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Using Baited Remote Underwater Video Systems (BRUVS) in the conservation of a popular aquarium species, *Metriaclima estherae* and *Potamonautes lirrangensis*, in Lake Malawi/Niassa/Nyasa

by

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DECLARATION

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ABSTRACT

The use of Baited Remote Underwater Video Systems (BRUVS) is a well-established monitoring technique used to obtain long-term monitoring data on aquatic species populations. However, the method is not commonly used in freshwater surveys despite the potential it has to be useful for collecting data. Since freshwater ecosystems are some of the most threatened natural systems in the world, it is beneficial to determine whether BRUVS are a viable monitoring tool to inform their management. The primary aim of this thesis was to determine if BRUVS could be used to extract critical population information about a small fish species and a crab species in the Meluluco reef system of Lake Malawi/Niassa/Nyasa.

BRUVS were deployed within 329 different localities encompassing a range of different habitats within the Meluluco reef system over a period of 3 years (2016 to 2018). The results of the study showed that BRUVS were effective at capturing data on the abundance and habitat preferences of both *Metriaclima estherae* and *Potamonautes lirrangensis*.

Potamonautes lirrangensis were more commonly observed in rocky substrate at shallower depths and seemed to be avoiding sandy substrate. Both male and female *M. estherae* were more frequently observed in rocky habitat, though males were more commonly found in sandier habitats in comparison to their female conspecifics. Stereo-Baited Remote Underwater Video Systems (Stereo-BRUVS) deployed in the year 2018 were able to accurately determine the lengths of *M. estherae* which displayed that males were larger on average in comparison to females and displayed a wider length distribution. The data also showed that smaller males were more commonly observed in sand dominated habitats, whereas larger males were found more frequently in rock dominated habitats.

Keywords: Freshwater, Lake Malawi, Lake Niassa, baited remote underwater video, BRUVS, ecological monitoring, management, *Metriaclima estherae*, *Potamonautes lirrangensis*

*Dedicated to Professor Olaf Weyl
who taught me so much in such a short time.
Rest Easy, Prof.*

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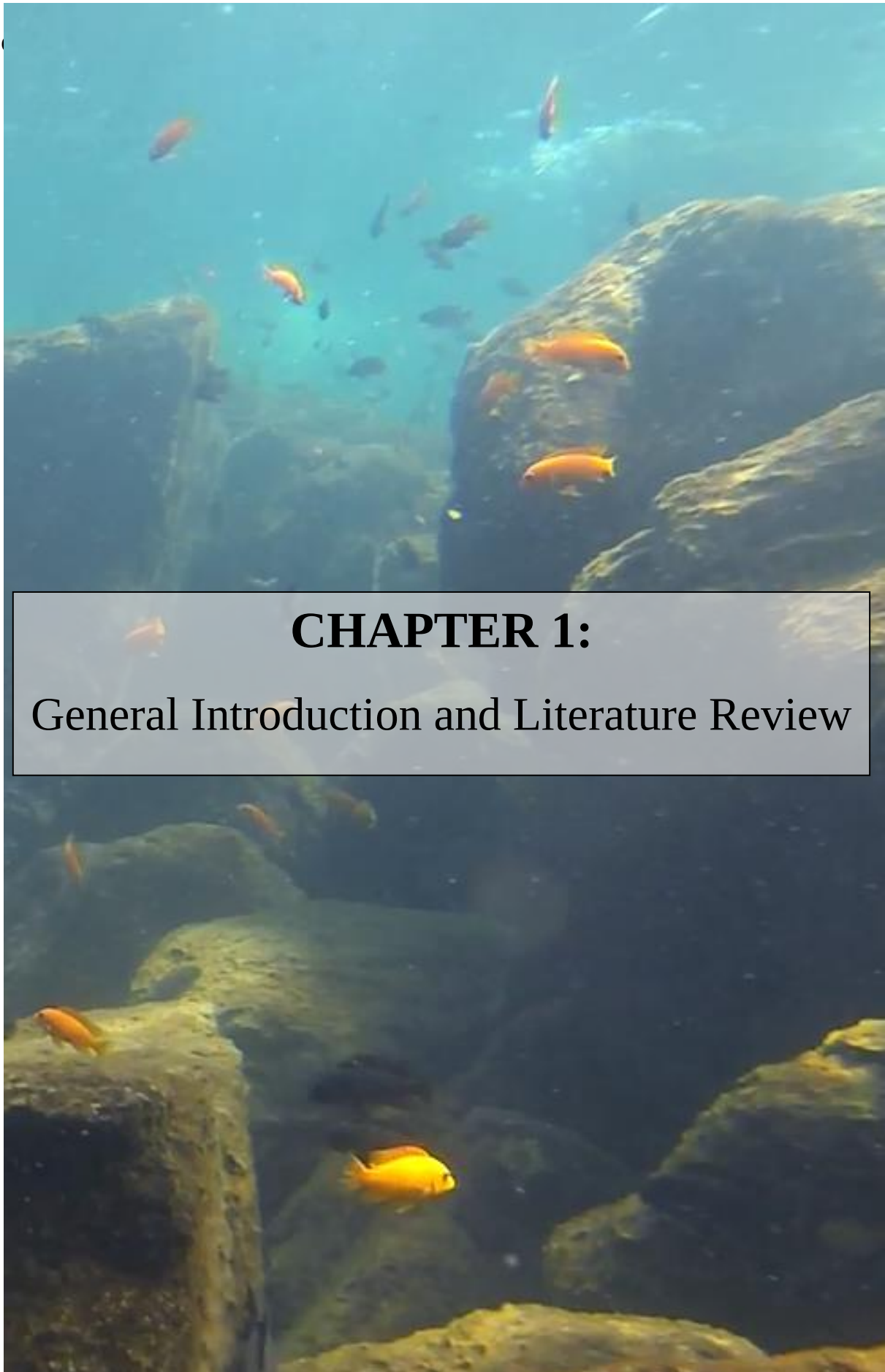
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CHAPTER 1:

General Introduction and Literature Review

The loss of biodiversity at an unprecedented rate is a global crisis that is accelerating both in scale and scope (Wood *et al.*, 2000). As a result of climate change and destructive human practices, biodiversity loss is a detrimental consequence for ecosystems which support and provide various services to human populations (Cardinale *et al.*, 2012; Proença *et al.*, 2017). This is particularly apparent in the case of freshwater ecosystems. Due to a combination of limited spatial extent and reliance on freshwater resources for biological necessity and other related services, freshwater ecosystems have become heavily altered and are therefore experiencing an exacerbated rate of biodiversity loss (Geist, 2011; Nobles and Zhang, 2011; Tickener *et al.*, 2020). Lake Malawi is no exception, with overfishing and habitat degradation driving collapses in local cichlid populations, (Palsson *et al.*, 2000; Banda *et al.*, 2005; Weyl *et al.*, 2010) the majority of which are endemic to the lake (Bootsma and Jorgensen, 2004).

1.1 Fish diversity and management in Lake Malawi/Niassa/Nyasa

Lake Malawi/Niassa/Nyasa is the most species rich lake in the world (Danley and Kocher, 2001). The lake is trans-boundary and is bordered by three countries, Malawi, Tanzania and Mozambique. It is particularly interesting due to the rapid speciation of fish fauna that has resulted in large assemblages of cichlid species with well over 400 species inhabiting the lake (Weyl *et al.*, 2010). The majority of these species exhibit local endemism to specific islands or rock structures in addition to being endemic to the lake itself, and thus hold high conservation value (Bootsma and Jorgensen, 2004). Furthermore, these fish are socio-economically valuable to the three countries bordering the lake as they provide food to local communities and draw in revenue through fishing, eco-tourism and via the aquarium trade (Sayer *et al.*, 2019). The lake is mainly surrounded by impoverished rural communities which are greatly dependent on the aquatic resources it provides, thus making it a critical area for conservation and management (Sayer *et al.*, 2019).

While there are some management strategies put in place on the lake, most are heavily focused on commercial fisheries and species with high monetary value which is not sufficient to preserve ecosystem integrity on the whole (Weyl, 2010). Other species which contribute to the overall functioning of the system are generally overlooked and as a result fish populations still show notable declines (Irvine *et al.*, 2019). In addition, due to Lake Malawi being a biodiversity hotspot, it is home to a large variety of species that are endemic to areas within the lake that hold value either ecologically or commercially in other sectors (Sayer *et al.*, 2019). This led to the suggestion that an ecosystem based management approach be adopted for Lake Malawi (Irvine *et al.*, 2019). In order to do this the IUCN assessed areas within the lake to be marked as Key Biodiversity Areas (KBA's). Key Biodiversity Areas are defined as sites which contribute significantly towards the global maintenance of biodiversity (IUCN, 2016). As Lake Malawi is already classified as a biodiversity hotspot, the establishment of KBAs within Lake Malawi was an efficient way to begin employing an ecosystem based approach to management on the lake (Sayer *et al.*, 2019).

1.2. Key Biodiversity Areas

Sites that qualify as KBAs meet at least one of the following criteria: they hold a significant number of threatened species or ecosystem types, they have a large proportion of species or ecosystem types that are geographically isolated, they are fully intact ecological communities that provide and sustain key services, they play important roles in biological processes such as provision of breeding grounds, ecological refugia and demographic aggregation or they are deemed highly irreplaceable through quantitative analysis (IUCN, 2016). Sites are delineated as KBAs in order to designate areas that are large enough to maintain ecological integrity and allow biodiversity to persist while also ensuring the practicality of efficient management (IUCN, 2016). In 2019, three sites with a combined area of 64.8km², namely Nkwichi,

Metangula and Minos Reef (Meluluco) became the first recognised KBA's on the Mozambican extent of Lake Malawi (Sayer *et al.*, 2019). This research project was conducted in one of these KBAs, Mino's Reef (Meluluco). Since the study site is located on the Mozambican extent of the lake, Lake Niassa will be used from this point on throughout the thesis as this is the official name given to the lake in Mozambique.

1.3. Using Baited Remote Underwater Video Systems to monitor remote freshwater populations

The countries bordering Lake Malawi are classified by the World Bank (2021) as low income (Malawi, Mozambique) and low to middle income (Tanzania) countries. This means that there are many rural, impoverished communities, and it is crucial to ensure that management practices can be employed with limited financial support (Sayer *et al.*, 2019). One of the challenges faced when developing effective management practices that promote the preservation of ecosystem integrity and maintenance of biodiversity in the lake is the implementation of a cost-effective, efficient monitoring plan within the KBA's (Sayer *et al.*, 2019). There are a number of surveying methods existing as a form of fauna monitoring on the lake that currently inform policy and are used to make management decisions. These include stock assessments performed on harvests from the trawl fisheries (Kanyerere *et al.*, 2018) as well as snorkel and scuba surveys for the observation of spawning behaviour and monitoring shallow living cichlid species (Ribbink *et al.*, 1983, Smith 2000). However, these techniques have been proven to be inefficient for long term monitoring because they are biased towards fishery species, subject to human error and do not occur frequently enough (Weyl *et al.*, 2010). Furthermore, the species composition in Lake Niassa is rapidly changing, and therefore adaptive management practices with consistent monitoring of species

composition will enable more efficient management of the lake as a resource (Weyl *et al.*, 2010).

The use of Baited Remote Underwater Video Systems (BRUVS) has proven to be both useful and cost-effective in marine environments (see Harvey *et al.*, 2013; Schobernd *et al.*, 2014; Walsh *et al.*, 2016; Roberts *et al.*, 2016; Harvey *et al.*, 2021). This method is non-extractive and relatively non-invasive and also negates the bias and human error associated with other monitoring methods currently used on the lake (Cappo *et al.*, 2006). In addition, BRUVS can be deployed at depths which cannot be accessed by SCUBA divers and sites can be sampled consecutively for as long as desired or required making it a highly efficient approach to monitoring (Watson *et al.*, 2007). It is also cost and time efficient in comparison to other methods such as SCUBA and snorkelling surveys (Harvey *et al.*, 2002b; Langlois *et al.*, 2010). A major limitation of the method is that only a relative estimate of density can be acquired since it is difficult to determine the exact size of the sampled area and there is a limit to the number of individuals that can be seen in frame, especially with regard to species that form dense schools (Willis *et al.*, 2000; van Looijengoed; 2014). In addition, the method is largely untested within freshwater systems, as shown in a literature study done by Whitmarsh *et al.* (2017) that indicated only 2% of studies included in the review were conducted in freshwater.

Nonetheless the method shows promise in its applicability and BRUVS have been successfully used in previous freshwater studies (see Ebner and Morgan 2013; Ebner *et al.*, 2015, Schmid *et al.*, 2017) as well as within Lake Niassa itself (Van Wyk, 2019). The BRUVS were used to monitor the Chambo complex, a group of species in the genus *Oreochromis* (mainly *Oreochromis lidole*, *Oreochromis karongae* and *Oreochromis*

squamipinnis) which contribute significantly towards Malawi's economy (Phiri *et al.*, 2013; Van Wyk, 2019). However, this research focused on large fisheries species and did not consider smaller fish species or other taxa such as the study species that were chosen for this particular research project, *Metriaclima estherae* (Red Zebra Cichlid) and *Potamonautes lirangensis* (Malawi Blue Crab).

1.4. Study species

1.4.1. *Metriaclima estherae*

Metriaclima estherae, previously known as *Pseudotropheus estherae*, sometimes referred to as *Maylandia estherae*, is a small cichlid species that is endemic to Lake Niassa (Konings, 1995; Konings, 2018). The species is part of the fish group known as the “Mbuna” which are a large group of haplochromine, rock dwelling cichlids, a large proportion of which are endemic to Lake Niassa (Turner, 1996; Genner and Turner, 2005). The Mbuna are a diverse group of fish species that hold a lot of significance to the scientific community as well the lake and its surrounding communities (Kanyumba *et al.*, 2011). These species vastly studied in terms of evolutionary biology due to their rapid speciation displaying evolutionary processes at appropriate scales for study (Genner and Turner, 2005). They also form a part of the lake's cultural identity and contribute to the classification of Lake Niassa as a World Heritage Site (Lake Malawi National Park, 2021). Furthermore, they are critical contributors to the income of surrounding countries through ecotourism and the aquarium trade. In the year 2019, export of live specimen, specifically in the group Mbuna, generated approximately 297 thousand US dollars (USD) (GoM, 2021). In 2021, this number decreased to around 138 thousand USD due to Covid-19 restrictions on export, but was still a significant contributor to

the Malawian economy (GoM, 2021). In addition, the sector is a major source of employment and showed a 7% increase in employment from 2019 to 2020 (GoM, 2021).

Metriaclima estherae, was chosen because of its distinct colouration as well as its commercial value in the aquarium trade and ecotourism. *Metriaclima estherae* is one of the most commonly kept freshwater ornamental species by hobbyists (Harrington, 2021; Sayer *et al.*, 2019) and attracts a large number of tourists who enjoy snorkelling and diving because of its bright appearance. The species is also most commonly captured within Mino's Reef (Meluluco), the study site chosen for this research project, as the most attractive colour morphs of this species are found in this area (Konings, 2001). Therefore, this is the area where the monitoring of this species is most critical. Mbuna species like *Metriaclima estherae* are known to have relatively small populations and overall low abundance which makes them vulnerable to rapid over-exploitation (Tweddle, 1992). Therefore, in order to prevent population crashes caused by this, monitoring of the species populations is necessary, especially within this area in which they are commonly harvested.

1.4.2. *Potamonautes lirrangensis*

Potamonautes lirrangensis is a widespread freshwater crab in Central Africa found in the upper Congo River basin and the African Rift Valley including Lake Niassa (Cumberlidge, 2018). It is a scavenge feeder and has a diet that is a combination of plant and animal food items (Weigand, 2014). The species is not endemic to the area but the subpopulation present in Lake Niassa is also known as the Malawi blue crab as it is the only known species of crab currently inhabiting the lake (Cumberlidge, 2018; Kochey *et al.*, 2019).

The species is most often caught for human consumption (Cumberlidge, 2018) and supports a small commercial fishery in Lake Niassa (Cumberlidge and Meyer, 2011; Cumberlidge, 2018;

Thiruvengadam, 2019). It is also collected for live trade and sold as an ornamental aquarium species (Dobson, 2004) and is sometimes sold under its pseudonym *Potamonautes orbitospinus* (Thiruvengadam, 2019). Furthermore, *Potamonautes lirrangensis* is also a critical prey species for other fish species caught by commercial fisheries in Lake Niassa (Cumberlidge and Meyer, 2011).

Dalu *et al.* (2017) showed that growing human populations have led to increased harvesting of freshwater crab species for human consumption in Zimbabwe. With populations on the shores of Lake Niassa also showing high growth rates (Jamu *et al.*, 2011), it is possible that *P. lirrangensis* could become a significant source of nutrition for the lake's communities. Furthermore, freshwater crabs play important roles in aquatic food webs and nutrient cycling (Cumberlidge *et al.*, 2009; Cumberlidge *et al.*, 2011; Daniels and Bayliss, 2012). This species was chosen in order to determine if BRUVS could be useful for monitoring non-vertebrate taxa in the lake.

The aim of this study was to determine whether BRUVS could be a viable tool for long term monitoring of smaller fish species and species belonging to different taxa in Lake Niassa. This was done by making use of BRUVS deployed in a number of different locales in Mino's reef, Lake Niassa, to extract population information on *Metriaclima estherae* and *Potamonautes lirrangensis*. In chapter 2 and 3, video footage collected from the BRUVS are used to determine the abundance of *M. estherae* and *P. lirrangensis* and see how their populations are influenced by habitat and depth. This will allow me to determine where these species are most commonly observed and what types of habitat they occupy. In Chapter 4, the BRUVS were used to determine the population structure of *M. estherae* as well as to

determine if there are differences in length ratios between sexes as well as between different habitat types and depth ranges.

1.5. Chapter summary

The thesis is made up of five research chapters. Following this chapter, which is a General Introduction and a Literature Review, Chapter 2, investigates the use of BRUVS to collect ecological data for the monitoring of a smaller, non-target fish species, *Metriaclima estherae*. This was done by recording the abundance of the species along sex, habitat and depth profiles in order to determine their population structure and where they are most commonly observed within the Meluluco reef system. Chapter 3 looked at using BRUVS to extract habitat use data for the crab species *Potamonautes lirrangensis* in order to see if they can successfully monitor large freshwater crustacea in the lake. The BRUVS were used to gather data about the habitat preferences of the species in order to determine areas of importance for the conservation of the species. Chapter 4 studies whether stereo-BRUVS can accurately determine the length distribution of smaller fish species in the lake by using *Metriaclima estherae* as a proxy. Finally, Chapter 5 provides a summary of findings and overall discussion which comments on whether BRUVS could be a viable management tool for the monitoring of smaller, non-fisheries associated species within Lake Niassa.



CHAPTER 2:

Assessing the abundance, habitat preferences and population structure of *Metriaclima estherae* in Lake Malawi/Niassa/Nyassas using Baited Remoted Underwater Video Systems (BRUVS)



INTRODUCTION

Lake Niassa is the most biodiverse lake in the world (Danley and Kocher, 2001) and has fascinated biologists due to the rapid speciation of fish fauna through adaptive radiation (Genner and Turner, 2005). Although the lake has been extensively studied in terms of evolutionary biology and biodiversity, there is a distinct lack of data on the lake in terms of resource use (Weyl *et al.*, 2010). Lake Niassa currently provides many ecosystem services to the people on its borders. Commercial and artisanal fisheries support the livelihood of over 1.6 million people and provide nutrition to surrounding communities of the three countries that border its shores (Banda *et al.*, 2005). Furthermore, live specimen collection for the international aquarium trade occurs in the lake as well as attracts ecotourists (Banda *et al.*, 2005). However, due to the high levels of poverty in the countries surrounding Lake Niassa, adequate management practices have yet to be implemented in order to ensure the long term sustainability of the lake as a resource (Weyl, 2010). The lake is already beginning to show declines in fish populations as a result of overfishing and inadequate fisheries management as well as effects of climate change and sedimentation or eutrophication due to poor agricultural practice (Munthali, 1997; Irvine *et al.*, 2019).

While there are some strategies put in place in the lake, these focus largely on species with high commercial value to industrial fisheries (Weyl, 2010) which may pose a problem for the maintenance of ecosystem integrity as a whole. Since the 90's there has been a shift in the economic development narrative to talking about concepts such as sustainability, maintenance of biodiversity and ecosystem integrity and natural resource management (Ferguson *et al.*, 1993). In order for natural resources to be able to continue providing for the human population, it is critical that they remain in a healthy, functioning state.

The sustainable management of Lake Niassa is critical to ensure that it will be able to continue providing for the people on its borders. In order for this to be successful,

management needs to take an ecosystem based approach (Irvine *et al.*, 2019). This is particularly difficult in the cases of transboundary lakes since compliance from all countries bordering the lake is required to ensure the adequate management of the lake as a whole (Servos *et al.*, 2013). In addition, when countries are developing, they do not necessarily have the financial capital to invest in management processes (Sayer *et al.*, 2019) as is the case with those surrounding Lake Niassa. In order for any management strategy to be effective, it would require consistent monitoring of exploited species populations to ensure that declines can be mitigated swiftly before causing any major knock on effects.

In an attempt to create management plans that promote the maintenance of ecosystem integrity, the IUCN designated 22 river, lake and wetland sites in and around the vicinity of Lake Niassa as Key Biodiversity Areas (Sayer *et al.*, 2019). A Key Biodiversity Area (KBA), as described in Chapter 1, is defined as a site that contributes significantly towards supporting biodiversity while being small enough to manage efficiently (IUCN, 2016). However, this does not necessarily combat the issue without the necessary consistent monitoring program. Monitoring methods that have been used in the past have involved stock assessments from fishery harvests (Kanyerere *et al.*, 2018) as well as snorkel and scuba surveys (Ribbink *et al.*, 1983, Smith 2000). Although these methods currently inform management decisions, they are inherently biased towards fishery species and are inadequate for long term monitoring (Weyl *et al.*, 2010).

The haplochromine Mbuna (Family Cichlidae; Tribe Haplochromini) of Lake Niassa dominate the rocky shores and is one of the most diverse fish groups in the world (Genner and Turner, 2005). The lake contains approximately 800 species of which the majority are haplochromines and only a small fraction of these species are not endemic to the lake (Turner, 1996). The Mbuna are some of the most studied cichlids from the African Great Lakes because they are a good example of rapid speciation and as a result display evolutionary

processes at an appropriate temporal scale for study (Genner and Turner, 2005). Although there has been an extensive amount of work done on their life history strategies, ecology and behaviour, there is a knowledge gap when it comes to their use as a resource and the faring of their populations under the stress of anthropogenic pressure. Although the Mbuna have little nutritional potential, live specimens are collected for the ornamental aquarium trade (Banda *et al.*, 2005). Furthermore, the group of fishes form an integral part of the Lake's identity and are part of the reason that Lake Niassa is considered a World Heritage Site (Lake Malawi National Park, 2021)

The Mbuna are relatively unexploited in terms of food resources (Munthali, 1997) but the species belonging to the group have relatively small populations and an overall low abundance, leaving them vulnerable to rapid overexploitation (Tweddle, 1992). In addition, with popular fishery species of Lake Niassa already in decline (Banda, 2005) studies by Munthali (1997) and Greenberg *et al* (2016) confirm that fishers would resort to exploiting ornamental fish species to retain their livelihoods. Without proper monitoring, these species could quickly succumb to the threats of overexploitation and due to high rates of endemism, this could have severe impacts on both the aquarium trade and the overall biodiversity of the lake (Tweddle, 1992). Mbuna species have already begun to show declines in species richness (Kanyumba *et al.*, 2012) and the lake is losing species quicker than new species are being observed (Kanyumba *et al.*, 2011).

In an attempt to combat the survey bias towards species that are harvested by fisheries, we propose Baited Remote Underwater Video Systems (BRUVS) as a viable alternative for Mbuna monitoring surveys. Baited Remote Underwater Video Systems have already proved to be both useful and cost effective in the marine environment (see Harvey *et al.*, 2013; Schobernd *et al.*, 2014; Walsh *et al.*, 2016; Roberts *et al.*, 2016; Harvey *et al.*, 2021). The method negates the bias associated with surveys done on fisheries harvests and is also both

non extractive and non-invasive as well as provides a closer look at species, decreasing the risk of human error which is high with methods such as scuba and snorkel surveys.

In order to see if this method will be useful for the smaller species in Lake Niassa, we need to determine whether the method can be used to extract ecological data for species that are not harvested by fisheries for the intent of consumption. Therefore the aim of this study was to use BRUVS to extract ecological data for a small haplochromine Mbuna species, *Metriaclima estherae*, in order to determine whether the BRUVS can be used to efficiently monitor smaller fish species in the lake. The study was conducted in the Meluluco area of the lake, which was designated as a Key Biodiversity Area in 2019, one of the first delineated on the Mozambique extent of the lake. Video footage collected between the years 2016 to 2018 was used to assess the abundance of this species primarily collected for sale in the aquarium trade. The extracted data was also used to assess the associated habitat preferences of the species by identifying the habitat variables in the areas in which *Metriaclima estherae* were most commonly observed.

METHODS AND MATERIALS

Study area

The study area for the research project was Lake Niassa, which has a surface area of 29 500km (ILEC, 2005) and a maximum depth of 700m (Bootsma and Jorgensen, 2004). The lake is bordered by three low to low-middle income countries, Malawi (low), Tanzania (low-middle) and Mozambique (low) (World Bank, 2021), all of which rely heavily on the lake for both social and economic purposes (Chafota, 2005). The lake is home to more than a thousand faunal species and is a biodiversity hotspot particularly well known for its vast array of cichlids (Chidammodzi and Muhandiki, 2015).

The lake is meromictic with an oxic-anoxic thermocline at around 250m in depth (Eccles, 1974). The Mozambican extent of the lake experiences a fixed rainy season between the months of November and April and a dry season between May and October (Halafo *et al.*, 2004). The surface water temperatures of the areas of lake encompassed by the Lake Niassa Reserve are relatively warm, ranging between 24 to 29°C with slightly alkaline pH ranging between 7.7 and 8.7 (Eccles, 1974). The available habitat along the Mozambican shoreline can be categorised into three dominant types, Vegetated Banks, Rocky Banks and Sandy Beaches (Halafo *et al.*, 2004).

The study itself was conducted in a small reef system approximately 7 km offshore of the Mozambican extent of the Lake and forms part of the Miluluka reef system (Konings, 1995). It consists of a series of rocky ridges separated by sandy tracts submerged between 5 to 7 meters below the surface of the lake (Konings, 2001). The reef is part of the Lake Niassa Reserve which was delineated by the WWF in 2011 spanning 478 km² and extending 4.83 km off the Mozambican shoreline (van Wyk *et al.*, 2018). It is important to note that while there is a lot of data on the resource use of the Malawian sectors of the lake, since it makes up the majority of the lakes borders, there is a data deficiency on the Mozambican extents where the Lake Niassa Reserve is located (van Wyk, 2019).

Meluluco was chosen because it was one of the areas chosen by the IUCN to be recognised as a Key Biodiversity Area in 2019, one of the first to be designated in Mozambique (Sayer *et al.*, 2019). Of particular interest was a shallow reef that occurs at approximately 7m depth within the Meluluco system, known as Mino's reef (Konings, 1995). This is where females of the study species, *Metriaclima estherae*, have the deepest orange colouration and are sought after for sale in the aquarium trade (Konings, 1995). Figure 2.1 indicates the 329 sites sampled as a part of the study in the Meluluco Reef System, Lake Niassa, Mozambique.

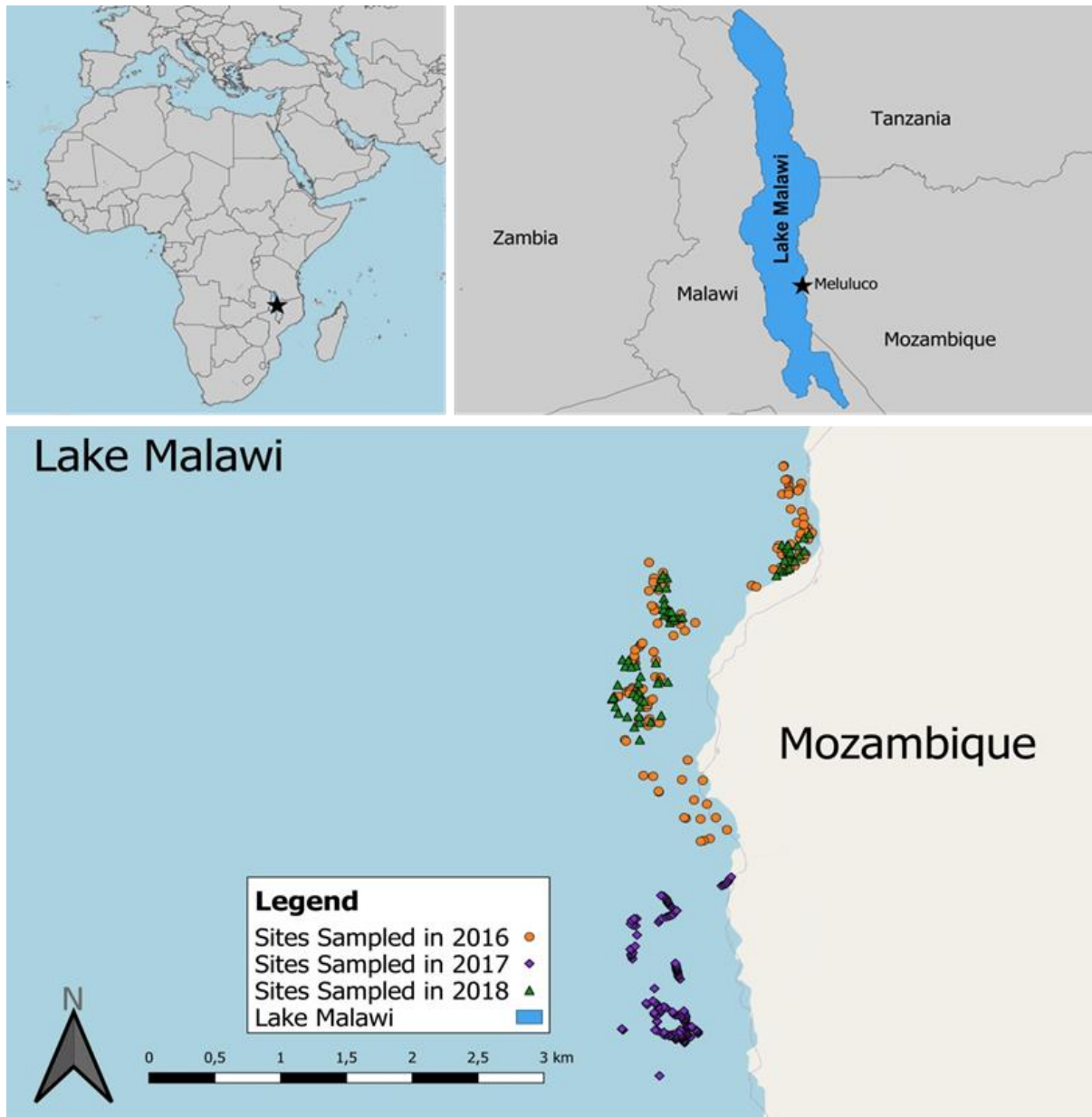


Figure 2. 1: The 329 sites sampled with the BRUVS in the Meluluco reef system, Lake Niassa, Mozambique, between 2016 and 2018 during the months of September October and November. Of these 329 sites sampled in total, the 68 sites that were sampled in the year 2018 made use of stereo-BRUVS.

Study species

Metriaclima estherae is laterally flattened with a terminal broad mouth (Konings 1995). The species is sexually dimorphic with females exhibiting a bright orange or yellow colouration with no bars on the body (Nyalungu and Couldrige, 2020). The males are blue with vertical bars on the body and yellow spots on the soft of the anal fin (Konings, 2001; Nyalungu and Couldrige, 2020) (Figure 2.2). Males are generally larger than females growing up to approximately 13cm (130mm) in total length and females growing to approximately 10cm (100mm) in total length (Konings, 1995). They occur in sediment free, rocky areas and feed on algae growing on these rocks (Konings, 2018). They are polygamous and males are territorial, defending areas approximately 1m in diameter (Konings, 2018). The most recent assessment by the IUCN categorises the species in Least Concern (Konings, 2018) but two prior assessments have assessed the species as Vulnerable (Kasembe, 2006; Kasembe, 2017), suggesting that proper management is critical to keep the population stable. For more information on *Metriaclima estherae* please refer to Chapter 1.

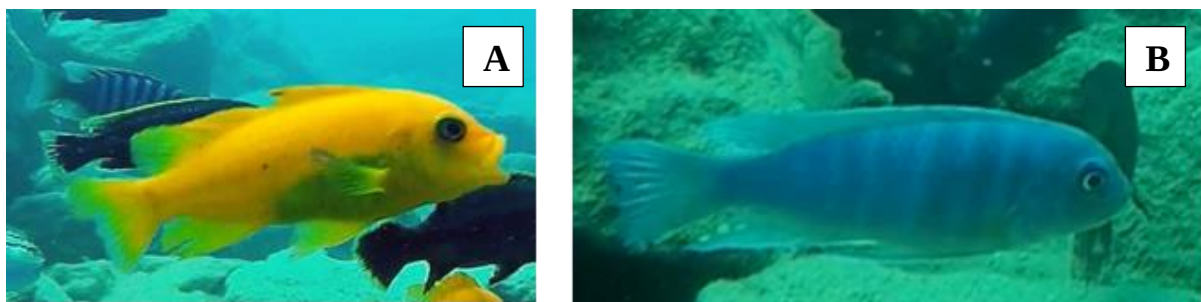


Figure 2. 2: *Metriaclima estherae* laterally flattened with a broad terminal mouth. A indicated the female of the species with its bright yellow colouration. B indicates the male, light blue with grey vertical bars and yellow egg spots on the anal fin. Images were taken as screenshots from the recorded video footage.

Experimental design and protocol

Deploying the Baited Remote Underwater Video System

The video footage analysed for this study made use of pre-collected data from van Wyk *et al.* (2018). The BRUVS were deployed at 329 sites in the Meluluco area over 3 years, (2016-2018), between the months of September and November. These sites varied in depth, substrate and vegetation and accounted for the three habitat classes identified by Eccles (1974). The sites were chosen by van Wyk *et al.* (2018) using a stratified random sampling design in order to ensure that a full range of available habitat was sampled.

Sampling that took place during the years 2016 and 2017 made use of 10 mono-Baited Remote Underwater Video Systems (mono-BRUVS) where a GoPro Hero 3 camera was mounted on a tripod made from a plastic base plate with steel legs. A PVC perforated bait container containing 100 g of crushed Usipa (*Engraulicypris sardella*), which is a readily available, abundant fish species native to Lake Niassa, was attached to the tripod with two steel arms, ensuring it was in view of the camera (Figure 2.3). Usipa (*Engraulicypris sardella*) was used in this study because it reanalysed video footage collected by van Wyk *et al.* (2018) and the species is a common type of bait used by commercial fisheries to catch the fish species which that study focused on.

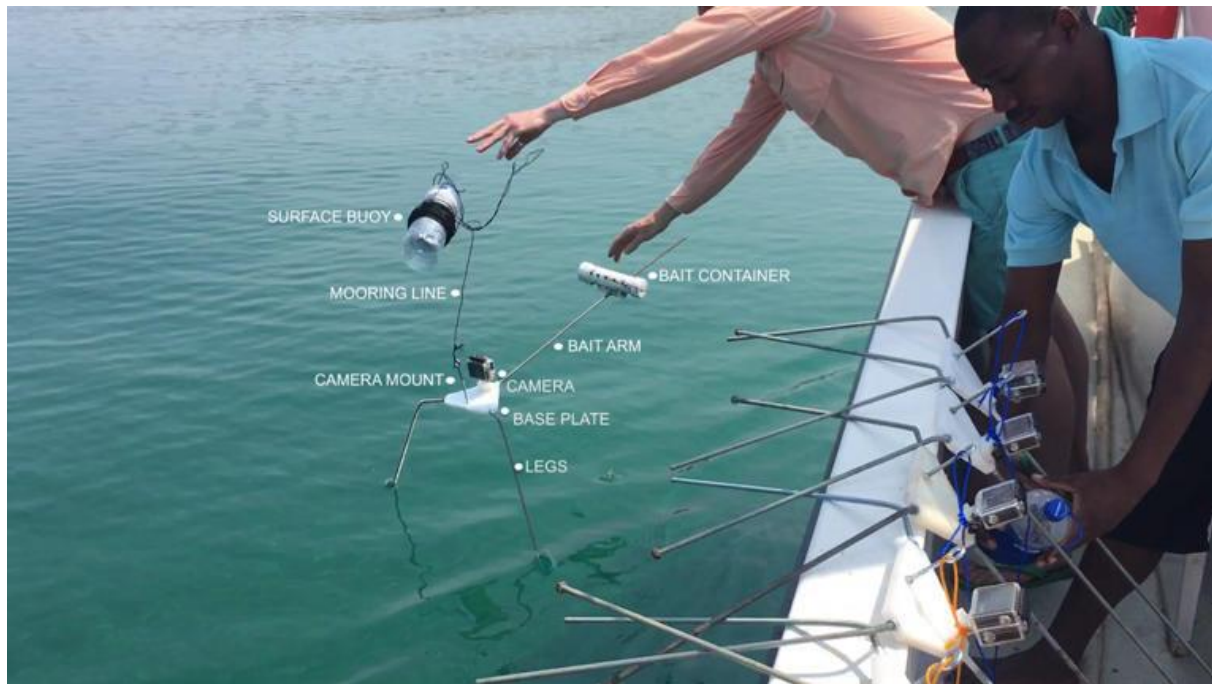


Figure 2. 3: Photograph of the mono-BRUVS used to sample sites in 2016 and 2017 with annotations (from van Wyk, 2019)

Sampling in the year 2018 made use of stereo-Baited Remote Underwater Video Systems (stereo-BRUVS), made up of a steel frame with two GoPro Hero 5 action cameras encased in aluminium housing. The perforated PVC bait container containing 100g crushed Usipa, was attached to a 1m bait arm to ensure it was in the field of view of the cameras. The cameras were mounted on either side of the steel frame, approximately 0.7m apart and facing inwards at an angle of 8° to allow for an overlapping field of view (Figure 2.4).



Figure 2. 4: Photograph of the stereo-BRUVS used to sample the sites in 2018 with annotations (from van Wyk, 2019)

Sampling protocol

The BRUVS were deployed at various localities at least 50 m apart at various depths, within the Meluluco area, ensuring that all available habitat types were accounted for through the sampling approach used by van Wyk *et al.* (2018). Each system was left to record for a minimum of 15 minutes beginning when the BRUV touched the lake floor (see sampling approach by van Wyk *et al.* 2018).

Video analysis

Video footage was analysed using EventMeasure (SeaGIS Pty. Ltd). The period creator function was used to create a standard watching period of 15 minutes to ensure that the video sample was observed within a standardised time frame unless the BRUV was flipped or obstructed in which case the video was analysed for as long as possible. Habitat variables

were determined as a proportion of the lake bed in field of view (Figure 2.5-2.8). These variables were Rock, Cobble, Sand, and Vegetation as described by Eccles (1974). The estimated abundance of *M. estherae* was recorded as a MaxN value by sex. The MaxN is the highest number of individuals per species, or in this specific case per sex, captured in a single frame of the video sample (Ellis and DeMartini, 1995). This is a conservative approach to ensure that the abundance is not inflated by counting the same individual multiple times (Ellis and DeMartini; 1995).



Figure 2. 5: Photograph of a site dominated by rocky habitat in the Meluluco Reef System, Lake Niassa, Mozambique, 2016-2018. Images were taken as screenshots from the recorded video footage.



Figure 2. 6: Photograph of a site dominated by cobble in the Meluluco Reef System, Lake Niassa, Mozambique, 2016-2018. Images were taken as screenshots from the recorded video footage.

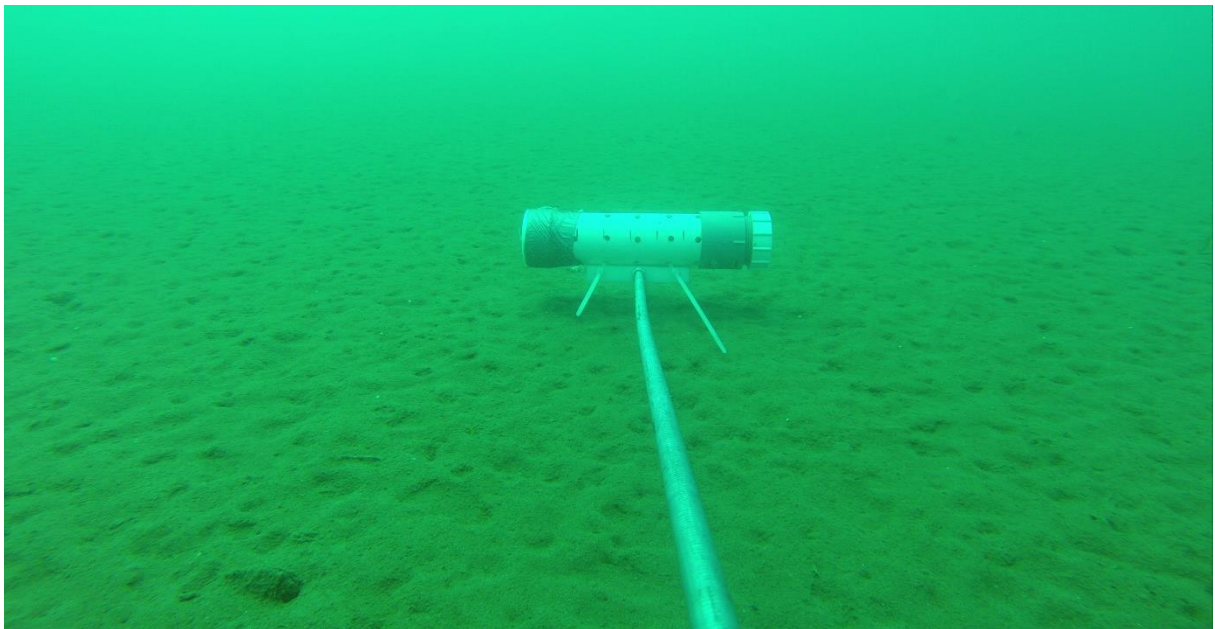


Figure 2. 7: Photograph of sand dominated habitat in the Meluluco Reef System, Lake Niassa, Mozambique, 2016-2018. Images were taken as screenshots from the recorded video footage.



Figure 2. 8: Photograph of vegetation dominated habitat in the Meluluco Reef System, Lake Niassa, Mozambique 2016-2018. Images were taken as screenshots from the recorded video footage.

Data analyses

CANOCO version 4.5 was used to conduct a Principal Component Analysis (PCA) to see which habitat variables were associated with the presence or absence of *M. estherae*. The PCA analysis compared habitat associations among sites characterised by male presence, female presence, both present and both absent. All data was tested for normality before choosing between a parametric test and its non-parametric equivalent.

R Studio version 1.4.1717 (R Development Core Team, 2021) was used to conduct a Chi-squared test of association between the habitat categories and the percentage abundance of sites with female presence, male presence, both present and both absent. This was to detect trends in the distribution of *Metriaclima estherae* across the different habitat classes.

In order to determine the relationship between *M. estherae* and depth by sex, Kruskal-Wallis tests were conducted to compare change in male and female abundance (using MaxN counts) across depth classes in increments of 10 ranging from 1 to 70 m deep. Furthermore, a chi-squared test was conducted to determine whether habitat was changing in relation to depth and a Kruskal-Wallis test was conducted on overall availability of habitat in order to determine which types occurred more frequently than others.

Finally, R Studio was used to fit binomial Generalised Linear Models (GLMs) to display the effect of major habitat drivers on male populations, female populations and the total population of *Metriaclima estherae* overall. The presence or absence data was incorporated as a categorical factor in order to compare the influence habitat variables had on the occurrence of *M. estherae* by sex.

RESULTS

The PCA (Figure 2.9) shows that the sites that have both male and female *Metriaclima estherae* present are correlated with high proportional abundance of rock or cobble. In comparison, the sites where no individuals are present are strongly associated with sand and vegetation. Sites that had females only showed a strong positive association with rock and a strong negative association with sand while sites that had males only showed less of a correlation to specific habitat and were more dispersed, only really being excluded by vegetation. While females seem to be excluded by all sand, males seem to associate with other substrates (Sand and Cobble). There is also a negative association with depth for *M. estherae* in general (Figure 2.9).

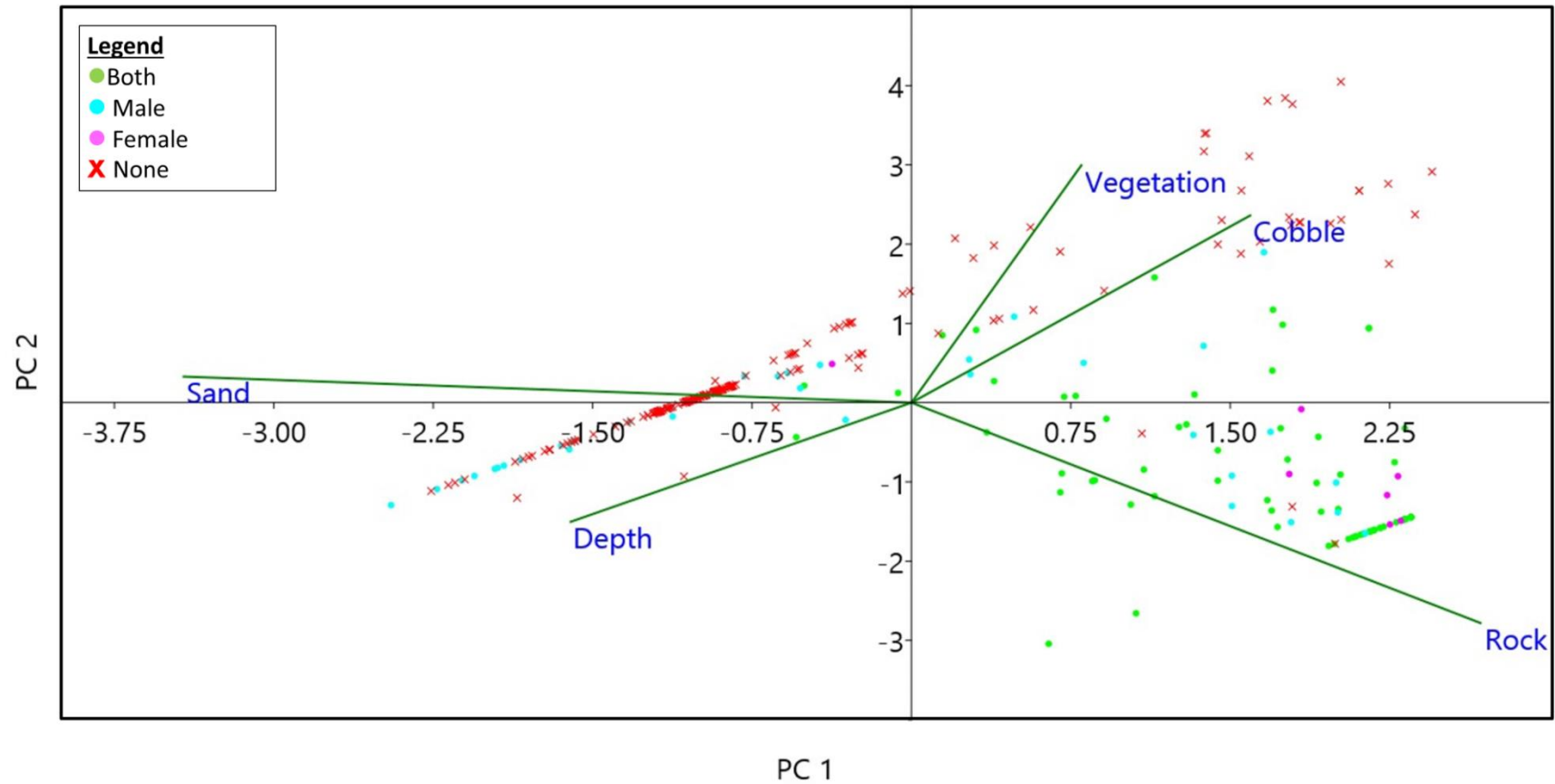


Figure 2. 9: Correlations between *Metriaclima estherae* population structure and habitat variables. PCA illustrates the association of habitat variables to sites which contained male only present, female only present, both male and female presence and all absent. Longer vectors indicate stronger influence on population structure.

Metriaclima estherae abundance significantly differed between habitat variables ($p < 0.01$, $\chi^2 = 206.88$, $df = 9$). Figure 2.10 shows that sandier habitats had the greatest percentage of sites where *M. estherae* was entirely absent, whereas rockier habitats showed the greatest percentage of sites with both males and females present. Males were more commonly found across all four habitat classes, whereas females show a clear preference for rocky habitat.

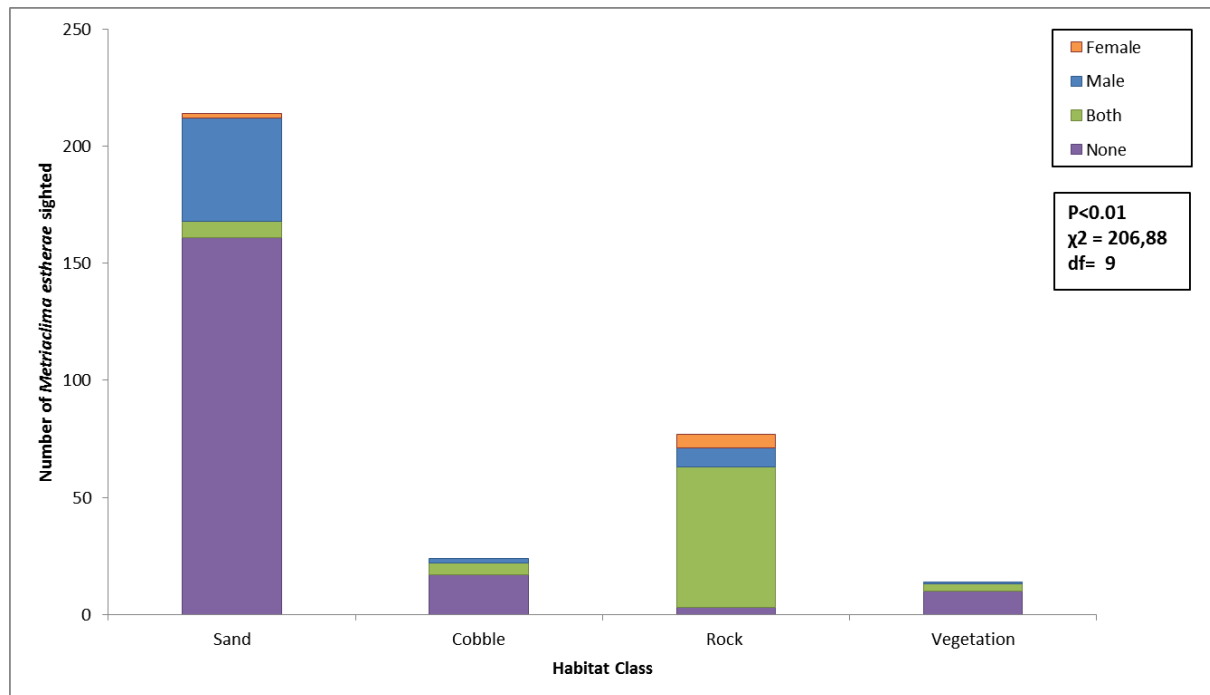


Figure 2. 10: *Metriaclima estherae* population structure in relation to the four major habitat variables in the Meluluco reef system, Lake Niassa, 2016-2018

Cobble and vegetation do not appear to affect *M. estherae* as significantly as the other two habitat variables. However, looking at the dataset as whole, these variables appear to be far less available than the other two habitat types. In order to test this, a Kruskal-Wallis test was conducted on the overall availability of habitat, independent of fish occupancy which showed that there was a statistically significant difference between the frequency of habitat occurrence (Kruskal-Wallis chi-squared = 102.19, $df = 3$, $p < 0.01$). A post hoc Kruskal-Wallis Multiple Comparisons Test revealed that rock and sand had occurred significantly

more often than cobble and vegetation but the occurrence of cobble and vegetation were not significantly different from each other (Table 2.1). This suggests that removing them from the analysis might depict a stronger result.

Table 2. 1: Kruskal-Wallis post-hoc comparison between the frequencies of occurrence of different habitat variables independent of fish occupancy. Results that show significant statistical differences are indicated with an “*”

	Observed Difference	Critical Difference	p-Value
Rock-Cobble	133.33	78.17	p<0.05 *
Rock-Sand	202.49	78.17	p<0.05 *
Rock-Vegetation	285.74	78.17	p<0.05 *
Cobble-Sand	69.16	78.17	p<0.05 *
Cobble-Vegetation	152.41	78.17	p>0.05
Sand-Vegetation	83.25	78.17	p<0.05 *

Therefore, in order to show a clearer picture of how substrate was affecting the distribution of *M. estherae*, the two main habitat drivers were plotted against *M. estherae* abundance (Figure 2.11). This clearly shows that *Metriaclima estherae* show preference for rockier habitats ($p<0.01$, $\chi^2=163.74$, $df=3$) (Figure 2.11). Males and females are more likely to appear together in rockier habitats. Sandier habitats are also more likely to have no individuals present at all. However, male *M. estherae* are more likely to appear alone in sandier habitats in comparison to rockier habitats, whereas females are rarely found in sandier habitats at all. It can also be noted that female abundance is much lower in comparison to male abundance.

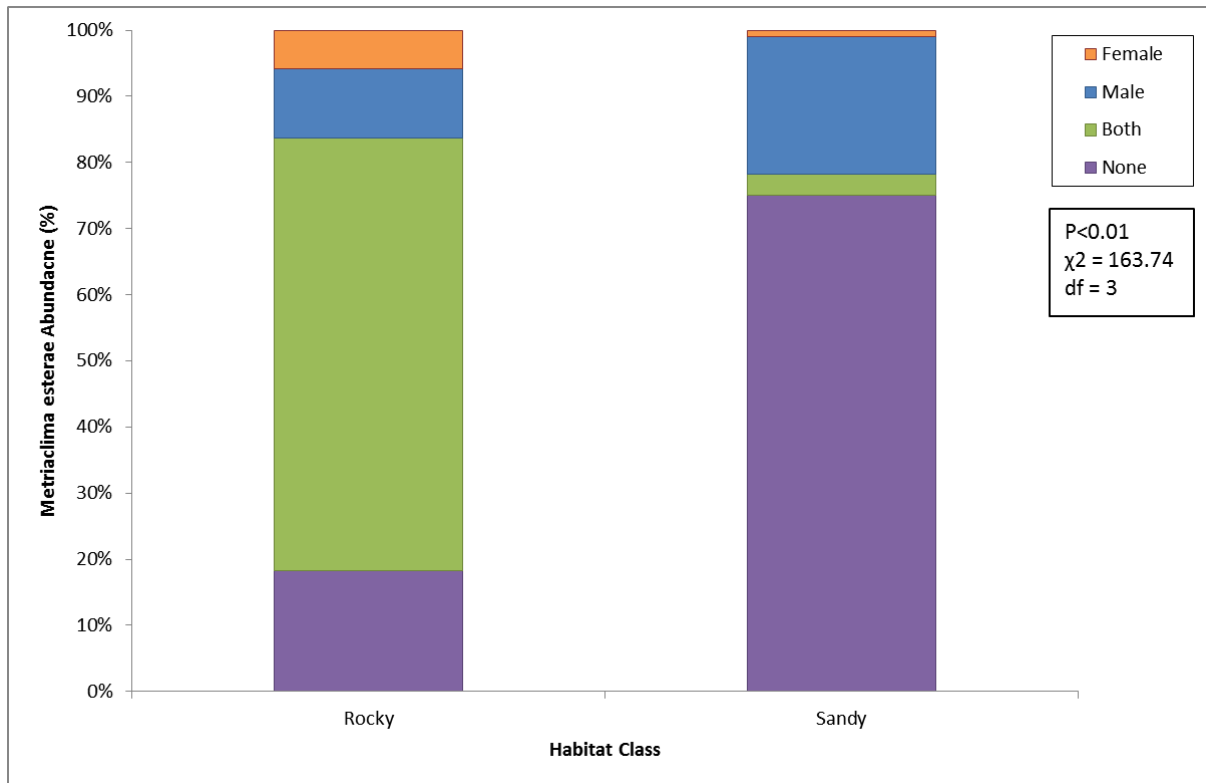


Figure 2. 11: *Metriaclima estherae* population structure in relation to the two major substrate variables in the Meluluco Reef System, Lake Niassa, Mozambique.

When looking at the associations with depth, *Metriaclima estherae* females were mostly observed in shallow sites (Figure 2.12). In comparison, *M. estherae* males were more abundant in the shallower sites but were found across all depth classes sampled (Figure 2.13). In order to determine whether available habitat could have an influence on this, habitat distribution across depth classes was plotted and revealed that rockier habitat was more common in the shallow sites whereas sandier habitat was common across all depth classes (Figure 2.14). Both males and females were recorded at deeper sites, males more commonly observed than females, but both were recorded in the depth classes between 41 to 50 meters and 61 to 70 meters deep in which rocky habitat was found.

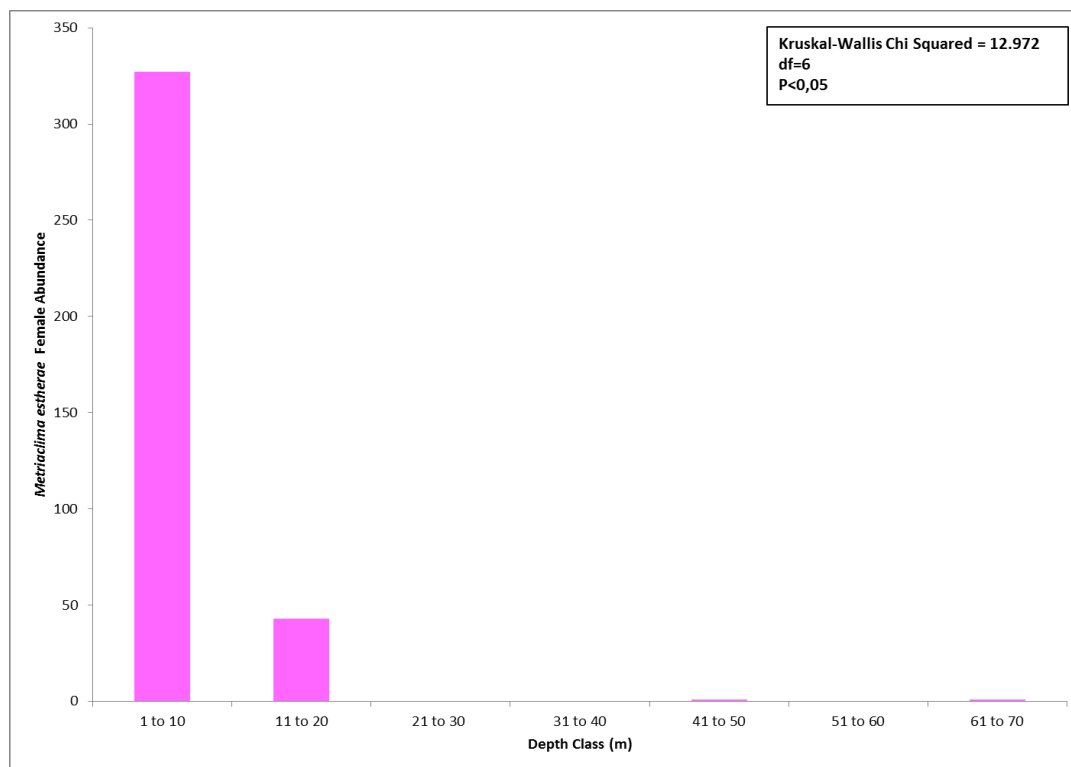


Figure 2. 12: *Metriaclima estherae* female distribution along depth classes in the Meluluco Reef System, Lake Niassa, Mozambique.

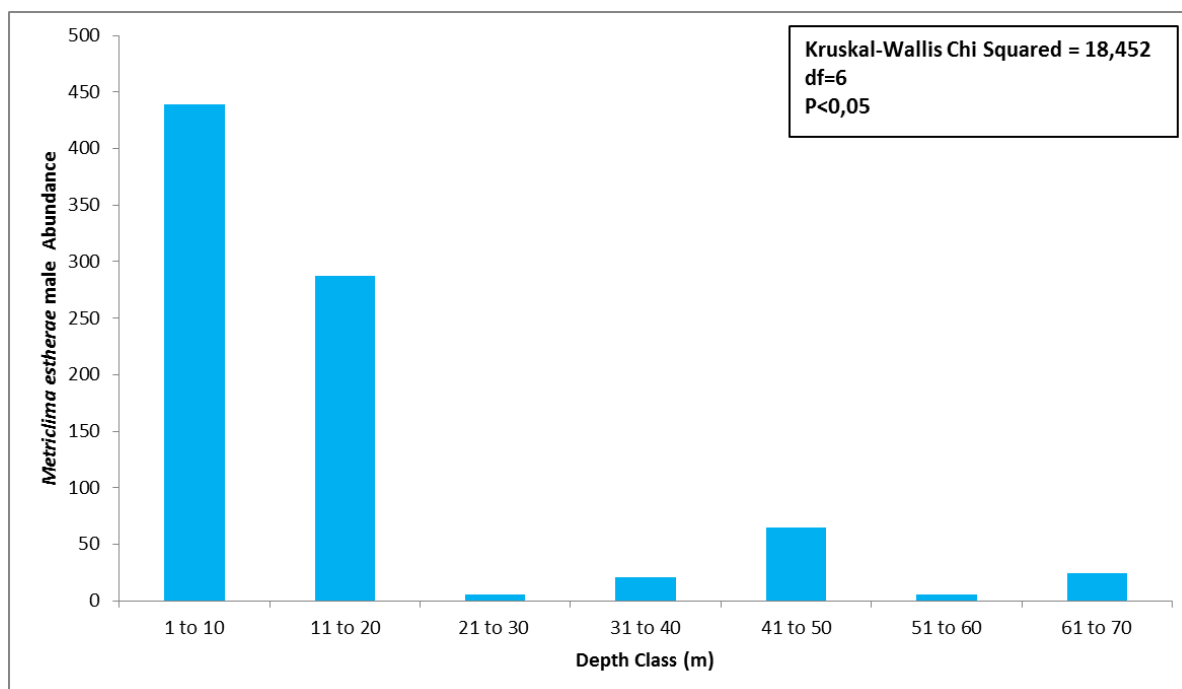


Figure 2. 13: *Metriaclima estherae* Male distribution along depth classes in the Meluluco Reef System, Lake Niassa, Mozambique.

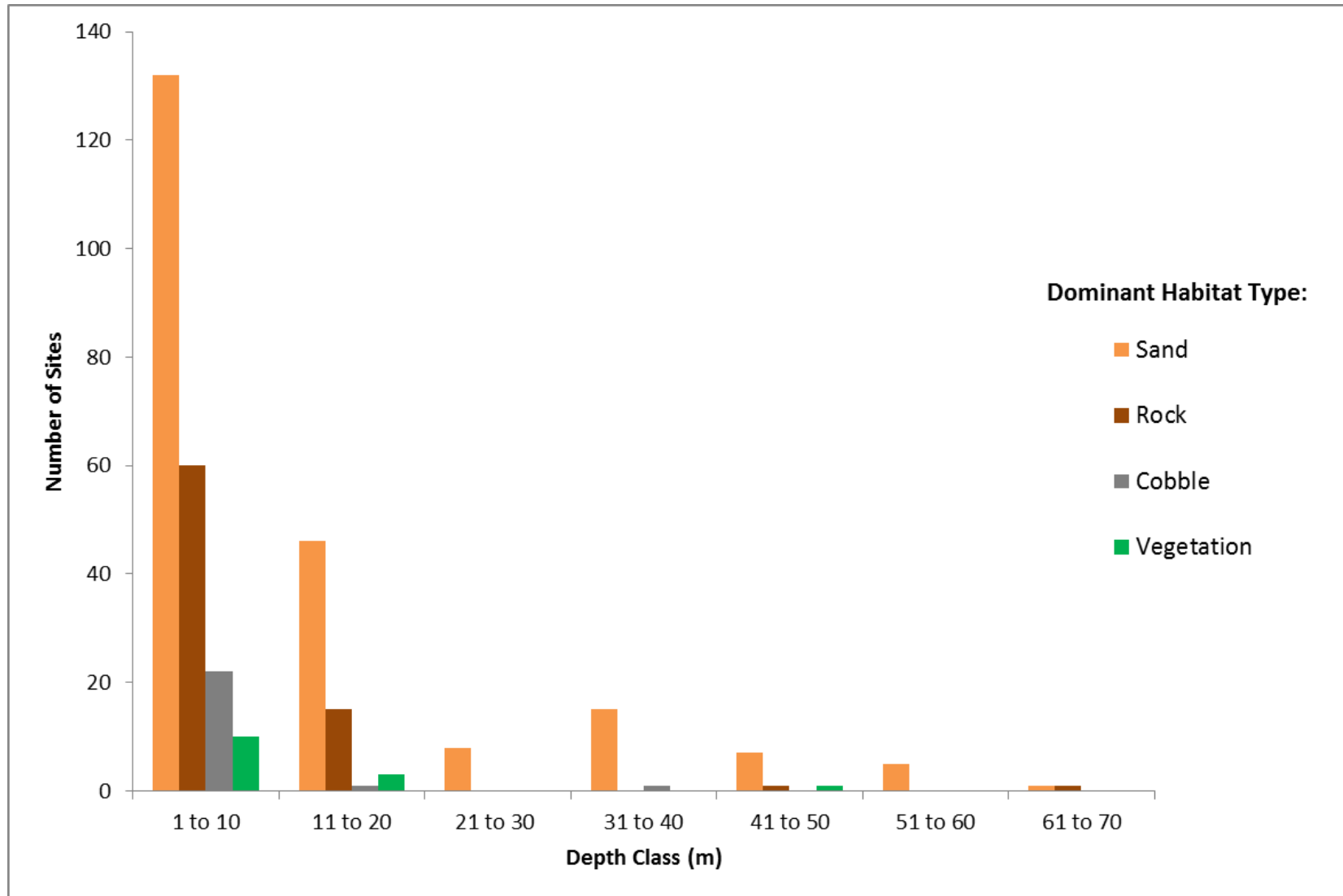


Figure 2. 14: Habitat frequency distribution along depth classes in the Meluluco Reef System, Lake Niassa, Mozambique.

The binomial GLM of *Metriaclima estherae* in Meluluco, Mozambique (Figure 2.15) indicates that Rock was the major explanatory variable for the variance observed in the *M. estherae* abundance data. There was also a significant interaction between sand and rock (SE = 0.51683, Z value= 3.984, $p < 0.001$), indicating that the *M. estherae* population can exist in the sandy reefs and are not entirely excluded by sand. Depth and sand on their own did not come out as significantly influencing the *M. estherae* population.

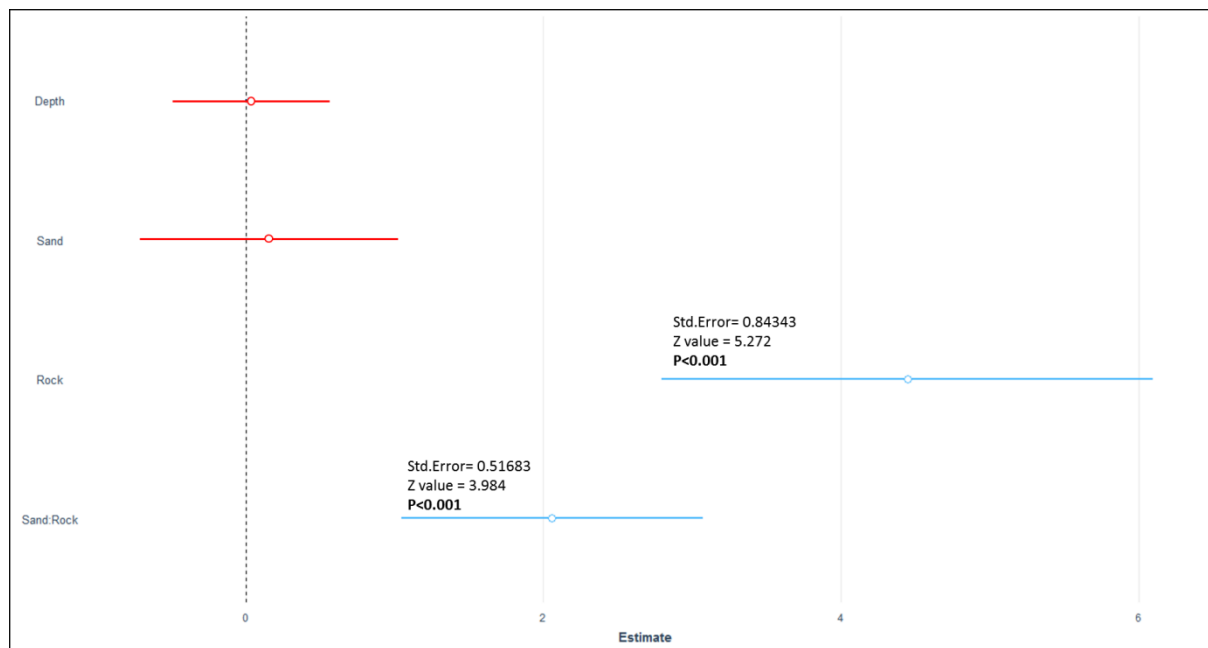


Figure 2. 15: Binomial general linear model coefficient plot for Total *Metriaclima estherae* abundance in Meluluco. Includes plotted Estimate points, Standard Error, z-value and $\Pr(>|z|)$. Blue lines indicate factors which significantly affect the abundance model ($P < 0.05$). Red lines indicate factors that do not ($P > 0.05$).

The GLM for *Metriaclima estherae* females (Figure 2.16) shows a strong negative association to sand and a strong positive association to rock with no significant interactions between the two. Depth also does not appear to significantly account for the variation in *M. estherae* female abundance.

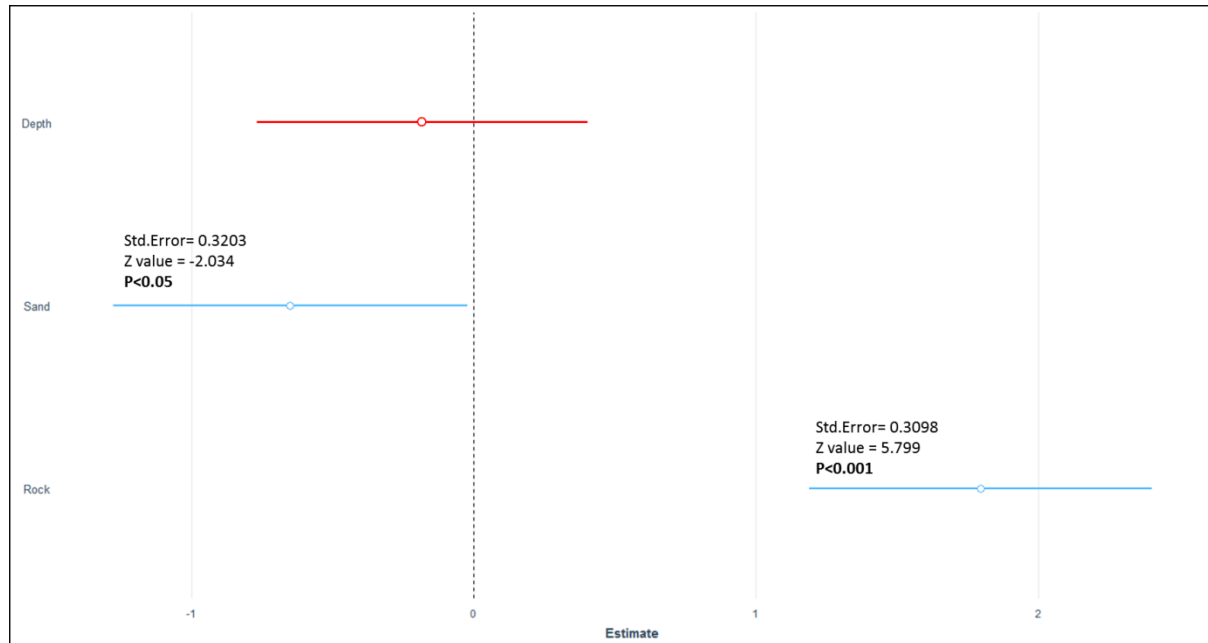


Figure 2. 16: Binomial general linear model coefficient plot for Female *Metriaclima estherae* abundance in Meluluco. Includes plotted Estimate points, Standard Error, z-value and $\Pr(>|z|)$. Blue lines indicate factors which significantly affect the abundance model ($P < 0.05$). Red lines indicate factors that do not ($P > 0.05$).

The GLM for *Metriaclima estherae* males (Figure 2.17) shows all three factors, depth, sand and rock to be positively associated with male abundance, with rock being more of an influencing factor than the other two. Again, there is an interaction between rock and sand that more significantly accounts for *M. estherae* male abundance, suggesting that males may show a preference for sandy reefs.

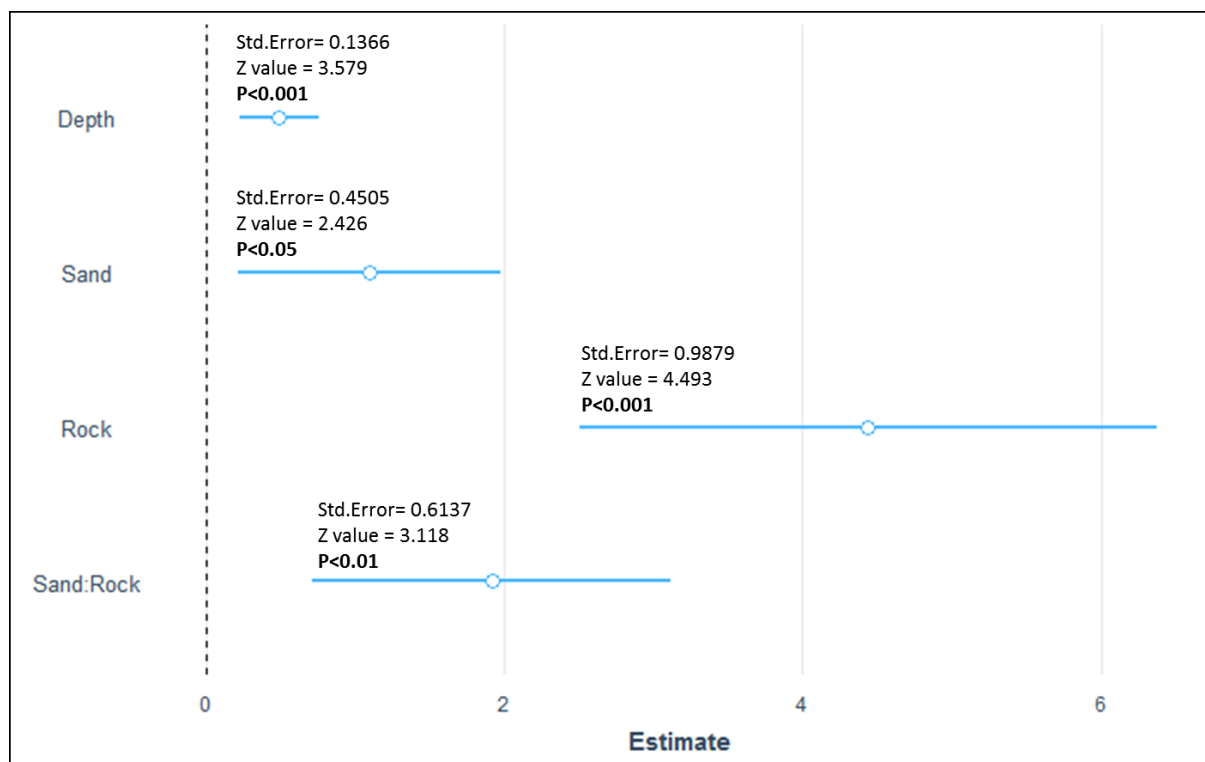


Figure 2. 17: Binomial general linear model coefficient plot for Male *Metriaclima estherae* abundance in Meluluco. Includes plotted Estimate points, Standard Error, z-value and $\Pr(>|z|)$. Blue lines indicate factors which significantly affect the abundance model ($P<0.05$). Red lines indicate factors that do not ($P>0.05$).

DISCUSSION

The results of the study indicate that the local population of *Metriaclima estherae* is most prominently influenced by substrate. They were shown to be most common around rocky reef habitat which is typical of most Mbuna species (Ribbink, 1983; Konings 2001). This is typical for rock dwelling Mbuna as individuals of the group of species are generally brightly coloured, even when exhibiting sexual dimorphism (Genner and Turner, 2005) and this makes them conspicuous to predators, meaning that they likely need the refugia provided by rocky habitat as hiding spaces (Ribbink, 1983). Also, the primary diet of *M. estherae* consists of algae that grow on the surfaces of rocks (Konings, 2018).

An interesting finding that arose from the data is that male and female individuals of the species show a clear difference in their habitat preferences. While female *M. estherae* show a highly negative correlation with sand, males of the species almost seem to benefit from the presence of other substrates, particularly sand. This is uncommon as much of the prior research on the species states that *M. estherae* are excluded in sandy habitat (Ribbink, 1983; Tweddle, 1992; Munthali, 1997; Konings, 1995; Konings 2001). However, *M. estherae* being a sexually dimorphic species in which males exhibit territoriality (Konings, 2018), it is actually more likely that females and males exhibit different tolerances to habitat variables.

Females of the species in the area exhibit a bright yellow colour that is conspicuous.

Furthermore, rocky habitat is far more common in the shallower reaches of the lake in comparison to the deep reaches. This means that against sandy substrate, female individuals would be far more conspicuous and much more at risk to predation by larger fish species and birds, in the shallower areas, than their male counterparts. Therefore, females of the species might be more reliant on the rocky substrate in order to avoid predation. In comparison, males with their light blue colouration and barring are more likely to blend in against the sandy substrate (Hendrik *et al.*, 2019) and thus are at much lower risk to predation when exposed in

sandier areas of the lake. This is important because males of the species and male Mbuna in general (Genner *et al.*, 1999) are known to exhibit territoriality (Konings, 2018) and need to cross less preferred habitat in order to claim their own territories. Knight *et al.* (1999) confirm that spatially adjacent female Mbuna are more likely to be related, whereas spatially adjacent male Mbuna display the opposite and are less likely to be related. This shows that there is male biased dispersal within Lake Niassa that is common to species that are territorial and polygamous (Knight *et al.*, 1999) such as *Metriaclima estherae*. This might explain why they are more commonly observed in sandy habitats than their female counterparts who do disperse very far from their place of birth.

Male *Metriaclima estherae* were found to be much more abundant than female individuals. This imbalance in sex ratio could be due to the fact that females are far more sought after for sale in the ornamental fish trade as a result of their bright colour (Tweddle, 1992). However, another explanation for this pattern might be siltation. A combined effect of poor agricultural practice in and around the lake, coupled with an increasing population in surrounding countries leading to industrial development on the lake's banks, has resulted in increased siltation (Ngochera, 2014). This poses a problem to *M. estherae* and Mbuna in general as their preferred habitat is becoming overlain with sediment. Mbuna in general have limited mobility and migration capacity as well as a very small range of habitat within the lake and thus this could lead to rapid declines in their populations (Tweddle, 1992; Ngochera, 2014). Since *Metriaclima estherae* females appear to be more restricted by sand, this effect may already be showing in their populations since female abundance was significantly lower than males. However, this does not mean that males will be entirely unaffected, since they too rely on rock for their primary food source (Ngochera, 2014) and could soon begin showing declines as a result of siltation.

When assessing sex-specific associations with depth, females seem to be completely restricted to the shallow regions whereas males appear to be more dispersed along the depth profiles. This again, supports the idea proposed by Knight *et al.* (1999) of male biased dispersion. However, whether this is related more to depth or habitat availability is unclear since the majority of the sites sampled at deeper parts of the lake were dominated by sand. Whether rocky reef type habitat is unavailable in deeper parts of the lake or if they were present but missed by the survey is a question that could be explored in a future study as this would have management implications for the species. The habitat distribution along depth did, however, show some presence of rocky habitat in the bands 41 to 50 and 61 to 70 meters deep and in response there was an associated increase in male abundance in those depth classes and the only female individuals observed in the deep were also recorded at those depths. This could show that *M. estherae* occupy much deeper areas than once thought, as they were always believed to be confined to shallower reaches of the lake (Konings, 1995; Konings, 2018)

In order to conserve the species, a necessary first step would be to target the habitat degradation problem that has arisen as a result of increased siltation. Although *Metriaclima estherae* display very distinct differences in habitat preferences by sex, both sexes prefer rocky habitat and preserving it would be beneficial for the conservation of the species as a whole. As the species, particularly the females, seem to be particularly reliant on the rocky substrate, the loss of this habitat coupled with extraction of individuals for ornamental trade could result in a rapid decline of population numbers, particularly as the species is already showing a male-skewed sex ratio.

Improvements to the study could be made to ensure that a full range of habitat is sampled across the range of depths. Since the study made use of video footage that was collected for the study of fishery based species, we believe that changing the bait from Usipa to common algae abundant in the rocky reefs of the area might improve the results. *Metriaclima estherae* have a primarily plant based diet (Konings, 1995; Konings, 2018) and did not display an attraction to the bait used. Since this study made use of pre-collected video footage and the bait was chosen to attract larger species caught by fisheries, it would be interesting to see how the inclusion of a more appropriate bait type for this species might influence the results. However, the results obtained were still useful and provided information about the species in terms of their habitat preferences. The results of the study confirm that the video system was effective in collecting population information on *Metriaclima estherae*, including habitat use and depth profiles, which could be used to determine key factors for the effective management of the species.



CHAPTER 3:

Using Baited Remote Underwater Video Systems (BRUVS) to determine the abundance and habitat preferences of *Potamonautes lirrangensis* in Lake Malawi/Niassa/Nyasa



INTRODUCTION

Freshwater crabs are widespread and present in almost all freshwater systems (Cumberlidge *et al.*, 2011). They are important freshwater invertebrates because they play key roles within their ecosystems as essential links within food webs (Cumberlidge *et al.*, 2011; Daniels and Bayliss, 2011). They act as detritivores, and therefore play an important role in nutrient cycling (Daniels and Bayliss, 2011; Cumberlidge *et al.*, 2009). They are an integral link in the food chain and are consumed by many other species such as fish, birds, otters, and crocodiles, to name a few (Daniels and Bayliss, 2011; Cumberlidge *et al.*, 2009). A large majority of freshwater crab species require near pristine conditions to survive and since they are found in all major freshwater systems, they are good indicators of water quality (Cumberlidge *et al.*, 2009). Freshwater crabs also have economic importance, especially in parts of Africa, as they are consumed by many people in rural communities and support small commercial fisheries (Reed and Cumberlidge, 2006; Cumberlidge and Meyer, 2011).

Cumberlidge *et al.* (2009) indicated that freshwater crabs are facing a high level of threat because they are sensitive to polluted water and excessive siltation caused by anthropogenic activities. Increasing human populations coupled with poverty has led to them being collected for human consumption more frequently (Dalu *et al.*, 2017). In addition, habitat degradation caused by industrial development, mining, deforestation and agriculture is also one of the main contributors to declines in freshwater crab species abundance (Cumberlidge *et al.*, 2011).

Potamonautes lirrangensis is a freshwater crab that is widely distributed in East Africa, found in a wide range of rivers and lakes in Congo, Malawi and Tanzania (Daniels and Bayliss, 2012). *Potamonautes lirrangensis* is not endemic to Lake Niassa, but the subpopulation which resides within the lake's depths is given the common name 'Malawi Blue Crab' because it is the only known freshwater crab species to inhabit the lake (Cumberlidge, 2018; Kochey *et al.*,

2019). The species is rated by the IUCN as Least Concern because of its wide distribution. However, this species is commercially exploited as a food resource and is collected from Lake Niassa for sale in the international aquarium trade (Thiruvengadam, 2019) which means that is important for the population to be monitored in order to prevent declines that may be caused by over-exploitation.

The aim of this study was to determine if Baited Remote Underwater Video Systems (BRUVS) can be used to extract habitat use data for *Potamonautes lirrangensis* in order to determine whether they can be used to efficiently monitor large freshwater crustacea. The study was conducted concurrently with the study performed on *Metriaclima estherae* described in Chapter 2 using the same video footage collected by BRUVS deployed in the Meluluco area of the lake from 2016 to 2018. This footage was used to assess the habitat preferences of this species by identifying the dominant habitat type in the areas in which *P. lirrangensis* were found to be most abundant.

METHODS AND MATERIALS

Study area

The study area is covered in depth in Chapter 2. The research was conducted within a small reef system 7km off shore of the Mozambican extent of Lake Niassa known as Meluluco. The Meluluco reef system was classified as a Key Biodiversity Area by the IUCN in the year 2019 and is one of the first to be designated within Mozambique (Sayer *et al.*, 2019). This reef was chosen because of its importance to the fish species *Metriaclima estherae*, which was the primary focus of the study. The reef has no biological significance to *Potamonautes lirrangensis* and they were captured in the footage of the BRUVS as by-catch.

Baited Remote Underwater Video systems were deployed at 329 sites in the Meluluco area over 3 years, (2016-2018), between the months of September and November. These sites varied in depth, substrate and vegetation and accounted for the three habitat classes identified by Eccles (1974). They were chosen using a stratified random sampling design, ensuring that a full range of available habitats were sampled according to the study done by van Wyk *et al.* (2018). Please refer to Figure 2.1 in Chapter 2 for a map illustrating the sampled sites in the Meluluco Reef System.

Study Species

Potamonautes lirrangensis is a relatively large species of crab with the carapace width of adult individuals ranging between 53-57mm (Cumberlidge *et al.*, 2021). They have a large, pointed exorbital tooth, a distinct complete postfrontal crest that is lined with small granules and smooth sidewalls on its carapace (Cumberlidge and Meyer, 2011). They are scavenging feeders with a combined diet of both plant and animal food types (Weigand and Plath, 2014). For more information on the species, please refer to Chapter 1.

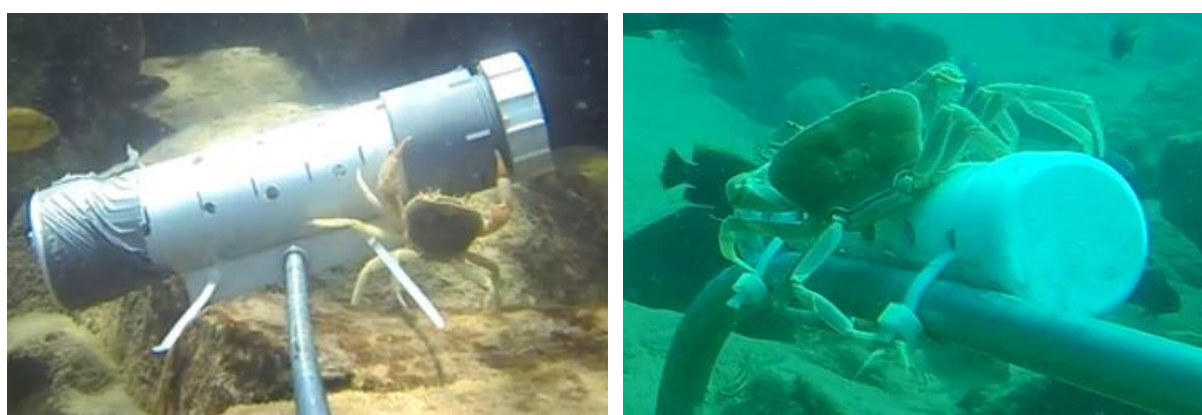


Figure 3. 1: *Potamonautes lirrangensis* also known as the Malawi Blue Crab. The only recorded crab species in Lake Niassa.

Experimental design and protocol

Deploying the Baited Remote Underwater Video Systems and video analysis

This study was conducted concurrently with the study done on *Metriaclima estherae* described in Chapter 2, using the same footage recorded by the BRUVS deployed in Meluluco from 2016 to 2018. Therefore, the methods used to deploy the BRUVS systems and analyse the footage collected by them are detailed in full within the methods and materials section of Chapter 2.

Data analyses

R Studio version 1.4.1717 (2021) was used to conduct data analysis. The data was tested for normality and a single factor ANOVA was used to compare the number of individuals sighted to the habitat categories, to determine if dominant habitat variable's had an effect on the overall abundance of *Potamonautes lirrangensis*.

A chi-squared test of association was conducted between the habitat categories and the percentage abundance of sites that showed presence or absence of *P. lirrangensis*. This was done to display the distribution of *P. lirrangensis* across habitat classes.

In order to determine if depth affected the abundance of the species, a Kruskal-Wallis test was conducted to compare *Potamonautes lirrangensis* abundance to depth classes, which were not normally distributed. Sites were grouped into depth classes in intervals of 10m starting from 1m deep to a maximum of 70m deep. The chi-square test conducted in Chapter 2 was used to provide a representation of the overall availability of habitat to see which were more frequently occurring than others.

Finally, a binomial Generalised Linear Model (GLM) was produced to display the effect of major habitat drivers on *P. lirrangensis* populations of the Meluluco area within Lake Niassa. A binomial GLM was used because the species data was input as a categorical value in the form of presence or absence data to see how the habitat drivers influenced *P. lirrangensis* occurrence.

RESULTS

Habitat dominated by rock showed the greatest abundance of *P. lirrangensis* (Figure 3.2). Rocky habitat had the greatest percentage of sites where *P. lirrangensis* was present, whereas sandier habitats had the greatest percentage of sights where the species was absent (Figure 3.3). This suggests that, similarly to *M. estherae*, *P. lirrangensis* has a preference for rocky substrate over sandy substrate. *Potamonautes lirrangensis* might also have an association to vegetation as it was sighted in a relatively large percentage of vegetated sites (Figure 3.3). However, since this habitat type was significantly less frequent than rocky and sandy habitat types (See Table 2.1 in Chapter 2), further testing would be required to determine the habitat association of *P. lirrangensis* with vegetation. *Potamonautes lirrangensis* appear to be actively avoiding sand as they were recorded in a very small proportion of sites dominated by sand.

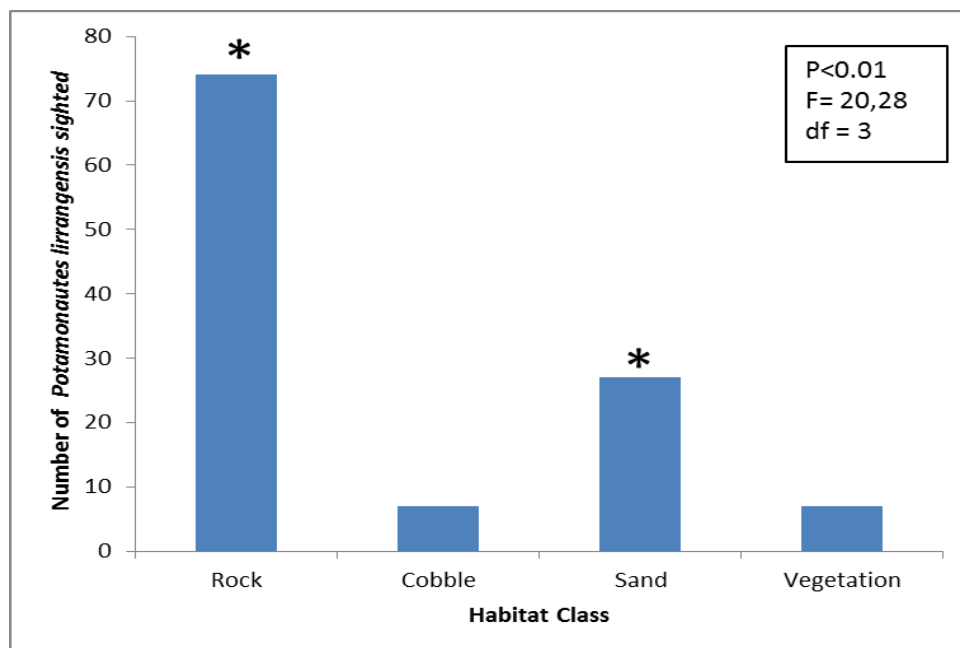


Figure 3. 2: *Potamonautes lirrangensis* occurrences on the major habitat types in Meluluco, Lake Niassa in 2017 – 2018. *Potamonautes lirrangensis* occurred significantly more frequently in rocky habitat in comparison to sandy habitat. There was no significant difference in occurrence between habitats dominated by cobble and vegetation.

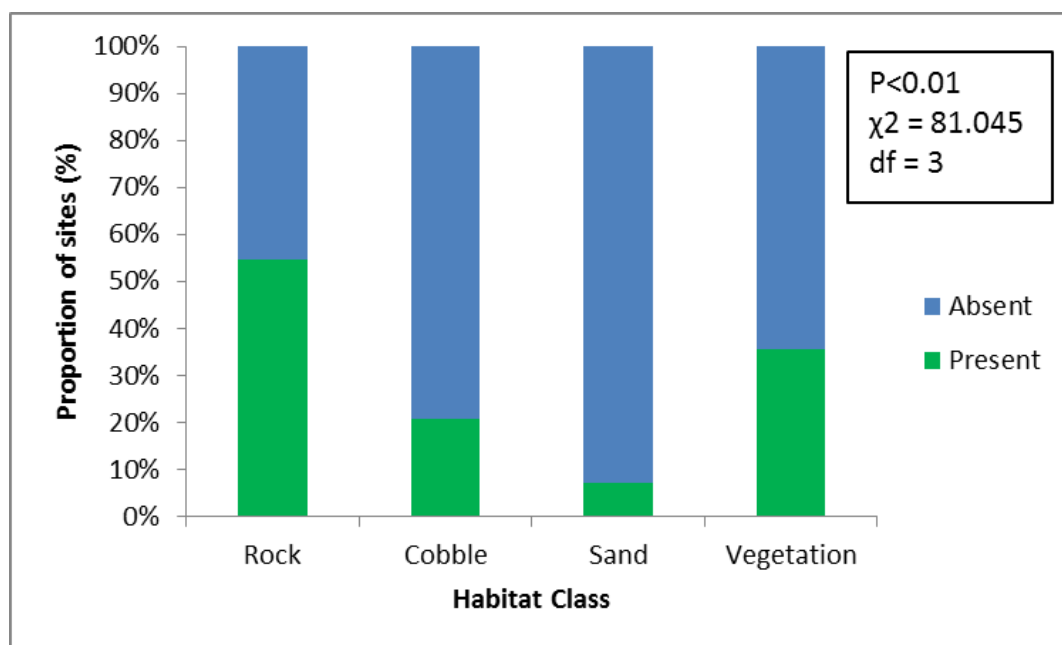


Figure 3. 3: The proportion of sites where *Potamonautes lirrangensis* was found present or absent in relation to the four major habitat variables.

Potamonautes lirrangensis were more commonly observed in the shallower sites (Figure 3.4). More than 70% of individuals were recorded at sites that were less than 10m deep (Figure 3.4). No crabs were observed in waters deeper than 40m.

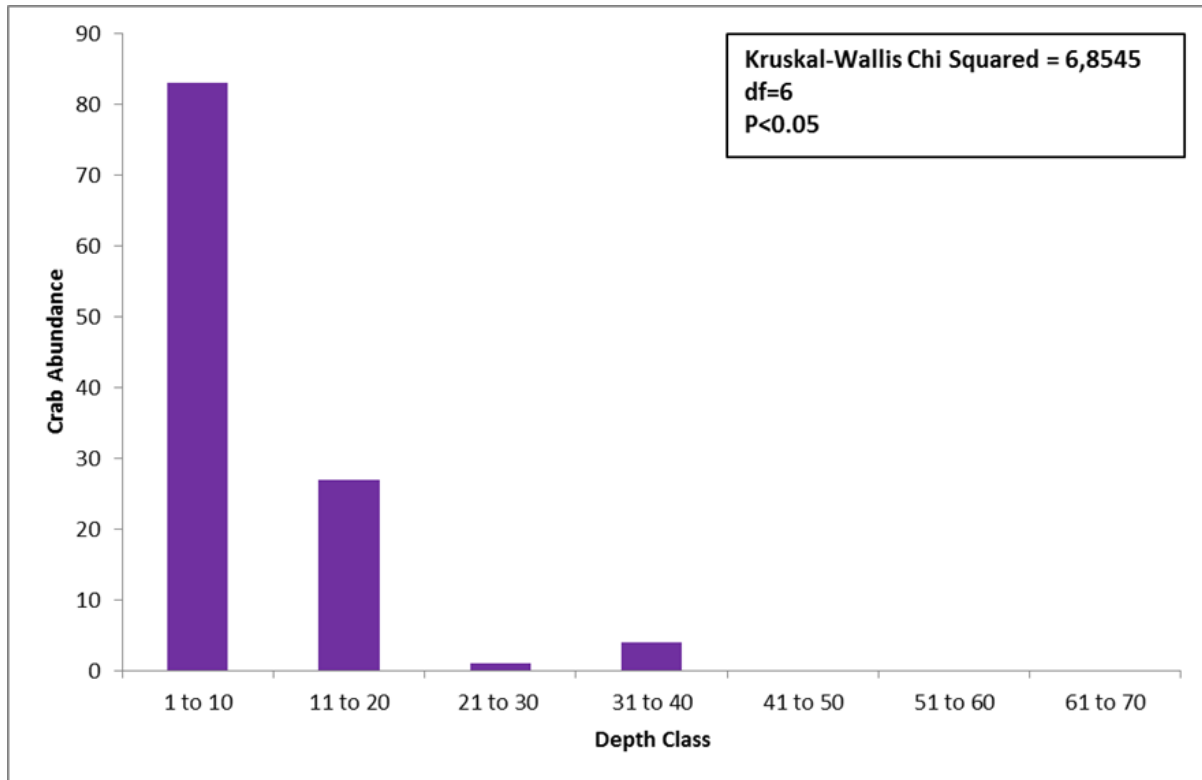


Figure 3. 4: *Potamonautes lirrangensis* distribution along depth gradient in the Meluluco Reef System, Lake Niassa, Mozambique.

Sand was the major explanatory variable for the variance observed in the *P. lirrangensis* abundance data (Std. error= 0.25084, z value= -3.179, $p < 0.001$) (Figure 3.5). They show a strong negative association to sand as well as a significantly positive association to rock (SE= 0.20726, z value= 2.128, $p < 0.05$) (Figure 3.5). This may suggest that although *P. lirrangensis* might prefer rocky habitats, it is the avoidance of sand that is more strongly affecting their abundance. This could explain why they were seen in many of the vegetated or cobble dominated sites (Figure 3.3) even though those habitat types were significantly less frequent

than Rocky and Sandy types (see table 2.1 in Chapter 2). Depth does not significantly account for the variation in *P. lirrangensis* abundance and does not seem to be influencing their population distribution (Figure 3.5).

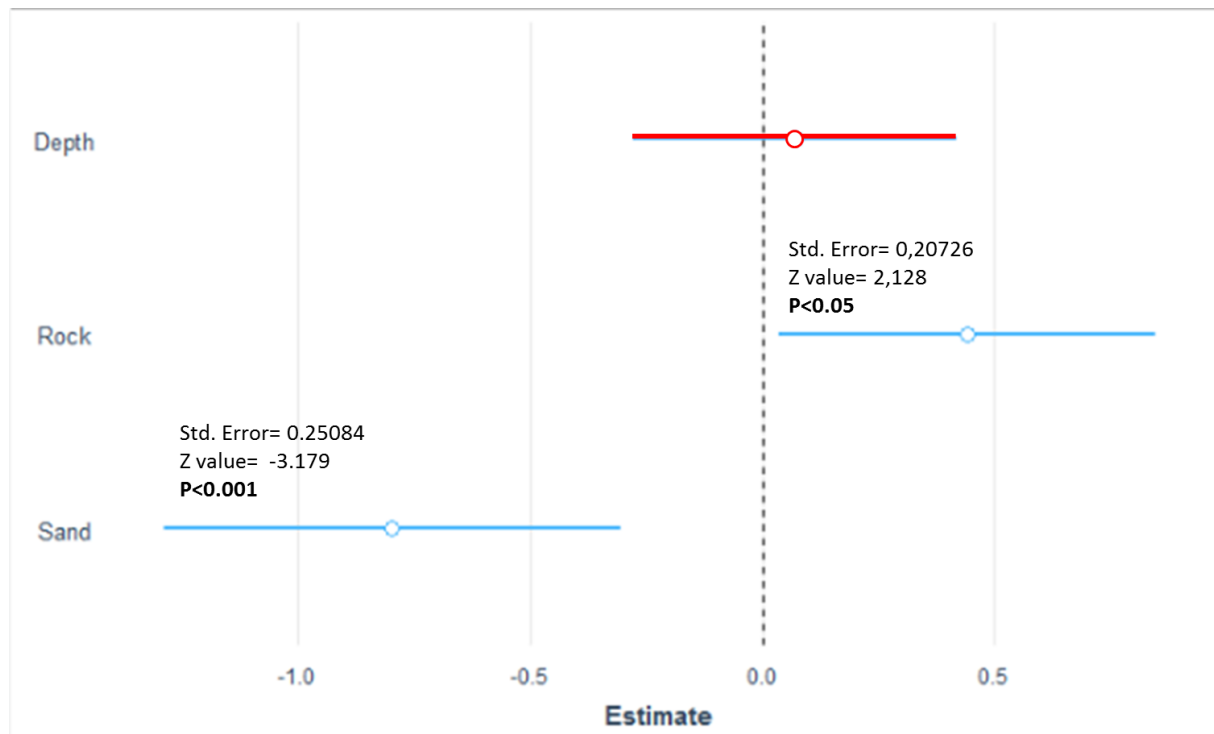


Figure 3. 5: Binomial general linear model coefficient plot for *Potamonautes lirrangensis* abundance in Meluluco. Includes plotted Estimate points, Standard Error, z-value and $\Pr(>|z|)$. Blue lines indicate factors which significantly affect the abundance model ($P < 0.05$). Red lines indicate factors that do not ($P > 0.05$).

DISCUSSION

At the studied sites in the Meluluco reef system, *Potamonautes lirrangensis* preferred rocky substrate. This is common for lake dwelling species (Marijnissen *et al.*, 2009) such as the crab species inhabiting Lake Tanganyika. This could be because *P. lirrangensis* is a fully aquatic crab that spends all of its life cycle living submerged in water (Cumberlidge *et al.*, 2021) and thus relies on submerged rock or other biological shelters, such as some types of vegetation, for protection against predation, as opposed to semi-terrestrial species which have the ability to burrow in mud (Okano *et al.*, 2000). The species faces high predation pressure (Johnson, 2019) from larger species in the lake such as predatory fish and birds (Kidd *et al.*, 2003; Johnston; 1989) and otters (Mgoola and Msiska, 2017), and therefore may require the cover provided by rocky substrate to avoid predation. The strong negative correlation with sandy substrate could be because they actively avoid open spaces where they are vulnerable to predation.

The species was most common in rocky habitat within the shallower areas of the lake at depths between 1 and 10m. Marijnissen *et al.* (2009) found a similar pattern where a comparable crab species inhabiting Lake Tanganyika were also found to be significantly more abundant in rocky habitat which was between the depths of 5 to 10 m. This was attributed to a greater abundance of food in the shallower regions of the lake (Marijnissen *et al.*, 2009). This could explain why *Potamonautes lirrangensis* displayed the same preferences. Since they are scavengers and detritivores that feed on both plant and animal material (Weigand and Plath, 2014), it is likely that they would prefer to live in these shallow areas as there is a greater quantity and variety of food available (Marijnissen *et al.*, 2009). The sites sampled in the deeper areas of the lake were mostly sandy and the preferred rocky habitat becomes significantly less frequent (see Figure 2.14 from Chapter 2). Therefore, *Potamonautes lirrangensis* may be more abundant in shallower areas due to a lack of suitable habitat. This

also conforms to the theory that they avoid sand because of the high predation pressure which they face as deeper sandy areas tend to be dominated by large-mouthed cichlids and catfish which prey on the species (Ribbink *et al.*, 1983).

Due to its widespread distribution range and its presence in different localities, *Potamonautes lirrangensis* is classified by the IUCN as Least Concern (Cumberlidge, 2018). However, management for the species and other freshwater crab species like it is necessary because of the vital role that they play as a part of the food web and as detritivores within the nutrient cycle (Daniels and Bayliss, 2012). Although the IUCN report identified no immediate threats to the species (Cumberlidge, 2018), in order to manage it efficiently it is important to identify which anthropogenic effects could possibly cause the population of *Potamonautes lirrangensis* in Lake Niassa to decline. Since they have preference for rocky substrate and the majority of the individuals identified were present in rocky areas, habitat degradation as a result of increased siltation could possibly threaten the *P. lirrangensis* population. It has already been noted that poor agricultural practices coupled with increased industrial development on the lake's shores as a result of an increasing human population has caused an increased sediment load to be washed into the lake (Ngochera, 2014). Similarly to *Metriaclima estherae* (see Chapter 2), this may pose a problem for *P. lirrangensis* should their preferred habitat become overlain with sand, leaving the bulk of their population vulnerable to predation.

Furthermore, the excess sediment washing into the lake increases the turbidity of the water which could be detrimental to the growth of submerged macrophytes and algae (Pullanikkatil *et al.*, 2015). These underwater plants and algae are primary sources of nutrition for *P. lirrangensis* (Hecky *et al.*, 2003). Furthermore, while fish are relatively tolerant of changes in water quality, invertebrates such as freshwater crabs, like *P. lirrangensis*, are more sensitive (Cumberlidge, 2009) and decreased water quality caused by poor agricultural practices and

eutrophication (Hecky *et al.*, 1999) could lead to population declines. In addition to this, increasing human populations on the lakes shores would increase the harvest demand (Dalu *et al.*, 2017) for *P. lirrangensis* which does support a small fishery and is captured for human consumption (Cumberlidge and Meyer, 2011; Thiruvengadam, 2019). As the commercial species of the lake are already showing severe population declines as a result of overfishing (Banda *et al.*, 2005, Weyl *et al.*, 2010), the demand for *P. lirrangensis* for human consumption could increase in response, leaving the population residing in Lake Niassa vulnerable to overexploitation.

Recent studies by Johnson (2019) and Cumberlidge *et al.* (2021) have suggested that the sub-population of *Potamonautes lirrangensis* in Lake Niassa is actually a divergent species that should be renamed to *Potamonautes orbitospinus* which is what it is commonly sold as in the aquarium trade. Although the Malawi Blue Crab is still most commonly recognised as *Potamonautes lirrangensis*, morphological and genetic characteristics indicate that the species found in Lake Niassa is entirely different and should be recognised as *Potamonautes orbitospinus* (Johnson, 2019). This would mean that the species would be endemic to Lake Niassa, as its variation was not recorded anywhere else and thus its distribution range would be significantly decreased (Cumberlidge *et al.*, 2021). Since the main reason that *Potamonautes lirrangensis* is classified by the IUCN as Least Concern is due to its wide distribution range (Cumberlidge, 2018), this reclassification of the Malawi Blue Crab as *Potamonautes orbitospinus* would mean that the red list rating would need to be reassessed and the species may be threatened but not classified as such due to data deficiency.

Since *Potamonautes lirrangensis* are omnivorous detritivores, the species did show attraction to the bait, even though it was chosen to attract different species (by van Wyk *et al* 2018, to study commercially important fisheries species). Future research might benefit from comparing un-baited video systems to BRUVS to determine whether the bait has an impact on

the detection rate for this species. It would also be interesting to determine if lack of preferred habitat is driving the absence of *P. lirrangensis* in the deeper reaches of the lake.

Improvements to the study could include sampling more sites dominated by cobble and vegetation in order to see if there is a significant interaction between those habitat types and the abundance of *P. lirrangensis*. Future research may also want to determine if there is a relationship between the size of the crabs and the habitat in which they occur.

The management of the *Potamonautes lirrangensis* population in Lake Niassa, while it is still healthy, is key in order to prevent future declines. This study revealed, that like *Metriaclima estherae* the protection of rocky reefs would be critical for maintaining *P. lirrangensis* populations in Lake Niassa. This would provide the species with adequate refugia to allow its populations to recover from any anthropogenic effects that could cause severe population declines. Furthermore for both species, it is critical that the siltation problem currently faced by Lake Niassa be mitigated.

CHAPTER 4:

Using Stereo BRUVS to determine the length distribution of *Metriaclima estherae* in Lake Malawi/Niassa/Nyasa



INTRODUCTION

Lake Niassa holds more than 800 species of haplochromine fishes which have diversified to fill nearly every available ecological niche in the lake (Moran and Kornfield, 1993). Only a small fraction of these haplochromines are not endemic to the waters of Lake Niassa and the group has been extensively studied because of its immense diversity (Moran and Kornfield, 1993; Turner, 1996). The “Mbuna” are a sub-group of haplochromine cichlid species which display complex evolutionary processes at an accelerated rate because of their rapid speciation (Genner and Turner, 2005).

The species are also valuable to the commercial and societal sectors of the countries surrounding the lake. They exhibit a variety of bright colouration and are often collected for sale in the aquarium trade (Banda *et al.*, 2005). The aquarium trade supported by the lake brings in a significant proportion of income to the countries on its borders, for example, the sale of live Mbuna specimen generated approximately 138 thousand USD in the year 2019 (GoM, 2021). They also form an integral part of the lake’s cultural identity, contributing to Lake Niassa being considered a World Heritage Site (Lake Malawi National Park, 2021), and thus bring in additional income to surrounding countries in the form of ecotourism (Banda *et al.*, 2005, Sayer *et al.*, 2019).

Due to the Mbuna undergoing rapid speciation, the species within the group tend to have small populations and occur in relatively low abundance which means that they are vulnerable to rapid overexploitation (Tweddle, 1992). Although the Mbuna are not currently exploited as a food resource (Tweddle, 1992), the overexploitation of other popular fishery species in the lake has already resulted in decreased harvests (Munthali, 1997; Banda *et al.*, 2005) which means that fishers in the area may have to resort to harvesting ornamental species as a source

of nutrition in the future to retain their livelihoods (Banda *et al.*, 2005; Munthali, 1997). The Mbuna are relatively small in size compared to more popular fisheries species and have low nutritional value (Munthali, 1997), meaning that larger harvests of these species would be needed to meet the demands of the growing population on the lake's borders (Donda *et al.*, 2014). This coupled with their relatively small populations, would have significant impacts on the aquarium trade and the overall genetic diversity of the lake, especially if the species are not carefully monitored.

Therefore, it is beneficial to ensure that these populations are managed and the harvesting of their stocks is carefully controlled in order to prevent rapid declines. Baited Remote Underwater Video Systems or BRUVS have already shown to be a viable management tool for extracting critical population data for the species *Metriaclima estherae* in Chapter 2. However, another important factor to consider is the size of fish removed from the population. Commercially targeted fish species undergo two types of overfishing. Recruitment overfishing occurs when fish are harvested before reproducing and as a result recruitment declines in direct proportion with the abundance of mature individuals (Allen *et al.*, 2013). Growth overfishing occurs when fish are harvested at sizes that are insufficient to meet the optimal yield per recruit, therefore resulting in more individuals being removed from the population in order to meet demand (Amarasinghe, 1988; Karjalainen and Marjomäki, 2005). This effect is exacerbated in species harvested for the ornamental trade as smaller, younger fish are targeted in order to maximise the amount of time that they will survive in captivity (Yanong, 1996). Hence understanding the length distribution of the species, will be beneficial for their management, especially for those which are harvested as ornamentals.

Therefore, the aim of this study was to determine if stereo-Baited Remote Underwater Video Systems (stereo-BRUVS) can be used to accurately draw length distribution information for the smaller fish species in the lake by using them to measure *Metriaclima estherae*. We then

used this data to see if we could determine biological information such as whether there is a size difference between males and females of the species as well as whether *M. estherae* length differs over different depth and habitat classes. This information may be useful for underpinning management protocols on the harvesting of *M. estherae* for the aquarium trade as they are usually removed at juvenile stage before they are given the opportunity to reproduce. Understanding length distribution could help inform more sustainable harvesting of the species.

METHODS AND MATERIALS

Study area

The study was conducted in a small reef system known as Meluluco, which occurs approximately 7km off the Mozambican extent of Lake Malawi/Niassa/Nyasa and was designated as a Key Biodiversity Area by the IUCN in the year 2019 (Sayer *et al.*, 2019). Particular focus was placed on a shallow reef in the system, about 7m deep, known as Mino's reef because of its importance to the study species *Metriaclima estherae* (Konings, 1995). This reef is where *M. estherae* is most commonly fished for sale in the aquarium trade as it is where the females of the species display the deepest orange/yellow colour which is attractive in live specimen kept by fish keepers (Konings, 1995; Harrington 2021).

See Chapter 2 for detailed information on the study area. Only video footage from the stereo-BRUVS deployed in the year 2018 was analysed for this study. Figure 2.1 indicates the 68 sites sampled in 2018 within the Meluluco Reef System.

Study Species

Metriaclima estherae is a small mbuna haplochromine cichlid that is endemic to Lake Niassa (Konings, 1995, Konings, 2018). The species is important to the international aquarium trade as it is one of the most commonly kept African cichlids by hobbyists (Sayer et al, 2019; Harrington, 2021). They are sexually dimorphic where females are a bright yellow and males a light blue with vertical grey bands and yellow egg spots on the anal fin (Konings, 2001; Nyalungu and Couldrige, 2020). Males are generally larger than females growing up to approximately 13cm (130mm) total length and females growing to approximately 10cm (100mm) total length (Konings, 1995). See the study species sections of Chapter 1 and 2 for detailed information on the study species *Metriaclima estherae*. Figure 2.2 in Chapter 2 provides a photograph of the study species.

Experimental design and protocol

Deploying the Baited Remote Underwater Video Systems and video analysis

In order to measure the lengths of fish species, it is necessary to use stereo- BRUVS. The stereo BRUVS were made up of a steel frame with two cameras mounted on either side 0.7m apart at an angle of 8° to create an overlapping field of view. This positioning allows for the collection of length measurements during the video analysis (Harvey and Mladenov, 2001; Harvey *et al.*, 2002a). A perforated PVC pipe was held on a 1m bait arm to ensure it was in the field of view of the camera and was filled with 100g crushed *Usipa (Engraulicypris sardella)*. For more details on the bait used, see the methods section of Chapter 2. The stereo-BRUVS were deployed at 68 different locations within the Meluluco reef system, each of which were at least 50m apart (van Wyk *et al.*, 2018). The system was allowed to record for a minimum of 15 minutes from when the stereo BRUV touched the lake floor.

Length analysis

Length data was obtained using EventMeasure (SeaGIS Pty. Ltd). The period creator function was used to create a standard watching period of 15 minutes to ensure that the collected data was observed within a standardised time frame, unless one or both of the cameras were flipped or obstructed in which case the video was analysed for as long as possible. Length data was fit to each individual in the MaxN frame which was determined by counting the highest number of individuals per species, per sex, captured in a single frame of the video sample (as defined by Ellis and DeMartini, 1995). Footage from both cameras was loaded into the software and each individual fish was followed starting from the MaxN frame to ensure individuals were not measured multiple times. Fish were followed individually until they were in line with both cameras, allowing them to be measured for total length. This was achieved by using the guidelines provided by EventMeasure (SeaGIS Pty. Ltd) software. By marking the centre of the tail and mouth of each individual fish on the footage obtained from each camera, the software generates an approximation of the individuals total length. In order to limit errors, measurements of fish that were flagged by the software for being obstructed, at too great an angle or too far away were discarded.

Data analyses

R Studio version 1.4.1717 (2021) was used to conduct data analysis. The data was tested for normality and non-parametric equivalents to tests were used if the data could not be transformed to fit a normal distribution. A Wilcoxin signed-rank test was used to compare the length data between males and females of the species. This was done to confirm if males were larger than their female counterparts. R Studio was also used to divide the length data into length classes of 10 mm increments ranging from 50mm to 130mm. A Chi-squared test of

association was done to see if there was a difference in abundance of males and females within the different length classes and a length frequency distribution, by sex, was drawn to illustrate the difference in size between males and females. Fisher's exact test was conducted on the male and female distributions individually in order to display the length distribution for each individual sex with relation to the main habitat drivers determined in Chapter 2 of the thesis. This was to determine if there was a possible relationship between habitat and length for males and females of the species.

In order to determine the relationship with depth, Kruskal Wallis tests were conducted between the length classes (ranging from 50mm to 130mm in increments of 10mm) and the depth classes (ranging from 1m to 70m in increments of 10m) in order to determine if length distribution changed according to changes in depth. This was done for the species as a whole and then again for each individual sex in order to determine if there was a relationship between length and depth.

RESULTS

The results show that, on average, *Metriaclima estherae* males were significantly larger ($W=23320$, $p<0.001$) than their female conspecifics. Figure 4.1 shows that most of the males recorded fell into the range 80 to 90 mm, whereas most of the females measured to 70 to 80mm. The length distribution (Figure 4.2) also shows that the males of the species have a larger size range ($\chi^2=54.161$, $df=6$, $p<0.001$) with individuals recording lengths of up to 130 mm, whereas the largest females recorded did not exceed 100mm. However, no individuals of either sex were recorded to be below 50mm in length (Figure 4.2).

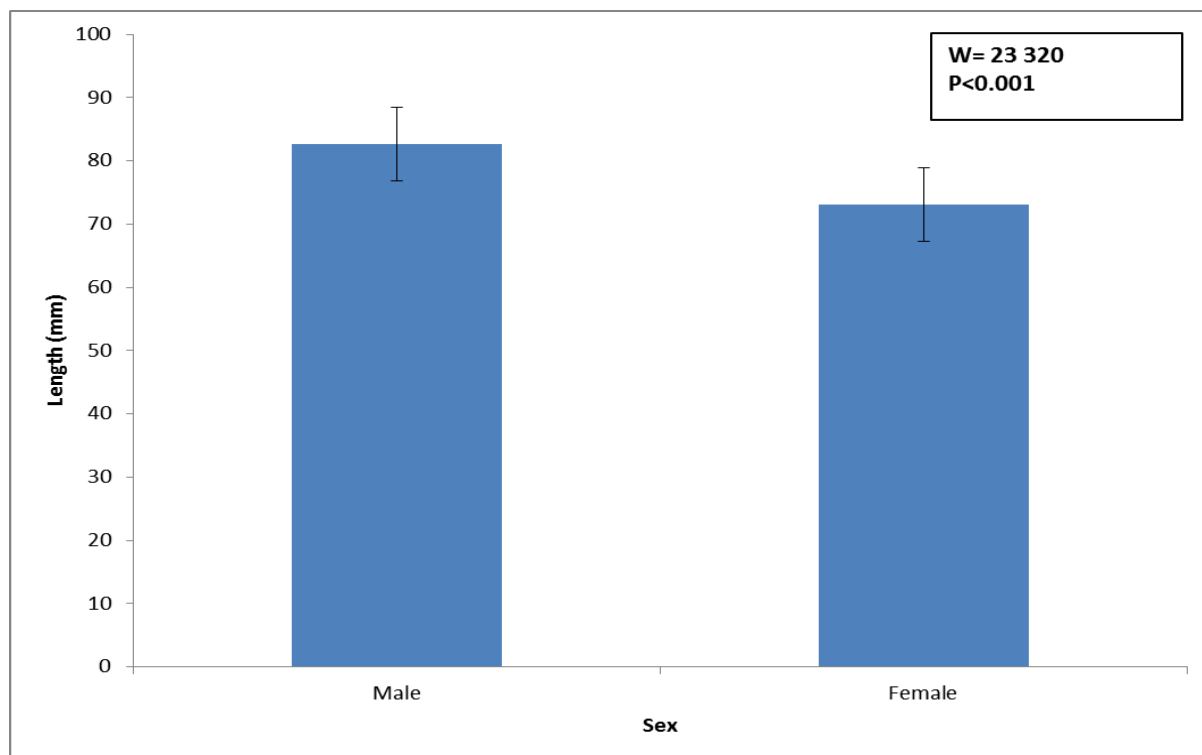


Figure 4. 1: Mean ($\pm$ SE) Length measurements between male and female individuals of *Metriaclima estherae* from the Meluluco reef system, Lake Niassa, in the year 2018.

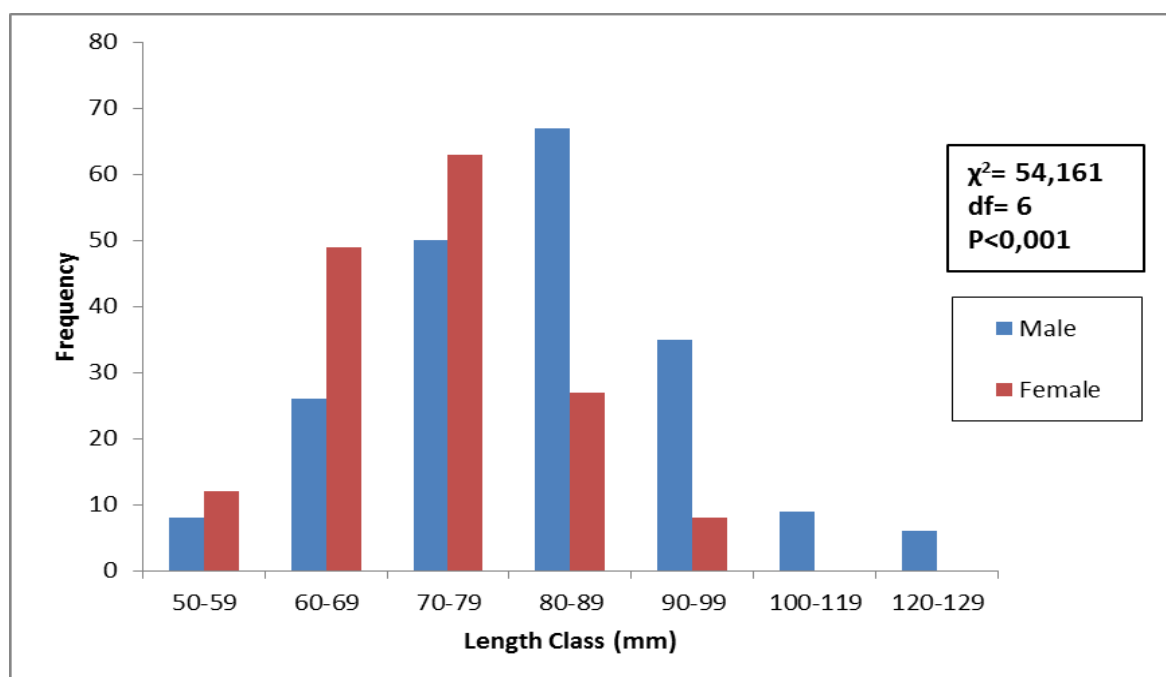


Figure 4. 2: *Metriaclima estherae* length distribution for male and female individuals of the species in the Meluluco reef system, Lake Niassa, 2018.

In general, the length distribution for males in relation to sandy and rocky substrate (Figure 4.3), (main habitat drivers, see Chapter 2), shows that male *Metriaclima estherae* are almost always more common in rocky habitat types regardless of their size. However, the smallest detected males (in the class 50 to 59mm) are more common in sandier habitats (Figure 4.3). In comparison, very few of the largest males observed (between 100 to 129 mm in length) are found in sandier habitats. In rocky habitat, the males showed a normal distribution along length, with the largest frequency of males recorded between 70 to 100mm.

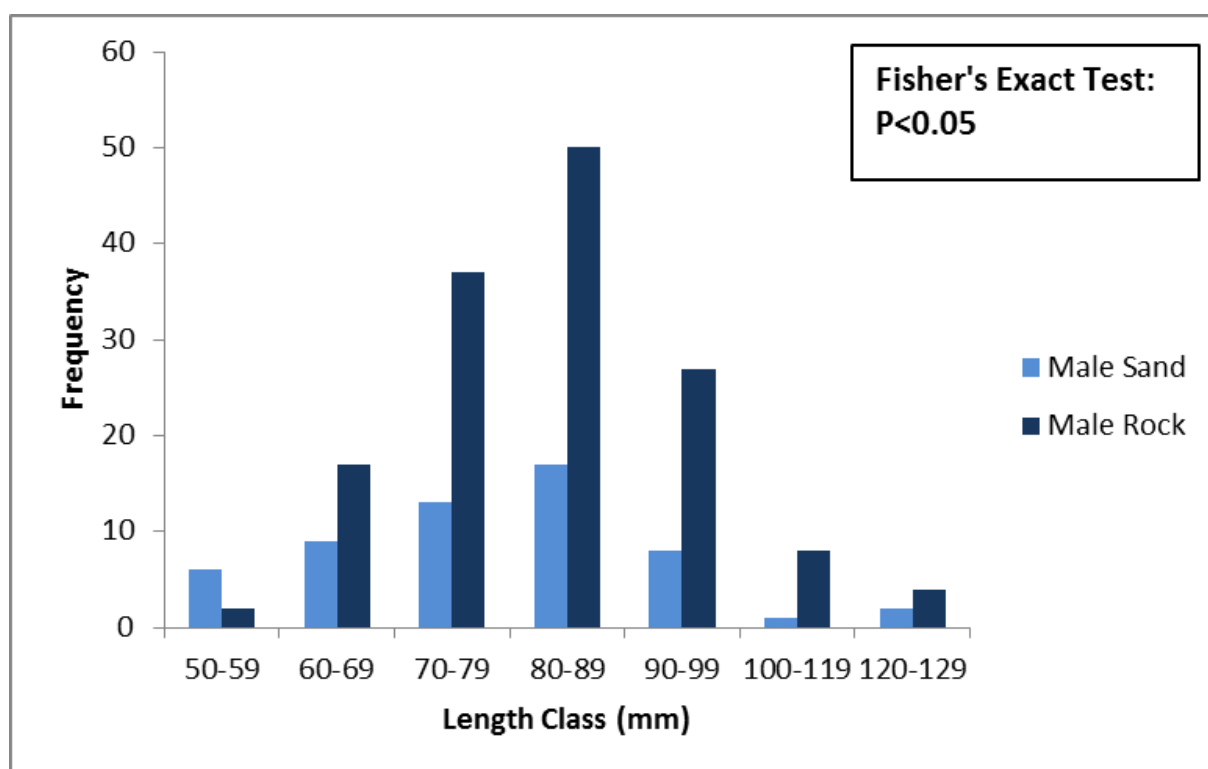


Figure 4. 3: *Metriaclima estherae* length distribution for Males of the species in relation to substrate, the main habitat driver for the species.

For female *M. estherae* (Figure 4.4) very few individuals were found in sandy habitat in general. However, smaller individuals (50 to 59mm) were always recorded in rocky habitat. Most of the females, spotted in sandy habitat, although still a comparably small proportion, were recorded in the length class 60 to 69mm and this proportion steadily decreased in frequency whereby a very minimal number of females in the size class 90 to 99mm were found in sandy habitat. Similarly to the males, in rocky habitat, female length frequencies followed a normal distribution, albeit over a smaller length range, with the largest frequency of females occurring between 60 to 79mm in length.

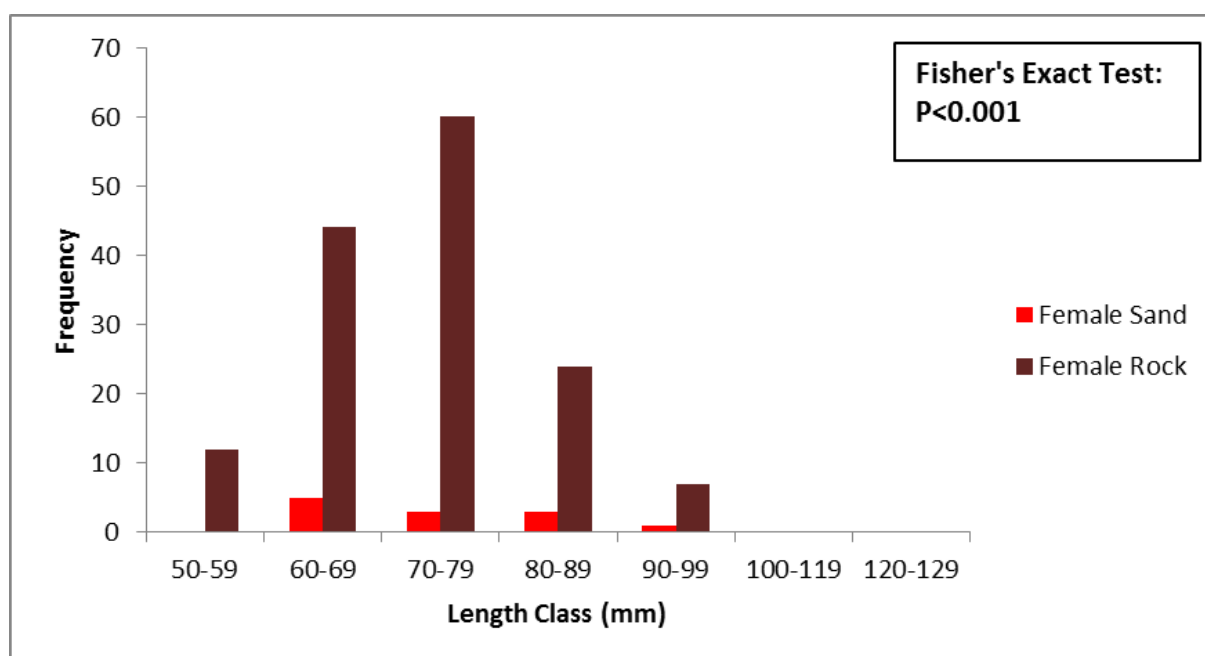


Figure 4. 4: *Metriaclima estherae* length distribution for Females of the species in relation to substrate, the main habitat driver for the species.

Finally, Kruskal-Wallis rank sum tests were conducted to explore the relationship between specimen length and habitat depth. The tests conducted between total length and depth as well as female length and depth both showed no statistical difference (Table 4.1). Therefore, for the species as a whole, or the female individuals, depth had no influence on the length distribution. However, the assessment of male length relative to depth showed that depth was influencing the length structure of the male *M. estherae* individuals. The percentage composition graph (Figure 4.5) further explored the relationship between male *M. estherae* and depth. It shows that depths between 1 and 20m show the largest range of length, while depths from 21 to 30m were dominated by smaller male fish (60 to 79mm). The deepest areas of the lake where male fish were recorded in 2018, 31 to 40m in depth, were dominated by fish that ranged between 60 to 69 mm in length. This shows that the larger fish are more common in shallow areas of the lake while the smaller fish dominate deeper areas. The smallest males, in the length class 50 to 59mm were only recorded in the shallowest depth class, between 1 and 10m in depth.

Table 4. 1: Summary statistics of the following Kruskal-Wallis rank sum tests. The table illustrates the results of the Kruskal-Wallis rank sum tests conducted between *Metriaclima estherae* total length with relation to depth, and the lengths of each individual sex and depth. Only the comparison between Male lengths and depth show statistical significance (indicated by the “*”).

	Kruskal Wallis Chi Squared	df	p-value
Length Vs Depth	1.1353	3	p>0.05
Male Length Vs Depth	8.1056	3	p<0.05 *
Female Length Vs Depth	0.096653	1	p>0.05

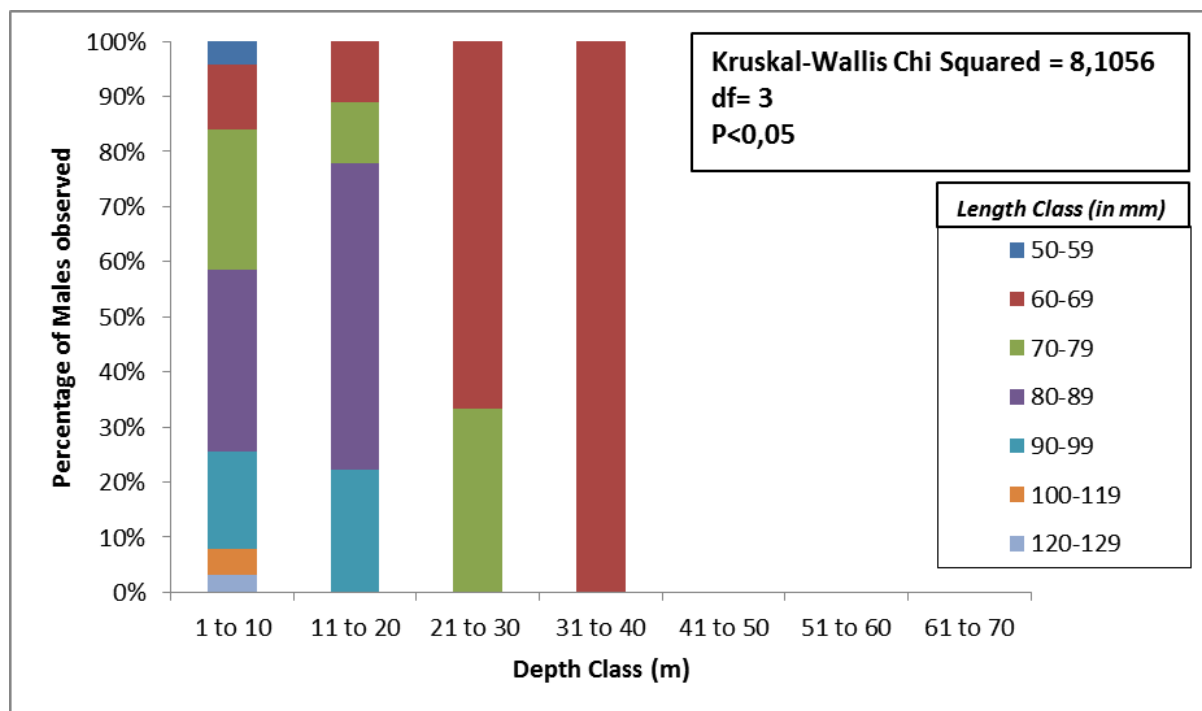


Figure 4. 5: *Metriaclima estherae* male length percentage composition over depth classes in the Meluluco reef system, Lake Niassa, 2018.

DISCUSSION

Males of *Metriaclima estherae* were found to be, on average, larger than their female conspecifics and had a wider length distribution, growing up to 130mm, whereas the largest females recorded were no bigger than 100mm. This is in line with the previous literature noting the size of the species (Yedier *et al.*, 2014; Genner and Turner 2015; Oliver, 2018; Unver *et al.*, 2020) and its initial description by Konings (1995).

In the sites that were surveyed, no individuals under 50mm were recorded. This could be because of one of two reasons, the first being that *M. estherae* are mouth brooders (Coffman 2011), which means that females hold their young within their mouths until they are several weeks old and until they are capable of free swimming (Wickler, 1962). Mbuna species are all mouth brooders which do not guard their young, but rather deposit them into sheltered areas

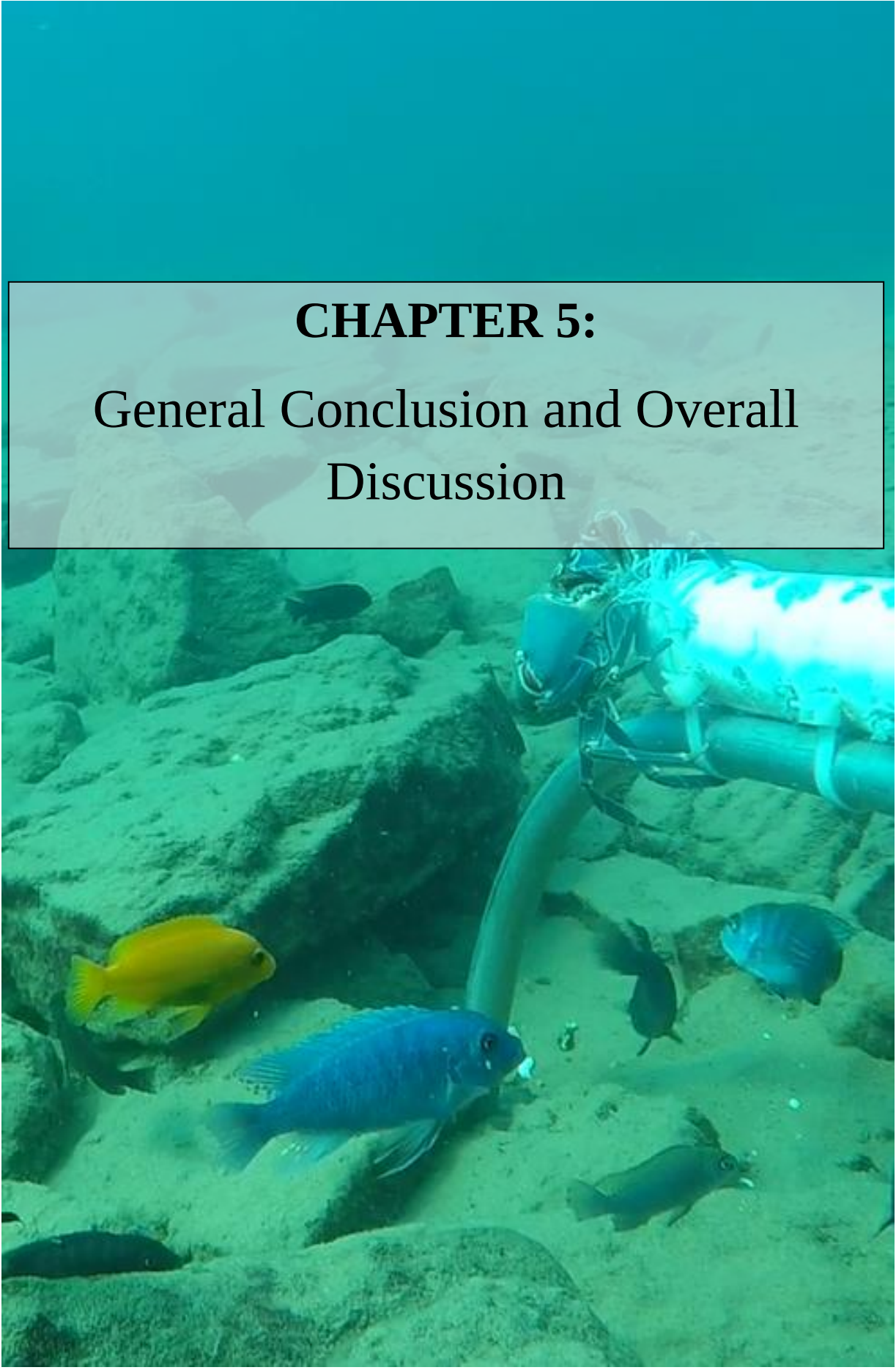
provided by the rocky reefs (Coffman, 2011; Trendall, 1988). Juveniles are deposited into rocky habitat at a standard length of 11mm (Trendall, 1988) and spend most of their time hiding in the crevices provided by the reefs (Coffman, 2011) where they are not in view of the camera. The second reason is because they are too small to identify. The study done by Yedier *et al.* (2014) noted that the colours of *M. estherae* become more apparent as they age and are also partially affected by their diet. Therefore, smaller individuals would be difficult to identify on camera as they would lack distinguishing features.

However, the camera systems were effective at picking up larger juveniles. *Metriaclima estherae* reach sexual maturity at approximately 70mm in length (Borstein, 2011; Robert, 2020). For males of the species, fish with lengths less than 70mm were more frequent in sandy habitat, especially those within the 50 to 59mm length class, whereas larger, older males were more frequent in rocky habitat. This could be because males of the species exhibit territoriality (Konings, 2018). The species is polygamous and males aggressively defend territories of approximately 1m in diameter (Konings, 2018). Therefore it is possible that small juvenile males are pushed out into less preferred habitat (sandy habitat—see results from Chapter 2) in order to search for and establish their own territories. Larger, older males are more common in the preferred rocky habitat, having already established a territory and being more capable of defending it. This male-biased dispersal, which is common in the Mbuna of Lake Niassa (Knight *et al.*, 1999) also accounts for the deeper areas of the lake being dominated by smaller male individuals as sandier habitat occurs more frequently in the deeper areas of the lake (See Figure 2.14 in chapter 2).

Since the females of the species do not have to disperse as far as the males, there is no association between their length distribution and depth and they are more commonly found in the shallower areas of the lake where their preferred habitat is more frequent (See Figure 2.14 in Chapter 2. This is in line with by the study conducted by Knight *et al.* (1999) which

showed that spatially adjacent female Mbuna are more likely to be related than spatially adjacent male Mbuna. The slight decreasing trend in females spotted within sandy habitat may be further explained by predation pressure. Since the bright yellow colour of females is already conspicuous, larger individuals would be more so, thus requiring the refugia provided by rocks to avoid predation (Ribbink, 1983).

This information could be useful for the implementation of adaptive management for *M. estherae* and other Mbuna species which exhibit similar traits. It can also be useful for identifying during which periods of time growth phases occur within species which can aid sustainable harvesting of the species for the aquarium trade (Ng and Tan, 1997). A growth phase refers to a period of time where juveniles are plentiful before the majority are lost to competition and predation (Ng and Tan, 1997). During this time juveniles can be harvested for sale as live specimen with a lower associated impact on the long term health of the population (Ng and Tan, 1997). Some improvements to the study could include changing the bait to the algae which makes up the primary diet of the species (Konings, 1995; Konings, 2018) and could improve the range of the measured length distribution. Future studies would also benefit from looking at a comparison between un-baited video systems and BRUVS to determine the role the bait plays in the effectiveness of the method as a monitoring tool. However, stereo-BRUVS are viable at obtaining critical measurement data for the species and others similar to it, which could be used to underpin the management of their populations.

An underwater photograph showing a diver in a white tank and blue gear on the right, reaching down towards a sandy seabed. Several colorful fish, including a prominent yellow one and a blue one, are swimming around. The background is a deep blue-green water with some rocky structures.

CHAPTER 5:

General Conclusion and Overall Discussion

Currently, the applicability of Baited Remote Underwater Video Systems (BRUVS) as a management tool for freshwater systems is not well studied (Whitmarsh *et al.*, 2017). Despite the method being cost-effective, non-invasive and proven to be quite useful in marine environments, there are very few reported instances where the method is being implemented in freshwaters (Whitmarsh *et al.*, 2017). However, the results of this study suggest that BRUVS can be used as a feasible long term monitoring tool for the fish populations in Lake Niassa. They have already been proven to be effective at monitoring the larger fishery species in the lake (van Wyk, 2019) and the findings of this study show that they can be used effectively to monitor smaller fish species as well as larger freshwater invertebrates.

The overarching aim of this research project was to determine if BRUVS could be used to extract critical population information on smaller species in the lake, such as species abundance, habitat associations and in the case of *Metriaclima estherae* population structure, and thus whether BRUVS could be a viable monitoring tool within the lake, particularly within areas which were designated as Key Biodiversity Areas (KBA's).

The IUCN designated KBA's within the lake as a means to employ an ecosystem based approach to management (Sayer *et al.*, 2019) through the protection of areas large enough to maintain biodiversity but small enough to be managed practically (IUCN, 2016). One of the challenges associated with using this approach is that these areas need to be frequently monitored (IUCN, 2016), in order for them to be effectively managed in the long term, while simultaneously limiting the financial cost to the countries surrounding the lake (Sayer *et al.*, 2019). The use of BRUVS would be an ideal solution as the method is tried and tested and in fact preferred in marine environments, and has the potential to be highly beneficial for the long term monitoring of freshwater ecosystems due to its non-extractive, non-invasive, cost-effective nature (see Bernard 2012; Bernard *et al.*, 2014; Cappo *et al.*, 2001; Cundy *et al.*, 2017; Logan *et al.*, 2017; Roberson *et al.*, 2017).

While the method has not been used extensively within freshwater ecosystems, this study and others (see Ebner and Morgan, 2013; Ebner *et al.*, 2015; Schmid *et al.*, 2017; Jones *et al.*, 2019; van Wyk, 2019) indicate that the implementation of this method in freshwater monitoring shows promise. The combined results of this study illustrate that BRUVS are able to accurately produce data on species populations, for both *Metriaclima estherae* and *Potamonautes lirrangensis*, which is required to develop management protocols within the Meluluco area.

In Chapter 2 the footage obtained from the BRUVS was used to show that *Metriaclima estherae* abundance is prominently driven by substrate and the species displayed a preference for rocky habitat. The BRUVS also showed that males and females of the species occupy slightly different niches. Despite both sexes being observed more frequently in rocky substrate, males were found to be more common in sandier substrate while females were almost always excluded by it. Furthermore, males of the species were more abundant than females. The results of Chapter 4 indicated that stereo-BRUVS could be used to accurately measure the lengths of identifiable *M. estherae* individuals, showing that males were larger on average and had a wider length distribution (recorded between 50mm and 130mm) than females (50mm-100mm) which is in line with previous studies regarding *M. estherae* length (Konings 1995, Yedier *et al.*, 2014; Genner and Turner 2015; Oliver, 2018; Unver *et al.*, 2020). Smaller males were more commonly associated with sandy substrate, which could be a result of intraspecific competition influencing the dispersal of male *M. estherae*. Larger, older males and females regardless of their size were more frequently recorded in rocky substrate, which is indicative of the importance of rocky habitat to breeding adults. As *M. estherae* are mouth-brooders, they hold their young in their mouths until they are free swimming but do not guard their young after this stage, meaning that the fry are reliant on the sheltered refugia

provided by crevices in rocky substrate in which they are deposited by breeding females (Wickler, 1962; Trendall, 1988; Coffman, 2011).

The findings of this study highlighted key conservation concerns for *M. estherae*. They provide evidence to suggest that the protection of rocky habitat is the most efficient way to conserve the species populations. The lake is already facing an issue with this regarding siltation, resulting in rocky habitat becoming overlain with sand due to industrial development and poor agricultural practices along its banks (Ngochera, 2014). It also highlighted that males are more abundant than females which is uncommon in species like *M. estherae* which are polygamous (Knight *et al.*, 1999). This supports the hypothesis that siltation could be affecting *M. estherae* as females would be more susceptible to the loss of rocky habitat since they seemed to be confined to it. In addition to this, females are more sought after in the ornamental trade due to their bright colouration (Tweddle, 1992). The results obtained from the length data also showed promise for management of the species. The data allowed us to determine useful patterns about *M. estherae*'s use of the environment at different life stages, which could be used to time harvest of juveniles for the aquarium trade within a "Growth Phase" (explained in the discussion of Chapter 4) to minimise the long term effect on the population (Ng and Tan, 1997).

The BRUVS also successfully monitored *Potamonautes lirrangensis*. In Chapter 3, results showed that the species had a preference for rocky substrate and also appeared to be more common in shallower areas of the reef system. *Potamonautes lirrangensis* was most abundant in rocky areas between 1 to 10m deep, which is common for other lake dwelling crabs (Marijnissen *et al.*, 2009). This finding would flag siltation as a conservation issue for *P. lirrangensis* as well (Ngochera, 2014). The excess sediment could also pose an additional threat to this species as it increases the turbidity of the water and shades out the light required

by submerged macrophytes and algae for growth (Pullanikkatil *et al.*, 2015), which are primary sources of food for the species (Hecky *et al.*, 2003).

Since the use of BRUVS is still limited in the freshwater space (Whitmarsh *et al.*, 2017), further research is required to determine whether the method is viable as a “blanket tool” for monitoring the vast array of fauna living within the lake. It might be useful to compare between un-baited video systems to determine the influence of the bait on the results obtained, particularly because *M. estherae* did not take to the crushed Usipa (*Engraulicypris sardella*) as bait. Future research might also benefit from baiting the BRUVS with a variety of bait types to include the preferred diets of a wider array of species. This may increase the detection rate and influence the results for species that have a more plant based diet, like *M. estherae* who they primarily feed on algae growing on the rocks in the reef (Konings, 1995; Konings, 2018). Future studies would also benefit from increasing the scope of the BRUVS deployments to include a wider array of habitat types in different areas and at different depths of the lake as well as areas within the other designated KBA’s delineated by the IUCN.

In conclusion, the BRUVS were able to extract viable population data on the abundances and preferences of *Metriaclima estherae* and *Potamonautes lirrangensis* and could be useful to inform the management of these species and others like it, at least in the Meluluco Key Biodiversity Area. The method would be highly beneficial to the management of the lakes KBAs as it can provide long term monitoring data for a wide array of species via a cost-effective, non-invasive, non-extractive means. The method should be tried and tested on other important biodiversity areas within the lake and other freshwater ecosystems because it has the ability to bolster management efforts by underpinning them with easily available, long term monitoring data.

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APPENDICES

Appendix A: Complete count data set for *Metriaclima estherae* showing the MaxN counts for both males and females in the Meluluco Reef System, Lake Niassa, Mozambique, between the years 2016-2018.

<i>Metriaclima estherae</i>					
Site Code	Year	MaxN Female	MaxN Male	Total	
332_2016	2016	0	0	0	
333_2016	2016	0	0	0	
334_2016	2016	0	0	0	
335_2016	2016	0	0	0	
336_2016	2016	0	0	0	
337_2016	2016	0	0	0	
338_2016	2016	0	0	0	
339_2016	2016	0	0	0	
340_2016	2016	0	0	0	
341_2016	2016	0	0	0	
342_2016	2016	0	0	0	
343_2016	2016	0	0	0	
344_2016	2016	0	0	0	
345_2016	2016	0	0	0	
347_2016	2016	0	0	0	
348_2016	2016	0	0	0	
349_2016	2016	1	1	2	
350_2016	2016	1	2	3	
351_2016	2016	0	0	0	
352_2016	2016	0	0	0	
354_2016	2016	0	0	0	
356_2016	2016	0	1	1	
357_2016	2016	0	0	0	
362_2016	2016	0	0	0	
363_2016	2016	0	0	0	
364_2016	2016	0	0	0	
365_2016	2016	0	0	0	
370_2016	2016	1	5	6	
371_2016	2016	0	7	7	
372_2016	2016	0	3	3	
373_2016	2016	1	6	7	

374_2016	2016	0	0	0
375_2016	2016	0	0	0
376_2016	2016	3	2	5
377_2016	2016	2	0	2
378_2016	2016	3	3	6
379_2016	2016	0	1	1
380_2016	2016	1	5	6
381_2016	2016	1	0	1
382_2016	2016	4	6	10
383_2016	2016	5	0	5
384_2016	2016	0	0	0
385_2016	2016	0	0	0
386_2016	2016	0	0	0
387_2016	2016	0	0	0
388_2016	2016	0	0	0
389_2016	2016	0	0	0
390_2016	2016	0	0	0
391_2016	2016	0	0	0
392_2016	2016	0	0	0
393_2016	2016	0	0	0
394_2016	2016	0	0	0
395_2016	2016	0	0	0
396_2016	2016	0	0	0
397_2016	2016	0	0	0
398_2016	2016	0	0	0
399_2016	2016	0	0	0
401_2016	2016	0	0	0
402_2016	2016	0	0	0
403_2016	2016	0	0	0
404_2016	2016	0	0	0
405_2016	2016	0	0	0
406_2016	2016	0	0	0
407_2016	2016	0	0	0
410_2016	2016	0	1	1
411_2016	2016	1	0	1
413_2016	2016	0	0	0
414_2016	2016	0	0	0
415_2016	2016	0	0	0
416_2016	2016	3	0	3
419_2016	2016	0	0	0
420_2016	2016	0	0	0

422_2016	2016	4	0	4
423_2016	2016	4	0	4
424_2016	2016	0	0	0
457_2016	2016	0	0	0
458_2016	2016	0	0	0
459_2016	2016	0	0	0
460_2016	2016	2	0	2
461_2016	2016	0	0	0
462_2016	2016	2	0	2
463_2016	2016	1	0	1
464_2016	2016	0	0	0
465_2016	2016	3	1	4
466_2016	2016	1	1	2
467_2016	2016	0	0	0
468_2016	2016	3	2	5
469_2016	2016	5	0	5
470_2016	2016	0	0	0
471_2016	2016	0	0	0
472_2016	2016	0	0	0
473_2016	2016	0	0	0
474_2016	2016	0	0	0
476_2016	2016	1	0	1
477_2016	2016	0	0	0
478_2016	2016	0	0	0
479_2016	2016	0	0	0
482_2016	2016	0	0	0
483_2016	2016	3	0	3
484_2016	2016	0	0	0
485_2016	2016	0	0	0
487_2016	2016	0	0	0
488_2016	2016	2	0	2
489_2016	2016	0	0	0
491_2016	2016	3	0	3
494_2016	2016	4	0	4
495_2016	2016	2	0	2
496_2016	2016	2	0	2
497_2016	2016	6	1	7
498_2016	2016	13	1	14
499_2016	2016	21	2	23
500_2016	2016	2	0	2
501_2016	2016	4	9	13

502_2016	2016	4	0	4
503_2016	2016	31	4	35
504_2016	2016	0	0	0
505_2016	2016	3	1	4
3661_2016	2016	9	8	17
3662_2016	2016	6	16	22
3663_2016	2016	7	10	17
3664_2016	2016	2	3	5
3671_2016	2016	6	5	11
3672_2016	2016	5	17	22
3673_2016	2016	3	5	8
3674_2016	2016	4	7	11
3681_2016	2016	4	6	10
3682_2016	2016	4	2	6
3683_2016	2016	2	3	5
3684_2016	2016	3	2	5
3691_2016	2016	0	0	0
3692_2016	2016	2	1	3
3693_2016	2016	2	3	5
3694_2016	2016	1	2	3
4072_2016	2016	0	0	0
552_2017	2017	0	0	0
553_2017	2017	0	0	0
554_2017	2017	0	0	0
555_2017	2017	0	0	0
556_2017	2017	0	0	0
558_2017	2017	0	0	0
559_2017	2017	0	0	0
560_2017	2017	0	0	0
561_2017	2017	0	0	0
562_2017	2017	0	0	0
563_2017	2017	0	0	0
564_2017	2017	0	0	0
565_2017	2017	1	0	1
566_2017	2017	1	0	1
567_2017	2017	0	0	0
568_2017	2017	0	0	0
569_2017	2017	0	0	0
570_2017	2017	0	0	0
571_2017	2017	0	0	0

572_2017	2017	0	0	0
573_2017	2017	0	0	0
574_2017	2017	0	0	0
575_2017	2017	0	0	0
576_2017	2017	0	0	0
577_2017	2017	0	0	0
578_2017	2017	1	0	1
579_2017	2017	0	0	0
580_2017	2017	0	0	0
581_2017	2017	0	0	0
582_2017	2017	0	0	0
583_2017	2017	0	0	0
584_2017	2017	2	0	2
585_2017	2017	0	0	0
586_2017	2017	0	0	0
587_2017	2017	0	0	0
588_2017	2017	0	0	0
589_2017	2017	0	0	0
590_2017	2017	0	0	0
591_2017	2017	0	0	0
592_2017	2017	4	0	4
593_2017	2017	3	0	3
594_2017	2017	3	0	3
595_2017	2017	4	0	4
596_2017	2017	13	2	15
597_2017	2017	14	0	14
598_2017	2017	15	0	15
599_2017	2017	1	0	1
600_2017	2017	21	0	21
601_2017	2017	13	4	17
602_2017	2017	11	4	15
603_2017	2017	8	6	14
604_2017	2017	34	1	35
605_2017	2017	38	5	43
606_2017	2017	33	4	37
607_2017	2017	9	0	9
608_2017	2017	24	3	27
609_2017	2017	13	5	18
610_2017	2017	9	7	16
611_2017	2017	11	8	19
612_2017	2017	0	0	0

613_2017	2017	0	0	0
614_2017	2017	0	0	0
615_2017	2017	0	0	0
616_2017	2017	0	0	0
617_2017	2017	0	0	0
618_2017	2017	0	0	0
619_2017	2017	0	0	0
620_2017	2017	0	0	0
621_2017	2017	0	0	0
622_2017	2017	0	0	0
623_2017	2017	0	0	0
624_2017	2017	0	0	0
625_2017	2017	0	0	0
626_2017	2017	0	0	0
627_2017	2017	0	0	0
628_2017	2017	0	0	0
629_2017	2017	4	0	4
630_2017	2017	0	0	0
631_2017	2017	0	0	0
632_2017	2017	0	0	0
633_2017	2017	0	0	0
634_2017	2017	0	0	0
635_2017	2017	0	0	0
636_2017	2017	0	0	0
637_2017	2017	0	0	0
638_2017	2017	3	0	3
639_2017	2017	0	0	0
640_2017	2017	4	0	4
641_2017	2017	3	0	3
642_2017	2017	0	0	0
643_2017	2017	0	0	0
644_2017	2017	4	0	4
645_2017	2017	0	0	0
646_2017	2017	0	0	0
647_2017	2017	0	0	0
648_2017	2017	0	0	0
649_2017	2017	0	0	0
650_2017	2017	0	0	0
651_2017	2017	0	0	0
652_2017	2017	0	0	0
653_2017	2017	0	0	0

654_2017	2017	0	0	0
655_2017	2017	0	0	0
656_2017	2017	4	0	4
657_2017	2017	4	0	4
658_2017	2017	0	0	0
660_2017	2017	3	0	3
661_2017	2017	0	0	0
662_2017	2017	0	0	0
663_2017	2017	4	0	4
664_2017	2017	0	0	0
665_2017	2017	0	0	0
666_2017	2017	0	0	0
667_2017	2017	0	0	0
668_2017	2017	0	0	0
669_2017	2017	0	0	0
670_2017	2017	0	0	0
671_2017	2017	3	0	3
672_2017	2017	5	0	5
674_2017	2017	9	0	9
675_2017	2017	12	0	12
676_2017	2017	6	0	6
677_2017	2017	4	0	4
678_2017	2017	34	1	35
679_2017	2017	16	1	17
680_2017	2017	8	0	8
681_2017	2017	6	0	6
44_2018	2018	0	0	0
45_2018	2018	0	0	0
46_2018	2018	0	0	0
47_2018	2018	0	0	0
48_2018	2018	0	0	0
49_2018	2018	0	0	0
50_2018	2018	3	0	3
51_2018	2018	0	0	0
52_2018	2018	0	0	0
53_2018	2018	0	0	0
54_2018	2018	0	0	0
55_2018	2018	0	0	0
56_2018	2018	6	14	20
57_2018	2018	4	11	15

58_2018	2018	8	2	10
60_2018	2018	6	6	12
61_2018	2018	31	4	35
62_2018	2018	3	3	6
63_2018	2018	22	5	27
64_2018	2018	9	8	17
65_2018	2018	4	15	19
66_2018	2018	7	6	13
67_2018	2018	11	24	35
330_2018	2018	0	0	0
331_2018	2018	0	0	0
332_2018	2018	1	1	2
333_2018	2018	3	6	9
334_2018	2018	4	2	6
335_2018	2018	5	2	7
336_2018	2018	3	2	5
337_2018	2018	2	1	3
338_2018	2018	0	0	0
343_2018	2018	0	0	0
344_2018	2018	0	0	0
345_2018	2018	0	1	1
346_2018	2018	0	0	0
347_2018	2018	1	2	3
348_2018	2018	0	0	0
349_2018	2018	0	0	0
350_2018	2018	0	0	0
351_2018	2018	0	0	0
352_2018	2018	3	0	3
353_2018	2018	0	0	0
354_2018	2018	0	0	0
357_2018	2018	0	0	0
358_2018	2018	0	0	0
359_2018	2018	1	0	1
360_2018	2018	0	2	2
361_2018	2018	0	0	0
362_2018	2018	1	0	1
363_2018	2018	0	0	0
364_2018	2018	3	0	3
365_2018	2018	0	0	0
366_2018	2018	0	0	0
367_2018	2018	0	2	2

368_2018	2018	1	1	2
369_2018	2018	0	0	0
370_2018	2018	1	2	3
371_2018	2018	15	10	25
372_2018	2018	5	2	7
373_2018	2018	6	5	11
375_2018	2018	5	4	9
376_2018	2018	10	2	12
377_2018	2018	8	3	11
378_2018	2018	9	6	15
379_2018	2018	7	5	12
380_2018	2018	4	5	9
381_2018	2018	10	2	12
Total		857	372	1229

Appendix B: Complete count data set for *Potamonautes lirrangensis* showing the MaxN counts for the species in the Meluluco Reef System, Lake Niassa, Mozambique, between the years 2016-2018.

<i>Potamonautes lirrangensis</i>			
SiteCode	Year	MaxN	
332_2016	2016	0	
333_2016	2016	0	
334_2016	2016	0	
335_2016	2016	0	
336_2016	2016	0	
337_2016	2016	0	
338_2016	2016	0	
339_2016	2016	0	
340_2016	2016	0	
341_2016	2016	0	
342_2016	2016	0	
343_2016	2016	0	
344_2016	2016	0	
345_2016	2016	0	
347_2016	2016	0	
348_2016	2016	0	
349_2016	2016	1	
350_2016	2016	0	
351_2016	2016	0	
352_2016	2016	0	
354_2016	2016	0	
356_2016	2016	0	
357_2016	2016	0	
362_2016	2016	0	
363_2016	2016	0	
364_2016	2016	0	
365_2016	2016	0	
370_2016	2016	1	
371_2016	2016	1	
372_2016	2016	0	

373_2016	2016	1
374_2016	2016	0
375_2016	2016	0
376_2016	2016	0
377_2016	2016	1
378_2016	2016	0
379_2016	2016	1
380_2016	2016	1
381_2016	2016	0
382_2016	2016	0
383_2016	2016	2
384_2016	2016	0
385_2016	2016	0
386_2016	2016	0
387_2016	2016	0
388_2016	2016	0
389_2016	2016	0
390_2016	2016	0
391_2016	2016	0
392_2016	2016	0
393_2016	2016	0
394_2016	2016	0
395_2016	2016	0
396_2016	2016	0
397_2016	2016	0
398_2016	2016	0
399_2016	2016	0
401_2016	2016	0
402_2016	2016	0
403_2016	2016	0
404_2016	2016	0
405_2016	2016	0
406_2016	2016	0
407_2016	2016	0

410_2016	2016	0
411_2016	2016	0
413_2016	2016	0
414_2016	2016	0
415_2016	2016	0
416_2016	2016	0
419_2016	2016	0
420_2016	2016	0
422_2016	2016	1
423_2016	2016	0
424_2016	2016	0
457_2016	2016	0
458_2016	2016	1
459_2016	2016	0
460_2016	2016	0
461_2016	2016	0
462_2016	2016	0
463_2016	2016	1
464_2016	2016	0
465_2016	2016	1
466_2016	2016	1
467_2016	2016	0
468_2016	2016	0
469_2016	2016	0
470_2016	2016	0
471_2016	2016	0
472_2016	2016	0
473_2016	2016	0
474_2016	2016	0
476_2016	2016	0
477_2016	2016	0
478_2016	2016	0
479_2016	2016	0
482_2016	2016	0

483_2016	2016	0
484_2016	2016	0
485_2016	2016	0
487_2016	2016	0
488_2016	2016	0
489_2016	2016	0
491_2016	2016	0
494_2016	2016	2
495_2016	2016	1
496_2016	2016	0
497_2016	2016	1
498_2016	2016	1
499_2016	2016	1
500_2016	2016	2
501_2016	2016	1
502_2016	2016	0
503_2016	2016	0
504_2016	2016	0
505_2016	2016	1
3661_2016	2016	0
3662_2016	2016	1
3663_2016	2016	1
3664_2016	2016	0
3671_2016	2016	0
3672_2016	2016	0
3673_2016	2016	0
3674_2016	2016	0
3681_2016	2016	0
3682_2016	2016	0
3683_2016	2016	1
3684_2016	2016	1
3691_2016	2016	1
3692_2016	2016	0
3693_2016	2016	1

3694_2016	2016	0
4072_2016	2016	0
552_2017	2017	0
553_2017	2017	0
554_2017	2017	0
555_2017	2017	0
556_2017	2017	0
558_2017	2017	0
559_2017	2017	0
560_2017	2017	0
561_2017	2017	0
562_2017	2017	1
563_2017	2017	0
564_2017	2017	0
565_2017	2017	0
566_2017	2017	0
567_2017	2017	0
568_2017	2017	0
569_2017	2017	0
570_2017	2017	0
571_2017	2017	0
572_2017	2017	0
573_2017	2017	0
574_2017	2017	0
575_2017	2017	0
576_2017	2017	0
577_2017	2017	0
578_2017	2017	0
579_2017	2017	0
580_2017	2017	0
581_2017	2017	0
582_2017	2017	0
583_2017	2017	0
584_2017	2017	0

585_2017	2017	0
586_2017	2017	0
587_2017	2017	0
588_2017	2017	0
589_2017	2017	0
590_2017	2017	0
591_2017	2017	0
592_2017	2017	0
593_2017	2017	0
594_2017	2017	0
595_2017	2017	2
596_2017	2017	8
597_2017	2017	1
598_2017	2017	1
599_2017	2017	3
600_2017	2017	3
601_2017	2017	4
602_2017	2017	2
603_2017	2017	1
604_2017	2017	3
605_2017	2017	3
606_2017	2017	3
607_2017	2017	0
608_2017	2017	2
609_2017	2017	2
610_2017	2017	0
611_2017	2017	3
612_2017	2017	0
613_2017	2017	0
614_2017	2017	0
615_2017	2017	0
616_2017	2017	0
617_2017	2017	0
618_2017	2017	0

619_2017	2017	0
620_2017	2017	0
621_2017	2017	0
622_2017	2017	0
623_2017	2017	0
624_2017	2017	0
625_2017	2017	0
626_2017	2017	0
627_2017	2017	0
628_2017	2017	0
629_2017	2017	0
630_2017	2017	0
631_2017	2017	1
632_2017	2017	0
633_2017	2017	0
634_2017	2017	0
635_2017	2017	2
636_2017	2017	0
637_2017	2017	0
638_2017	2017	0
639_2017	2017	0
640_2017	2017	0
641_2017	2017	0
642_2017	2017	0
643_2017	2017	0
644_2017	2017	0
645_2017	2017	0
646_2017	2017	0
647_2017	2017	0
648_2017	2017	0
649_2017	2017	0
650_2017	2017	1
651_2017	2017	0
652_2017	2017	0

653_2017	2017	0
654_2017	2017	0
655_2017	2017	0
656_2017	2017	0
657_2017	2017	0
658_2017	2017	0
660_2017	2017	0
661_2017	2017	0
662_2017	2017	0
663_2017	2017	0
664_2017	2017	0
665_2017	2017	0
666_2017	2017	0
667_2017	2017	0
668_2017	2017	0
669_2017	2017	0
670_2017	2017	0
671_2017	2017	0
672_2017	2017	0
674_2017	2017	0
675_2017	2017	0
676_2017	2017	0
677_2017	2017	0
678_2017	2017	0
679_2017	2017	0
680_2017	2017	0
681_2017	2017	0
44_2018	2018	0
45_2018	2018	0
46_2018	2018	0
47_2018	2018	0
48_2018	2018	0
49_2018	2018	0
50_2018	2018	0

51_2018	2018	0
52_2018	2018	0
53_2018	2018	0
54_2018	2018	0
55_2018	2018	0
56_2018	2018	2
57_2018	2018	2
58_2018	2018	1
60_2018	2018	2
61_2018	2018	1
62_2018	2018	0
63_2018	2018	0
64_2018	2018	0
65_2018	2018	0
66_2018	2018	0
67_2018	2018	0
330_2018	2018	0
331_2018	2018	1
332_2018	2018	0
333_2018	2018	1
334_2018	2018	0
335_2018	2018	0
336_2018	2018	1
337_2018	2018	1
338_2018	2018	0
343_2018	2018	0
344_2018	2018	0
345_2018	2018	0
346_2018	2018	0
347_2018	2018	0
348_2018	2018	0
349_2018	2018	1
350_2018	2018	0
351_2018	2018	0

352_2018	2018	0
353_2018	2018	0
354_2018	2018	0
357_2018	2018	0
358_2018	2018	0
359_2018	2018	0
360_2018	2018	1
361_2018	2018	0
362_2018	2018	3
363_2018	2018	0
364_2018	2018	0
365_2018	2018	0
366_2018	2018	0
367_2018	2018	0
368_2018	2018	1
369_2018	2018	0
370_2018	2018	0
371_2018	2018	3
372_2018	2018	5
373_2018	2018	0
375_2018	2018	1
376_2018	2018	3
377_2018	2018	0
378_2018	2018	3
379_2018	2018	1
380_2018	2018	3
381_2018	2018	2
Total		115

Appendix C: Complete habitat variable data set for showing the depth and the habitat variables present (in %) for each of the 329 sites sampled in the Meluluco Reef System, Lake Niassa, Mozambique, between the years 2016-2018.

SiteCode	Year	Habitat				
		Depth	Rock (%)	Cobble (%)	Sand (%)	Vegetation (%)
332_2016	2016	2.4	10	0	80	10
333_2016	2016	5.4	15	80	5	0
334_2016	2016	10.5	0	0	100	0
335_2016	2016	17.2	0	0	100	0
336_2016	2016	1.7	15	60	0	25
337_2016	2016	5.4	0	50	25	25
338_2016	2016	10.7	0	0	100	0
339_2016	2016	15.4	0	0	100	0
340_2016	2016	2.4	0	75	5	20
341_2016	2016	5.4	0	20	80	0
342_2016	2016	9.8	0	0	100	0
343_2016	2016	16.2	0	0	100	0
344_2016	2016	2.6	0	0	100	0
345_2016	2016	5	0	0	100	0
347_2016	2016	8.5	0	0	100	0
348_2016	2016	15.4	0	0	100	0
349_2016	2016	2.4	80	10	10	0
350_2016	2016	4.5	70	30	0	0
351_2016	2016	10.5	85	5	10	0
352_2016	2016	12.8	0	0	100	0
354_2016	2016	9.2	0	0	100	0
356_2016	2016	5.5	75	10	15	0
357_2016	2016	15	0	0	100	0
362_2016	2016	6.4	0	10	90	0
363_2016	2016	5.8	0	40	60	0
364_2016	2016	5.2	0	0	100	0
365_2016	2016	5.4	0	0	100	0
370_2016	2016	5.8	100	0	0	0
371_2016	2016	6	90	10	0	0
372_2016	2016	4.5	85	15	0	0
373_2016	2016	5	90	0	10	0
374_2016	2016	5.6	0	0	100	0
375_2016	2016	5	0	0	100	0
376_2016	2016	3.7	0	60	40	0
377_2016	2016	3.7	60	20	20	0
378_2016	2016	5	40	40	20	0
379_2016	2016	5	55	30	15	0
380_2016	2016	5.5	80	20	0	0
381_2016	2016	4.7	0	0	100	0
382_2016	2016	8.2	100	0	0	0

383_2016	2016	8.9	80	0	20	0
384_2016	2016	9.1	0	0	100	0
385_2016	2016	9	0	0	100	0
386_2016	2016	1.7	0	0	100	0
387_2016	2016	1.7	0	0	90	10
388_2016	2016	1.7	0	0	90	10
389_2016	2016	1.9	0	10	0	90
390_2016	2016	2.9	0	0	90	10
391_2016	2016	2.1	0	0	80	20
392_2016	2016	2.4	0	0	80	20
393_2016	2016	2.1	0	0	100	0
394_2016	2016	2.6	0	0	80	20
395_2016	2016	2.2	0	0	10	90
396_2016	2016	2.1	0	0	90	10
397_2016	2016	2.1	0	0	50	50
398_2016	2016	5.3	0	0	80	20
399_2016	2016	9.8	0	0	100	0
401_2016	2016	2.5	0	0	90	10
402_2016	2016	4.8	0	0	85	15
403_2016	2016	4.4	0	0	100	0
404_2016	2016	5.3	0	0	100	0
405_2016	2016	5.4	0	0	100	0
406_2016	2016	5.6	0	0	100	0
407_2016	2016	5.3	0	0	100	0
410_2016	2016	5.7	0	0	100	0
411_2016	2016	4.8	0	0	100	0
413_2016	2016	10.6	0	0	100	0
414_2016	2016	10.3	0	0	100	0
415_2016	2016	8.9	0	0	100	0
416_2016	2016	9	0	0	100	0
419_2016	2016	10.1	0	0	100	0
420_2016	2016	10.4	0	0	100	0
422_2016	2016	12	25	50	25	0
423_2016	2016	10.6	0	0	100	0
424_2016	2016	10.5	0	0	100	0
457_2016	2016	15.3	0	0	100	0
458_2016	2016	15.8	0	0	90	10
459_2016	2016	14.8	0	0	100	0
460_2016	2016	15.3	0	0	100	0
461_2016	2016	15.3	0	0	100	0
462_2016	2016	15.6	0	0	100	0
463_2016	2016	15.8	0	0	100	0
464_2016	2016	15.6	0	0	100	0
465_2016	2016	15.2	30	30	40	0
466_2016	2016	15.5	60	0	40	0
467_2016	2016	15.8	0	0	100	0

468_2016	2016	15.5	100	0	0	0
469_2016	2016	15.3	0	0	100	0
470_2016	2016	15	0	0	100	0
471_2016	2016	16	0	0	100	0
472_2016	2016	13.9	0	0	100	0
473_2016	2016	8.3	0	0	100	0
474_2016	2016	10.3	0	0	100	0
476_2016	2016	10.6	0	0	100	0
477_2016	2016	15.5	0	0	100	0
478_2016	2016	13.3	0	0	100	0
479_2016	2016	15.5	0	0	100	0
482_2016	2016	10	0	0	100	0
483_2016	2016	15.5	0	0	100	0
484_2016	2016	4.1	0	0	100	0
485_2016	2016	3.9	0	0	100	0
487_2016	2016	3.5	0	0	100	0
488_2016	2016	5.4	0	0	95	5
489_2016	2016	4.8	0	0	100	0
491_2016	2016	6.2	0	0	100	0
494_2016	2016	9.7	15	25	60	0
495_2016	2016	9.1	100	0	0	0
496_2016	2016	14.9	0	0	100	0
497_2016	2016	13.4	60	10	30	0
498_2016	2016	12.4	40	35	25	0
499_2016	2016	15.3	40	25	35	0
500_2016	2016	14.6	20	40	40	0
501_2016	2016	10.7	25	60	15	0
502_2016	2016	15.8	80	20	0	0
503_2016	2016	16.2	0	45	55	0
504_2016	2016	14.5	0	0	100	0
505_2016	2016	14.5	100	0	0	0
3661_2016	2016	1	100	0	0	0
3662_2016	2016	1	35	55	10	0
3663_2016	2016	1	35	55	10	0
3664_2016	2016	1	100	0	0	0
3671_2016	2016	1	100	0	0	0
3672_2016	2016	1	100	0	0	0
3673_2016	2016	1	100	0	0	0
3674_2016	2016	1	100	0	0	0
3681_2016	2016	1	100	0	0	0
3682_2016	2016	2.3	100	0	0	0
3683_2016	2016	2.3	100	0	0	0
3684_2016	2016	2.3	100	0	0	0
3691_2016	2016	1.9	50	10	40	0
3692_2016	2016	1.9	100	0	0	0
3693_2016	2016	1.9	100	0	0	0

3694_2016	2016	1.9	60	20	20	0
4072_2016	2016	5.5	0	0	100	0
552_2017	2017	2.7	0	70	20	10
553_2017	2017	3	0	60	30	10
554_2017	2017	3	0	70	25	5
555_2017	2017	3.5	0	10	90	0
556_2017	2017	3.2	0	80	15	5
558_2017	2017	2.8	0	0	100	0
559_2017	2017	2.5	0	0	100	0
560_2017	2017	2.9	0	0	100	0
561_2017	2017	3.2	0	0	80	20
562_2017	2017	4.8	0	20	80	0
563_2017	2017	4.7	0	10	90	0
564_2017	2017	4.6	0	20	80	0
565_2017	2017	5.2	0	10	90	0
566_2017	2017	5.8	0	15	85	0
567_2017	2017	5.5	0	0	100	0
568_2017	2017	5.5	0	0	90	10
569_2017	2017	5.2	0	0	95	5
570_2017	2017	4.6	0	0	100	0
571_2017	2017	4.4	0	0	80	20
572_2017	2017	9.5	0	0	100	0
573_2017	2017	7.5	0	0	100	0
574_2017	2017	4.1	0	0	100	0
575_2017	2017	5.7	0	0	100	0
576_2017	2017	7.9	0	0	100	0
577_2017	2017	7.2	0	0	100	0
578_2017	2017	7.7	0	0	100	0
579_2017	2017	7.9	0	0	100	0
580_2017	2017	7.3	0	0	100	0
581_2017	2017	7.4	0	0	100	0
582_2017	2017	2.4	0	0	70	30
583_2017	2017	2.6	0	0	100	0
584_2017	2017	2.5	60	0	30	10
585_2017	2017	2.2	0	0	100	0
586_2017	2017	2.3	0	0	100	0
587_2017	2017	2.3	0	0	100	0
588_2017	2017	2.4	0	0	100	0
589_2017	2017	2.7	0	0	100	0
590_2017	2017	8.5	0	0	100	0
591_2017	2017	3.1	0	0	100	0
592_2017	2017	13	0	0	100	0
593_2017	2017	10.2	0	0	100	0
594_2017	2017	9.1	0	0	100	0
595_2017	2017	9.5	0	45	55	0
596_2017	2017	9.4	60	0	40	0

597_2017	2017	9.7	70	10	20	0
598_2017	2017	10.3	90	0	10	0
599_2017	2017	9.7	0	80	20	0
600_2017	2017	10.3	10	30	60	0
601_2017	2017	8.3	90	5	5	0
602_2017	2017	9.8	60	0	40	0
603_2017	2017	10.7	70	0	30	0
604_2017	2017	11.5	35	10	55	0
605_2017	2017	12.2	70	10	20	0
606_2017	2017	12.7	90	0	10	0
607_2017	2017	14.7	90	10	0	0
608_2017	2017	15.3	80	10	10	0
609_2017	2017	13	60	20	20	0
610_2017	2017	11.3	100	0	0	0
611_2017	2017	7.5	100	0	0	0
612_2017	2017	17.2	0	0	100	0
613_2017	2017	15.2	0	0	100	0
614_2017	2017	13.6	0	0	100	0
615_2017	2017	11.8	0	0	100	0
616_2017	2017	13.6	0	0	100	0
617_2017	2017	14.9	0	0	100	0
618_2017	2017	16.3	0	0	100	0
619_2017	2017	1.7	0	0	60	40
620_2017	2017	1.1	0	70	30	0
621_2017	2017	1.2	0	20	50	30
622_2017	2017	1.1	0	70	20	10
623_2017	2017	1	0	80	0	20
624_2017	2017	1.2	0	70	10	20
625_2017	2017	1.3	0	70	20	10
626_2017	2017	1.2	0	70	10	20
627_2017	2017	1.3	0	80	15	5
628_2017	2017	2	0	65	20	15
629_2017	2017	6.9	0	10	90	0
630_2017	2017	6.8	0	40	60	0
631_2017	2017	5.6	0	25	15	60
632_2017	2017	5.1	0	10	20	70
633_2017	2017	5.2	0	10	5	85
634_2017	2017	5	0	40	20	40
635_2017	2017	5.4	0	5	5	90
636_2017	2017	6.1	0	45	55	0
637_2017	2017	7	0	20	80	0
638_2017	2017	13.9	0	0	100	0
639_2017	2017	13.8	0	0	100	0
640_2017	2017	10.1	0	0	100	0
641_2017	2017	15.8	0	0	100	0
642_2017	2017	18	0	0	100	0

643_2017	2017	15	0	0	100	0
644_2017	2017	10	0	0	100	0
645_2017	2017	11	0	0	100	0
646_2017	2017	10.4	0	0	100	0
647_2017	2017	35.4	0	0	100	0
648_2017	2017	38.2	0	0	100	0
649_2017	2017	35.7	0	70	20	10
650_2017	2017	32.2	0	0	100	0
651_2017	2017	30.1	0	0	100	0
652_2017	2017	34.5	0	0	100	0
653_2017	2017	39.2	0	0	100	0
654_2017	2017	49.5	0	0	100	0
655_2017	2017	40.6	0	0	100	0
656_2017	2017	42.6	0	0	100	0
657_2017	2017	44.2	0	0	100	0
658_2017	2017	49	0	10	20	70
660_2017	2017	50	0	0	100	0
661_2017	2017	52.1	10	0	90	0
662_2017	2017	52.4	0	0	100	0
663_2017	2017	47.8	0	0	100	0
664_2017	2017	55.4	0	0	100	0
665_2017	2017	51.2	0	0	100	0
666_2017	2017	29.5	0	0	100	0
667_2017	2017	22.9	0	0	100	0
668_2017	2017	31.4	0	0	100	0
669_2017	2017	34.5	20	0	80	0
670_2017	2017	37.6	0	0	100	0
671_2017	2017	30.1	0	0	100	0
672_2017	2017	32.5	0	0	100	0
674_2017	2017	39.7	0	0	100	0
675_2017	2017	43.7	0	0	100	0
676_2017	2017	40.9	0	40	60	0
677_2017	2017	43.7	0	10	90	0
678_2017	2017	49.5	100	0	0	0
679_2017	2017	64.9	100	0	0	0
680_2017	2017	62.5	0	0	100	0
681_2017	2017	54.4	0	0	100	0
44_2018	2018	5.6	0	0	100	0
45_2018	2018	5.5	0	0	100	0
46_2018	2018	7	0	0	100	0
47_2018	2018	8.6	0	0	100	0
48_2018	2018	5.5	0	0	100	0
49_2018	2018	9.1	0	0	100	0
50_2018	2018	6	20	0	80	0
51_2018	2018	6.8	0	0	100	0
52_2018	2018	4.9	0	0	100	0

53_2018	2018	6.3	0	0	100	0
54_2018	2018	4.2	0	0	100	0
55_2018	2018	2.7	0	0	100	0
56_2018	2018	6.2	70	15	15	0
57_2018	2018	6.4	100	0	0	0
58_2018	2018	9.8	15	15	70	0
60_2018	2018	7.5	65	25	10	0
61_2018	2018	8.2	5	10	85	0
62_2018	2018	10.7	100	0	0	0
63_2018	2018	6.5	20	60	20	0
64_2018	2018	6.4	100	0	0	0
65_2018	2018	9.4	100	0	0	0
66_2018	2018	10.9	30	25	45	0
67_2018	2018	10.8	100	0	0	0
330_2018	2018	34.6	0	0	100	0
331_2018	2018	30.1	0	0	100	0
332_2018	2018	7.6	100	0	0	0
333_2018	2018	8	50	20	30	0
334_2018	2018	9.8	60	0	40	0
335_2018	2018	12	100	0	0	0
336_2018	2018	14.9	70	0	30	0
337_2018	2018	14.7	20	0	80	0
338_2018	2018	3.7	0	0	70	30
343_2018	2018	8.9	0	0	100	0
344_2018	2018	3.3	0	0	55	45
345_2018	2018	10	0	20	80	0
346_2018	2018	2.8	0	0	20	80
347_2018	2018	8.3	100	0	0	0
348_2018	2018	2.5	0	0	20	80
349_2018	2018	14.4	100	0	0	0
350_2018	2018	3.9	0	30	70	0
351_2018	2018	13.1	0	0	100	0
352_2018	2018	6	0	0	100	0
353_2018	2018	6.9	0	0	100	0
354_2018	2018	20.2	0	0	100	0
357_2018	2018	30.7	0	0	100	0
358_2018	2018	3.1	0	10	90	0
359_2018	2018	20.5	0	0	100	0
360_2018	2018	2.8	100	0	0	0
361_2018	2018	26.8	0	0	100	0
362_2018	2018	31.8	0	15	85	0
363_2018	2018	34.5	0	0	100	0
364_2018	2018	30.7	0	0	100	0
365_2018	2018	20.9	0	0	100	0
366_2018	2018	6.5	10	0	90	0
367_2018	2018	4.7	100	0	0	0

368_2018	2018	5.1	20	20	60	0
369_2018	2018	4.1	0	0	100	0
370_2018	2018	3.6	100	0	0	0
371_2018	2018	9.9	100	0	0	0
372_2018	2018	9.5	0	35	65	0
373_2018	2018	8.2	100	0	0	0
375_2018	2018	7.4	100	0	0	0
376_2018	2018	7.8	85	0	15	0
377_2018	2018	6.7	50	20	30	0
378_2018	2018	6.6	80	10	10	0
379_2018	2018	9.2	100	0	0	0
380_2018	2018	8.1	100	0	0	0
381_2018	2018	9.3	55	0	45	0

Appendix D: Complete length data set for *Metriaclima estherae* showing the length (in mm) for males and females of the species in the Meluluco Reef System, Lake Niassa, Mozambique, in the year 2018.

Site Code	Fish	Sex	Length (mm)
7	1	Male	120.7
7	2	Male	69.9
7	3	Male	62.8
13	1	Male	88.2
13	2	Male	71.1
13	3	Male	87.2
13	4	Male	80
13	5	Male	88.4
13	6	Male	86.1
13	1	Female	67.8
13	2	Female	85.2
13	3	Female	72
13	4	Female	71.4
13	5	Female	70
13	6	Female	62
13	7	Female	73.2
13	8	Female	76.3
13	9	Female	77.2
13	10	Female	77.8
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15	4	Male	74.4
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