontade. Ao concluir esta pesquisa, você NÃO renuncia a quaisquer reivindicações, direitos ou recursos legais.

Este formulário tem 40 perguntas, que são a opção MAIS MÚLTIPLA, e não deve demorar mais de 10 a 15 minutos para ser concluído. O objectivo destas questões é obter uma melhor compreensão da pesca recreativa no rio Kwanza, como funciona e quais são as percepções dos pescadores sobre a biologia e a sustentabilidade do gigante africano threadfin / barbudo, historicamente e actualmente.

Há uma seção adicional que é OPCIONAL e contém 20 perguntas sobre o barbudo para aquelas pessoas que se consideram especialistas em barbudo!

Todas as questões da pesquisa referem-se apenas às atividades de pesca no rio Kwanza e não em qualquer outro lugar.

Continuar com esta pesquisa indica que você está ciente de que:

1. O objectivo do projecto de investigação é investigar a pesca recreativa de threadfin / barbudo no rio Kwanza.

2. A Universidade de Rhodes forneceu esclarecimento ético a este projeto de pesquisa (Número de Ética 2019-0178-820) E você pode pedir para ver o certificado de liberação.

3. Ao participar deste projeto de pesquisa, você estará contribuindo para o desenvolvimento de uma base de conhecimento, que ajudará a melhorar a sustentabilidade da pesca.

4. Você participará do projeto participando e respondendo às perguntas da pesquisa com o melhor de sua capacidade.

5. A sua participação é totalmente voluntária e se, em qualquer altura, desejar desistir de participar, poderá fazê-lo sem quaisquer consequências negativas.

6. Seus pontos de vista e conhecimento não serão associados a você como um indivíduo e, portanto, não deve haver riscos ou retornos previsíveis para você como indivíduo.

7. O pesquisador pretende publicar os resultados da pesquisa na forma de teses de PhD / apresentações em conferências / artigos revisados por especialistas. No entanto, a confidencialidade e o anonimato dos registros serão mantidos e seu nome e identidade não serão revelados a ninguém.

8. Quaisquer outras perguntas que você possa ter sobre a pesquisa ou a minha participação foram respondidas e você está livre para enviar qualquer pergunta para ed.butler@live.co.za.

9. Ao marcar a caixa abaixo, você não está renunciando a quaisquer reivindicações legais, direitos ou recursos.

10. Uma cópia desta declaração de consentimento informado estará disponível para mim, e o original será mantido em registro.

☐ Eu entendo e estou ciente dos pontos acima e estou disposto a proceder voluntariamente

**English:**

Project title: Understanding a West-African recreational fishery as a complex socio-ecological system

You have been invited by Ed Butler from the Department of Ichthyology and Fisheries Science, Rhodes University to participate in research focusing on the giant African threadfin or barbudo. Your participation in this survey is voluntary and you may decide at any point that you are not willing to partake. The information collected will form part of a doctoral thesis and may be published in the future, including in scientific journals.

However, this process DOES NOT require you to provide your name and therefore the answers you give are completely ANONYMOUS. Additionally, the data collected will be stored securely and with complete confidentiality. Therefore, there is no personal risk involved with completing this survey. Furthermore, if you feel uncomfortable with any of the questions found in this survey, you are not obliged to answer and may leave out questions at will. This survey has been approved by the Rhodes University ethics committee with ethics no. 2019-0178-820 and you are may request to see this certificate at your will. By completing this survey, you DO NOT waiver any legal claims, rights or remedies.

This form has 40 questions which are MOSTLY MULTIPLE CHOICE and should take no-longer than 10-15 minutes to complete. The purpose of these questions is to gain a better understanding of the recreational fishery on the Kwanza River, how it operates and what fishermen's perceptions are on the biology and sustainability of the giant African threadfin / barbudo historically and currently.

There is an additional section which is OPTIONAL and contains 20 questions about barbudo for those people who consider themselves barbudo experts!

All questions in the survey are pertaining to fishing activities in the Kwanza River only and not anywhere else.

Proceeding further with this survey indicates that you are aware that:

11. The purpose of the research project is to investigate the recreational fishery for threadfin / barbudo on the Kwanza River.

12. Rhodes University has given ethical clearance to this research project (***Ethics number*** 2019-0178-820) and you may request to see the clearance certificate.

13. By participating in this research project you will be contributing towards the development of a knowledge base, which will aid in improving the sustainability of the fishery.

14. You will participate in the project by taking part and answering the questions on the survey to the best of your ability.

15. Your participation is entirely voluntary and should you at any stage wish to withdraw from participating further, you may do so without any negative consequences.

16. Your views and knowledge will not be associated with you as an individual and therefore there should be no foreseeable risks or comebacks to you as an individual.

17. The researcher intends publishing the research results in the form of a PhD thesis / conference presentations / peer-reviewed papers. However, confidentiality and anonymity of records will be maintained and your name and identity will not be revealed to anyone.

18. Any further questions that you might have concerning the research or your participation have been answered and you are free to email any queries to ed.butler@live.co.za.

19. By checking the box below, you are not waiving any legal claims, rights or remedies.

20. A copy of this informed consent declaration will be available to you, and the original will be kept on record.

☐ **I am 18 years of age and I understand and agree to the above points and am willing to proceed voluntarily**

# Pesquisa do barbudo / threadfin survey

Portuguese: Obrigado por concordar em preencher este formulário. As informações coletadas farão parte de uma tese de doutoramento e poderão ser publicadas no futuro.
No entanto, este processo não exige que você forneça seu nome e, portanto, as respostas que você dá são completamente ANÓNIMAS.
Este formulário tem 40 perguntas que são na sua maioria de escolha múltipla e que não deverão demorar mais de 10-12 minutos a completar.
Existe uma secção adicional que é OPCIONAL e que contém 20 perguntas sobre o Barbudo, para aqueles que se consideram especialistas em Barbudo.
Todas as questões da pesquisa referem-se apenas às atividades de pesca no rio Kwanza e não em qualquer outro lugar.
A continuação desta pesquisa indica que:
- você leu as informações acima
- você concorda voluntariamente em participar
- você tem pelo menos 18 anos de idade

English: Thank you for agreeing to fill out this form. The information collected will form part of a doctoral thesis and may be published in the future.
However, this process DOES NOT require you to provide your name and therefore the answers you give are completely ANONYMOUS.
This form has 40 questions which are MOSTLY MULTIPLE CHOICE and should take no-longer than 10-15 minutes to complete.
There is an additional section which is OPTIONAL and contains 20 questions about barbudo for those people who consider themselves barbudo experts!
All questions in the survey are pertaining to fishing activities in the Kwanza River only and not anywhere else.
Proceeding further with this survey indicates that:
- you have read the above information
- you voluntarily agree to participate
- you are at least 18 years of age

* Required

1. **Língua: / Language:** *
   *Mark only one oval.*
   - ( ) Portuguese *Skip to question 2.*
   - ( ) English *Skip to question 54.*

## Untitled Page

2. **Sexo:**
   *Mark only one oval.*
   - ( ) Feminino
   - ( ) Masculino

3. **Idade?**

   _______________

4. **Qual das seguintes alternativas melhor descreve você?**
*Mark only one oval.*

- Cidadão Angolano
- Emigrantes vivendo em Angola
- Turista
- Outros
- Other: ____________________

5. **Há quanto tempo você pesca no rio Kwanza?**
Por favor, forneça um valor em anos

____________________

## Conhecimento local

6. **Notou algum aumento ou diminuição do número de barbudo desde que começou a pescar no rio Kwanza?**
*Mark only one oval.*

- diminuiu muito
- diminuiu um pouco
- permaneceu o mesmo
- aumentou um pouco
- aumentou muito
- não tenho certeza

7. **Notou algum aumento ou diminuição no número de barbudos grandes (acima de 30 kg) desde que começou a pescar no rio Kwanza?**
*Mark only one oval.*

- diminuiu muito
- diminuiu um pouco
- permaneceu o mesmo
- aumentou um pouco
- aumentou muito
- não tenho certeza

8. **Pensa que vai pescar menos, mais ou a mesma quantidade de barbudo daqui a dez anos?**
*Mark only one oval.*

| | 1 | 2 | 3 | 4 | 5 | |
|---|---|---|---|---|---|---|
| menos | | | | | | mais |

9. **Porque você pensa isso?**
pode escolher mais de uma opção
*Check all that apply.*

- [ ] mudanças no meio ambiente
- [ ] mudanças no fluxo de água (barragens etc.)
- [ ] sobrepesca (cana e carreto / anzol e linha)
- [ ] sobrepesca (redes)
- [ ] sobrepesca (palangre / kimdamba )
- [ ] poluição
- [ ] não tenho certeza
- [ ] outros
- [ ] Other: ______________________

## Pesca

10. **Quando você vem pescar barbudo no rio Kwanza, você…**
escolha quais as opções que descrevem você (pode escolher mais de uma opção)
*Check all that apply.*

- [ ] Pesca da margem
- [ ] Pesca usando o seu próprio barco ou barco particular
- [ ] Arrenda um barco (chata) dos pescadores locais
- [ ] Arrenda um barco do hotel
- [ ] outros

11. **Como você pesca barbudo?**
pode selecionar mais de uma opção
*Check all that apply.*

- [ ] rapala
- [ ] jigheads e plásticos (dropshot)
- [ ] isca viva
- [ ] isca morta
- [ ] outros

12. **Quando pesca um peixe, como coloca o peixe no barco?**
*Mark only one oval.*

- ( ) à mão
- ( ) com um arpão / bicheiro
- ( ) com uma rede
- ( ) outros
- ( ) Other: ______________________

## Quantos de cada um você possuí?

Apenas seleccione itens que você usa para pescar barbudo.

13. **barcos de pesca**
*Mark only one oval.*

- 0
- 1
- 2
- 3
- 4
- 5
- mais de 5

14. **cana de pesca**
*Mark only one oval.*

- 0
- 1-2
- 3-4
- 5-6
- 7-8
- 9-10
- mais de 10

## Onde você compra seu…

Deixe em branco se não tem.

15. **barco de pesca e motores**
*Check all that apply.*

- [ ] localmente (em Angola)
- [ ] Namíbia
- [ ] África do Sul
- [ ] em outros lugares na África
- [ ] Europa, América ou Ásia
- [ ] outros
- [ ] Other: ____________________

16. **cana e carretel de pesca**
*Check all that apply.*

- [ ] localmente (em Angola)
- [ ] Namíbia
- [ ] África do Sul
- [ ] em outros lugares na África
- [ ] Europa, América ou Ásia
- [ ] outros
- [ ] Other: ____________________

17. **linha**
*Check all that apply.*

- [ ] localmente (em Angola)
- [ ] Namíbia
- [ ] África do Sul
- [ ] em outros lugares na África
- [ ] Europa, América ou Ásia
- [ ] outros
- [ ] Other: ____________________

18. **rapalas e iscas**
*Check all that apply.*

- [ ] localmente (em Angola)
- [ ] Namíbia
- [ ] África do Sul
- [ ] em outros lugares na África
- [ ] Europa, América ou Ásia
- [ ] outros
- [ ] Other: ____________________

19. **jigheads e plásticos (dropshot)**
*Check all that apply.*

- [ ] localmente (em Angola)
- [ ] Namíbia
- [ ] África do Sul
- [ ] em outros lugares na África
- [ ] Europa, América ou Ásia
- [ ] outros
- [ ] Other: ____________________

20. **anzóis**
*Check all that apply.*

- [ ] localmente (em Angola)
- [ ] Namíbia
- [ ] África do Sul
- [ ] em outros lugares na África
- [ ] Europa, América ou Ásia
- [ ] outros
- [ ] Other: ______________________

## Untitled Page

21. **Costuma comer o peixe que você pesca no rio Kwanza?**
*Mark only one oval.*

- ( ) sim, todo o peixe capturado
- ( ) sim, geralmente a maioria dos peixes
- ( ) sim, mas apenas 1 ou 2
- ( ) ocasionalmente 1 peixe
- ( ) nunca
- ( ) de outros
- ( ) Other: ______________________

22. **Quais as tipos de peixes você vai manter para comer?**
Classifique estas 5 espécies de 1 a 5 em ordem de desejo. (espécies de peixes capturadas no rio Kwanza)
*Mark only one oval per row.*

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| barbudo | ( ) | ( ) | ( ) | ( ) | ( ) |
| barracuda / pescada | ( ) | ( ) | ( ) | ( ) | ( ) |
| pargo | ( ) | ( ) | ( ) | ( ) | ( ) |
| corvina | ( ) | ( ) | ( ) | ( ) | ( ) |
| macoa | ( ) | ( ) | ( ) | ( ) | ( ) |

23. **Em media, quantos barbudo você mantém por dia?**
Se você capturasse 10 barbudos, quantos você manteria?
*Mark only one oval.*

- 1
- 2
- 3
- 4
- 5
- 6
- 7
- 8
- 9
- 10

24. **Alguma vez vende ou troca qualquer peixe que apanhe no rio Kwanza?**
*Mark only one oval.*

- vende
- troca
- ambos: vende e troca
- nem vende nem troca
- Eu preferiria não dizer

25. **Se você vende ou troca seu peixe, onde você faz isso?**
*Mark only one oval.*

- com amigos
- com colegas de trabalho
- com os clientes
- eu não faz isso

26. **Pensa que deveria existir restrições legais em Angola para o tamanho (RESTRIÇÃO POR TAMANHO) e/ou número (LIMITE DE SACO) de barbudos que uma pessoa pode pescar e levar para casa?**
*Mark only one oval.*

- Devem existir restrições legais ao número de barbudos que uma pessoa pode pescar e levar para casa (LIMITE DE SACO)
- Devem existir restrições legais ao tamanho dos barbudos que uma pessoa pode pescar e levar para casa (RESTRIÇÃO POR TAMANHO)
- Deve existir tanto RESTRIÇÃO POR TAMANHO como LIMITE DE SACO
- Não há necessidade nem de RESTRIÇÃO POR TAMANHO nem de LIMITE DE SACO
- outros
- Other: ____________________

## Despesas

Estas são despesas incorridas durante a pesca no Kwanza para barbudo. Esta secção destina-se a pescadores recreativos que vivem em Angola e pode ser deixada de fora para os turistas.

27. **Durante que meses pescam o barbudo no rio Kwanza?**

pode escolher mais de uma opção

*Check all that apply.*

- [ ] Janeiro
- [ ] Fevereiro
- [ ] Março
- [ ] Abril
- [ ] Maio
- [ ] Junho
- [ ] Julho
- [ ] Agosto
- [ ] Setembro
- [ ] Outubro
- [ ] Novembro
- [ ] Dezembro

28. **Com que frequência você pesca no rio Kwanza?**

Por favor, forneça um valor em termos do número de viagens realizadas em média por ano.

*Mark only one oval.*

- ◯ 1-2 viagens por ano
- ◯ 3-5 viagens por ano
- ◯ 5-10 viagens por ano
- ◯ 10-20 viagens por ano
- ◯ mais de 20 viagens por ano

29. **EM MÉDIA, quantas pessoas pescam com você?**

Em viagens ao rio Kwanza

*Mark only one oval.*

- ◯ 1
- ◯ 2
- ◯ 3
- ◯ 4
- ◯ 5
- ◯ mais de 5

## Em média, quanto você gasta com o seguinte por cada viagem de pesca feita ao rio Kwanza para pescar barbudo?

Por favor liste a moeda

30. **Combustível para o barco**

31. **Combustível para o carro (transporte para o Kwanza)**

32. **Comida e bebida**

33. **Alojamento**

34. **Equipamento**

35. **Outro (explicar)**

## Aluguer de barcos

36. **Você aluga o seu barco a outros pescadores recreativos?**
*Mark only one oval.*

- sim
- não *Skip to question 40.*
- Eu não tenho barcos *Skip to question 40.*

## Untitled Page

37. **Quanto cobra para arrendar seu barco por um dia?**

38. **Em média, com que frequência você aluga o seu barco por mês?**
*Mark only one oval.*

- 1-2 vezes por mês
- 3-4 vezes por mês
- 5-10 vezes por mês
- mais de 10 vezes por mês

39. **Em média, quanto combustivel você usa para o aluguer de um dia?**

_______________________________

*Skip to question 40.*

## Quão bem conhece a pesca de barbudo?

PARABÉNS, completou o questionário!

Contudo, existe mais uma secção opcional para aqueles que tenham disponibilidade ou que sejam especialistas em Barbudo! Se conheçe bem este tipo de pesca, iremos valorizar a informação que partilhar connosco e encorajamo-lo a completar a secção extra (20 perguntas). Se não conheçe bem este tipo de pesca ou não tem disponibilidade para completar esta secção extra, pode enviar já o questionário.

Muito obrigado!

40. *

*Mark only one oval.*

- ( ) ENVIAR *Stop filling out this form.*
- ( ) Secção extra (opcional)

## Conhecimento local

41. **Quantos tipos de barbudo você conhece? (de Angola)**

*Mark only one oval.*

- ( ) 0
- ( ) 1
- ( ) 2
- ( ) 3
- ( ) 4
- ( ) 5
- ( ) mais de 5

42. **Quando você acha que o barbudo chega ao rio Kwanza em cada ano?**
*Mark only one oval.*

- Janeiro
- Fevereiro
- Março
- Abril
- Maio
- Junho
- Julho
- Agosto
- Setembro
- Outubro
- Novembro
- Dezembro

43. **Quando pensa que o barbudo deixa o rio Kwanza todos os anos?**
*Mark only one oval.*

- Janeiro
- Fevereiro
- Março
- Abril
- Maio
- Junho
- Julho
- Agosto
- Setembro
- Outubro
- Novembro
- Dezembro

44. **Por que você acha que eles vêm para o rio Kwanza?**

45. **Onde estão os barbudos pequenos (menos de 1kg)?**

46. **Quando é que o barbudos grande estão no rio? (mais de 30 kg)?**
selecione os meses (pode escolher mais do que uma opção)
*Check all that apply.*

- [ ] Janeiro
- [ ] Fevereiro
- [ ] Março
- [ ] Abril
- [ ] Maio
- [ ] Junho
- [ ] Julho
- [ ] Agosto
- [ ] Setembro
- [ ] Outubro
- [ ] Novembro
- [ ] Dezembro

47. **Os peixes pequenos são machos, fêmeas ou ambos?**
*Mark only one oval.*

- ( ) macho
- ( ) fêmea
- ( ) ambos
- ( ) Eu não sei

48. **Porque você pensa isso?**

____________________
____________________
____________________
____________________
____________________

49. **Os peixes grandes (mais de 30 kg) são machos ou fêmeas ou ambos?**
*Mark only one oval.*

- ( ) macho
- ( ) fêmea
- ( ) ambos
- ( ) Eu não sei

50. **Porque você pensa isso?**

51. **Qual é o local mais acima no rio onde você ouviu falar que existe barbudo?**
Escreva "inseguro" se você não sabe

52. **Onde você acha que o barbudo se reproduz?**
Escreva "inseguro" se você não sabe

53. **E quando você acha que eles se reproduzem?**
Escreva "inseguro" se você não sabe

*Stop filling out this form.*

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54. **Sex:**
*Mark only one oval.*
- Female
- Male

55. **How old are you?**

56. **Which of the following best describes you?**
*Mark only one oval.*
- Angolan national
- Expatriate living in Angola
- Tourist
- Other: ____________________

57. **How long have you been fishing in the Kwanza River?**
Please provide a value in years

## Perceptions about the state and management of the fishery

58. **Have you noticed an increase or decrease in the number of threadfin since you began fishing in the Kwanza River?**
*Mark only one oval.*

- strong decrease
- weak decrease
- it has remained the same
- weak increase
- strong increase
- I am not sure

59. **Have you noticed an increase or decrease in the number of large (over 30 kg) barbudo (threadfin) since you began fishing in the Kwanza River?**
*Mark only one oval.*

- strong decrease
- weak decrease
- it has remained the same
- weak increase
- strong increase
- I am not sure

60. **Do you think you will catch less, more or the same amount of barbudo (threadfin) in ten years time?**
*Mark only one oval.*

| | 1 | 2 | 3 | 4 | 5 | |
|---|---|---|---|---|---|---|
| less | | | | | | more |

61. **Why? (previous question)**
you can select more than one option
*Check all that apply.*

- [ ] environmental changes
- [ ] water flow (dams etc.)
- [ ] too much fishing (rod-and-reel)
- [ ] too much gill-netting
- [ ] pollution
- [ ] unsure
- [ ] longline fishing
- [ ] Other: ______________________

## Fishing

62. **When you come fish at the Kwanza River for barbudo (threadfin), you...**
choose which options describes you (you can choose more than one option)
*Check all that apply.*

- [ ] Fish from the bank
- [ ] Fish using my own boat/ private boat
- [ ] Charter a boat (chata) from the local fishermen
- [ ] Charter a boat from the lodge
- [ ] Other: ______________________

63. **How do you fish for barbudo (threadfin)?**
you can select more than one option
*Check all that apply.*

- [ ] rapala
- [ ] jigheads and plastics / dropshot
- [ ] live-bait
- [ ] dead bait
- [ ] Other: ______________________

64. **When you catch a fish, how do you get it into the boat?**
*Mark only one oval.*

- ( ) by hand
- ( ) with a gaff
- ( ) with a landing net
- ( ) Other: ______________________

## How many of each do you own?

Only list items that you use to fish for barbudo (threadfin). write 0 if you do not own any.

65. **fishing boats**
*Mark only one oval.*

- ◯ 0
- ◯ 1
- ◯ 2
- ◯ 3
- ◯ 4
- ◯ 5
- ◯ more than 5

66. **fishing rods**
*Mark only one oval.*

- ◯ 0
- ◯ 1-2
- ◯ 3-4
- ◯ 5-6
- ◯ 7-8
- ◯ 9-10
- ◯ more than 10

## Where do you buy your...

leave blank if you do not own any of the following items

67. **fishing boats and motors**
*Check all that apply.*

- ☐ Locally (Angola)
- ☐ Namibia
- ☐ South Africa
- ☐ Elsewhere in Africa
- ☐ Europe, Asia or America
- ☐ Other: ______________________

68. **fishing rods and reels**
*Check all that apply.*

- [ ] Locally (Angola)
- [ ] Namibia
- [ ] South Africa
- [ ] Elsewhere in Africa
- [ ] Europe, Asia or America
- [ ] Other: ____________________

69. **fishing line**
*Check all that apply.*

- [ ] Locally (Angola)
- [ ] Namibia
- [ ] South Africa
- [ ] Elsewhere in Africa
- [ ] Europe, Asia or America
- [ ] Other: ____________________

70. **rapalas and lures**
*Check all that apply.*

- [ ] Locally (Angola)
- [ ] Namibia
- [ ] South Africa
- [ ] Elsewhere in Africa
- [ ] Europe, Asia or America
- [ ] Other: ____________________

71. **jigheads and plastics / dropshot**
*Check all that apply.*

- [ ] Locally (Angola)
- [ ] Namibia
- [ ] South Africa
- [ ] Elsewhere in Africa
- [ ] Europe, Asia or America
- [ ] Other: ____________________

72. **hooks**

*Check all that apply.*

- [ ] Locally (Angola)
- [ ] Namibia
- [ ] South Africa
- [ ] Elsewhere in Africa
- [ ] Europe, Asia or America
- [ ] Other: ______________________

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73. **Do you ever keep any fish that you catch in the Kwanza River to eat?**

*Mark only one oval.*

- ◯ yes, all of the fish caught
- ◯ yes, usually most of the fish
- ◯ yes, but only 1 or 2 fish
- ◯ sometimes 1 fish
- ◯ never
- ◯ Other: ______________________

74. **Which fish species will you keep to eat?**

Rank these 5 species in order of desirability (fish species caught in the Kwanza River)

*Mark only one oval per row.*

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| threadfin / barbudo | ◯ | ◯ | ◯ | ◯ | ◯ |
| barracuda | ◯ | ◯ | ◯ | ◯ | ◯ |
| snapper / pargo | ◯ | ◯ | ◯ | ◯ | ◯ |
| corvina | ◯ | ◯ | ◯ | ◯ | ◯ |
| jack / macoa | ◯ | ◯ | ◯ | ◯ | ◯ |

75. **On average, how many barbudo (threadfin) would you keep per day?**
If you caught 10 fish, how many would you keep?
*Mark only one oval.*

- 0
- 1
- 2
- 3
- 4
- 5
- 6
- 7
- 8
- 9
- 10

76. **Do you ever sell or barter any of the fish that you catch in the Kwanza River?**
*Mark only one oval.*

- sell
- barter
- both sell and barter
- neither sell nor barter
- I'd rather not say

77. **If you sell or barter your fish, where do you do so?**
*Mark only one oval.*

- with friends
- with work colleagues
- with customers
- I do not do this
- Other: ____________________

78. **Do you think that there should be lawful restrictions for the sizes (size-restrictions) and/or numbers (bag-limits) of threadfin/barbudo a person may keep per day in Angola?**
*Mark only one oval.*

- There should be restrictions on the number of barbudo kept per person per day (BAG-LIMITS)
- There should be restrictions on the size of the barbudo allowed to be kept (SIZE RESTRICTIONS)
- There should be both SIZE RESTRICTIONS and BAG-LIMITS for barbudo
- There is no need for either SIZE RESTRICTIONS or BAG-LIMITS for barbudo
- Other: ______________________

## Expenses

These are expenses incurred while fishing at the Kwanza for barbudo (threadfin). This section is intended for recreational fishermen living within Angola and can be left out by tourists.

79. **During which months do you target barbudo (threadfin) in the Kwanza River?**
you can select more than one option
*Check all that apply.*

- [ ] January
- [ ] February
- [ ] March
- [ ] April
- [ ] May
- [ ] June
- [ ] July
- [ ] August
- [ ] September
- [ ] October
- [ ] November
- [ ] December

80. **How often do you fish in the Kwanza River?**
Please provide a value in terms of the number of trips undertaken ON AVERAGE per year.
*Mark only one oval.*

- 1-2 trips per year
- 3-5 trips per year
- 6-10 trips per year
- 11-20 trips per year
- more than 20 trips per year

81. **ON AVERAGE, how many people fish with you?**
On trips to the Kwanza River
*Mark only one oval.*

- 0
- 1
- 2
- 3
- 4
- 5
- more than 5

## On average, how much do you spend on the following per each fishing trip made to the Kwanza River to target barbudo (threadfin)

please list the currency

82. **Fuel for the boat**

83. **Fuel for the car (transport to the Kwanza)**

84. **Food and drink**

85. **Accommodation**

86. **Tackle and equipment**

87. **Other (state)**

## Chartering

88. **Do you charter your boat to other recreational fishermen?**
*Mark only one oval.*

- yes
- no *Skip to question 92.*
- I don't own a boat *Skip to question 92.*

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89. **What do you charge to charter your boat for a day?**

90. **On average, how often do you charter your boat per month?**
*Mark only one oval.*

- 1-2 times per month
- 3-4 times per month
- 5-10 times per month
- more than 10 times per month

91. **On average, how much fuel do you use for a day's charter?**

*Skip to question 92.*

## How well do you know the barbudo fishery?

CONGRATULATIONS, you have completed the survey!

However, there is one more optional section for those that have the time or are barbudo experts! If you know the fishery very well we would value your information and would encourage you to complete the extra section (20 questions). If you do not know the fishery very well or you do not have the time to complete the extra section, you may submit now.

Thank you very much!

92. *
*Mark only one oval.*

- SUBMIT *Stop filling out this form.*
- Extra section (optional) *Skip to question 93.*

## Extra Section - fisher local ecological knowledge

93. **How many types of barbudo (threadfin) do you know of from Angola?**
*Mark only one oval.*

- ◯ 0
- ◯ 1
- ◯ 2
- ◯ 3
- ◯ 4
- ◯ 5
- ◯ more than 5

94. **When do you think the barbudo (threadfin) arrive at the Kwanza River each year?**
*Mark only one oval.*

- ◯ January
- ◯ February
- ◯ March
- ◯ April
- ◯ May
- ◯ June
- ◯ July
- ◯ August
- ◯ September
- ◯ October
- ◯ November
- ◯ December

95. **When do you think the barbudo (threadfin) leave the Kwanza River each year?**
*Mark only one oval.*

- ◯ January
- ◯ February
- ◯ March
- ◯ April
- ◯ May
- ◯ June
- ◯ July
- ◯ August
- ◯ September
- ◯ October
- ◯ November
- ◯ December

96. **Why do you think they come to the Kwanza River?**

97. **Where are the very small barbudo (threadfin)? (Less than 1 kg)**

98. **When are the big barbudo (threadfin) in the river? (more than 30 kg)**
select which months
*Check all that apply.*

- [ ] January
- [ ] February
- [ ] March
- [ ] April
- [ ] May
- [ ] June
- [ ] July
- [ ] August
- [ ] September
- [ ] October
- [ ] November
- [ ] December

99. **Are the small fish male or female or both?**
*Mark only one oval.*

- ◯ male
- ◯ female
- ◯ both
- ◯ I don't know

100. **Why do you think that?**

101. **Are the big fish (more than 30 kg) male or female or both?**

*Mark only one oval.*

- male
- female
- both
- I don't know

102. **Why do you think that?**

103. **What is the furthest location up river that you have heard of there being barbudo?**

Write 'unsure' if you do not know

104. **Where do you think the barbudo reproduce?**

Write 'unsure' if you do not know.

105. **And when do you think they reproduce?**

Write 'unsure' if you do not know