Management of water hyacinth (*Pontederia crassipes*) on the Hartbeespoort Dam in the North West, South Africa: An impact assessment.

by

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Declaration

All the work described in this thesis is my own and has never been submitted for examination with any University. It is submitted to Rhodes University for the degree of Doctor of Philosophy.

DEDICATION

This thesis is dedicated to my late mother, Desia Tsema Sebola (24 April 1955 – 21 November 2022). Thank you for teaching us the importance of education and reminding me that greatness requires resilience.

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Abstract

Invasion of freshwater bodies in South Africa by Invasive Alien Plants (IAPs) is common. This is primarily due to the construction of impoundments to meet water demands of the water-scarce country which have altered the hydrology of rivers, and this linked to anthopogenically driven eutrophication creates the ideal habitat for these plants. The Hartbeespoort Dam, a hypertrophic urban freshwater system in a temperate region of South Africa, is prone to aquatic weed infestations and algal blooms owing to the influx of nutrient from the urban spaces and agricultural activities upstream of the Dam. *Pontederia crassipes* (water hyacinth) first infested the dam in the early 1970s, leading to a 24-year chemical control programme which ended in 2016 with a moratorium on herbicide use. Biological control agents, introduced to the dam in the 1980s, had been hindered by the constant use of herbicides, and the moratorium enabled the proliferation of these agents. Although the *Neochetina* weevil spp. *N. eichhorniae,* and *N. bruchi* as well as the mite, *Orthogalumna terebrantis*, mirid, *Eccritotarsus catarensis*, and the moth, *Niphograpta albuguttalis*, were present, the weed was still not under control. The hypertrophic state of the dam helped the plants compensate for herbivory by the agents while the cool winters with frequent frosting events experienced in the highveld had a deleterious impact on the biological control.

The main aim of this thesis was to evaluate the impact of *Megamelus scutellaris,* a newly introduced water hyacinth biological control agent, on water hyacinth coverage on Hartbeespoort Dam. The second aim was to compare the impact biological control and mechanical control (manual removal) had on the aquatic ecosystem and if monocultural stands could still provide ecosystem services. The final aim was to establish the perception residents and visitors had about water hyacinth and to determine the most suitable methods for funding biological control activities

The hypothesis that augmentative releases of the newly introduced plant hopper, *Megamelus scutellaris* would reduce the water hyacinth coverage on the dam was not rejected, as, in January 2020 the insect density for *M. scutellaris* exceeded 6000 insects/m^2 which coincided with the reduction of water hyacinth coverage to below 5%. Monthly plant parameters and insect densities were assessed from October 2020- October 2022 to establish impact the introduction of *M. scutellaris* had on plant parameters and overall coverage of the dam by water hyacinth as confirmed through satellite imagery. Annually, in the spring there was a reinfestation of the dam through water hyacinth seedling recruitment necessitating the annual augmentative releases of *M. scutellaris.* The cold winters and frost adversely impacted

insect numbers resulting in the spring recruitment of seedlings being largely free of insect damage. To reduce the lag phase between the spring growth of water hyacinth coverage and the increase in agent populations augmentative releases of the insects are essential. The involvement of community-based satellite mass-rearing stations assisted with the release of high numbers of healthy insects into the system, even during the colder months. This is the first study where biological control alone has managed to reduce water hyacinth coverage on a high elevation, cool, temperate hypertrophic system. This approach is contrary to previous literature which indicated that an integrated management method that integrates elements of mechanical, chemical and biological control would be the only way to achieve control of water hyacinth.

Prior to 2020, the residents around the dam had used manual removal and mechanical control to manage the weed. The impact of mechanical and biological control on biodiversity of a previously colonized aquatic ecosystem was assessed. This was used to acquire empirical evidence that would inform future management strategies for water hyacinth. Mechanical removal leads to a drastic increase of nutrients in the water column which led to a proliferation of cyanobacterial blooms and therefore macrophyte removal has a positive impact on phytoplankton which is in direct competition with water hyacinth for nutrients and light. For other biodiversity indices macroinvertebrates decreased with macrophyte removal while removal had no impact on zooplankton. Comparatively, biological control allows the slow recovery of native macrophytes which led to a more diverse macrophyte population, responsible for keeping cyanobacteria numbers low. However, the biological control did lead to an increase in sedimentation. This can be reduced by integrating physical removal as the plants display severe leaf necrosis and browning. An undesired impact of the temporal absence of water hyacinth due to biological control facilitated the rapid increase in the invasive alien floating fern, *Salvinia minima* on the Dam.

Hartbeespoort Dam's revenue is generated through tourism and residential estate developments; therefore, the pristine state of the dam is essential for business, residents and visitors. A socio-economic survey was used to determine respondents' view of water hyacinth as a nuisance and their willingness to pay for its management. Additionally, the socio-economic factors that might influence willingness to pay were assessed. 299 electronic and printed surveys were completed but only 281 surveys were used for data analysis. Willingness to pay was not significantly influenced by the negative perception that respondents have of the aquatic weed, instead the respondent's gross income and residential status were the most influential factors for willingness to pay. Their willingness to pay was not influenced by the clearance level for the weed.

In conclusion the biological control is a better method for the management of water hyacinth and the dam’s biodiversity, however if the high nutrient influx continues unabated then the Hartbeespoort Dam will continue to have invasiv mass development through what is referred to as the invasive cascade, where one weed species is replaced by another after control. Aside from willingness to pay for its management an option of contributing labour should be given for residents to get involved in the management of water hyacinth by maintaining insect stocks at satellite mass rearing sites over winter and throughout the summer. A secondary biological control programme is needed for *S. minima*. Lastly, the management of water hyacinth in cool temperate regions with high levels of eutrophication requires strategic adaptive management.

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Chapter 1: General Introduction and Literature Review

1.1 Problem Statement

Since the 1500s, the number of people moving around the world has increased significantly, and as a consequence, the number of organisms introduced to regions where they are not native has also increased (Faulkner *et al*., 2020). Although only a small percentage of naturalized plant species become invasive, the ones that do have severe effects on native species diversity and ecosystem services provided by invaded habitats; with increasing international trade and globalization, introduction and naturalization of plant species outside their native range is likely to intensify (Hinz *et al*., 2019).

With its high environmental diversity in nine biomes, ranging from deserts to rainforests, South Africa is considered one of the planet's eighteen megadiverse countries as defined by Conservation International as those nations that harbour the majority of the Earth's species, with high numbers of endemic species (Van Wilgen *et al*., 2020). However, South Africa has experienced waves of colonization and migration, which have resulted in the deliberate introduction of plants and animals (Van Wilgen *et al*., 2020): bamboo came with the slaves from Java; medicinal plants with the indentured labourers from India; Australian *Acacia* and eucalyptus – plants for agriculture, horticulture, angling, medicinal purposes, animals as pets and ornamental plants. Although some invaders gained commercial importance, such as trees of the genera *Acacia*, *Eucalyptus* and *Pinus* which are used for timber and fuelwood, many of these introductions later became invasive species, (Richardson *et al*., 2020, Van Wilgen *et al*., 2020), among them is water hyacinth, *Pontederia* (=*Eichhornia*) *crassipes* Pellegrini and Horn (Pontederaceae) (Faulkner *et al*., 2020), the topic of this thesis.

Pontederia crassipes, commonly known as water hyacinth, was introduced to South Africa as an ornamental plant (Faulkner et al., 2020) for ponds because of its beautiful and attractive flowers (Figures 1.1. and 1.2) (Dechassa, 2020). It was first recorded in South Africa on the Cape Flats in 1908 and introduced to KwaZulu-Natal about the same time (van Wyk & van Wilgen, 2002).

Figure 1.1. Flowering water hyacinth plants on the Hartbeespoort Dam

Figure 1.2. The beautiful water hyacinth flower which led to it becoming an ornamental plant (Image from Hartbeespoort Dam).

Water hyacinth, a perennial, free-floating aquatic plant from the Amazon Basin in South America, spread in the late 1800s across continents and was shared between regions that have common watersheds (Hill & Coetzee, 2008). It has established in tropical and subtropical countries of the world, where it has become invasive in many of the water bodies (Hill & Coetzee, 2008; Faltlhauser *et al*., 2022). Waterbody managers have used chemical, physical or biological control methods to keep the weed at acceptable levels.

This thesis focuses on the management of water hyacinth on a freshwater system, the Hartbeespoort Dam located in the North West Province of South Africa, where this plant is invasive. A moratorium on the use of chemical control of the dam opened an opportunity to focus on biological control in addition to physical or mechanical removal as the control measures available for use. Biological control of water hyacinth has been successful in a large number of tropical water bodies, mainly in sub-Saharan Africa (Hill & Coetzee, 2008). In contrast, despite the release and establishment of a suite of biological control agents on the Hartbeespoort Dam, control had not been achieved. Arguably this is due to cold winter temperatures experienced at Hartbeespoort Dam, which is in the highveld region of South Africa, and is characterised by cold temperate conditions, which limits control agent population increases. Furthermore, the hypertrophic status of the water body allows the plants to thrive even under herbivore pressure.

1.2 Freshwater Invasions

The proliferation of IAPs in South Africa's freshwater bodies began in the late 1800s with the introduction of trout and water hyacinth (Hill *et al*., 2020). Invasion is usually driven by disturbance (Uyà *et al*., 2018) and thus, in South Africa, invasion of the freshwater environment is invariably a symptom of eutrophication or nutrient loading, and the change in hydrological flow regimes through the construction of weirs and dams into impoundments (Byrne *et al*., 2010, Coetzee *et al*., 2012). Eutrophication is the process of excessive nutrient enrichment of waters that typically results in problems associated with invasive aquatic plants, algal and cyanobacterial growth (Pannard *et al*., 2024). High nutrient concentrations are the result of natural and cultural nutrient influxes (Van Ginkel, 2011). Natural eutrophication is the influx of nutrients from natural sources such as rocks, soil, and other natural sources within the catchment area; it is thus irreversible and uncontrolled, but contributes very little, whereas cultural eutrophication is related to anthropogenic activities, that is, human, social and economic activities (Van Ginkel, 2011). The main cause of nutrient accumulation is industrialization and rapid urbanization, with storm-water runoff and discharge of sewage into lakes being the two most common ways nutrients enter the aquatic ecosystem (Dhote, 2007). In theory, this form of eutrophication is controllable as people can minimize the impact of their activity on the waterbody (Van Ginkel, 2011).

Over the course of the past 40 years, eutrophication has become an increasing threat to the sustainability of South Africa's freshwater resources (Van Ginkel, 2011). South Africa has some of the most eutrophic aquatic ecosystems in the world, due to an increase in pollution resulting from a developing economy, urbanisation, coupled with failing wastewater infrastructure (Coetzee *et al*., 2012). Like many developing countries, South Africa is characterized by rapid rates of urbanization (Chapungu *et al*., 2018). As the urban centres grow spatially and demographically, developing countries are confronted by waste disposal challenges that often result in water pollution (Chapungu *et al*., 2018) and because the majority of South African reservoirs and impoundments are located downstream of densely populated urban areas, they receive improperly treated waste

water (Coetzee *et al*., 2012).

Chamier *et al*. (2012) found that the disturbance caused by increased nutrient concentrations contributes to the eutrophication process, resulting in toxic algal (cyanobacterial) blooms and excessive macrophyte growth. Many cyanobacterial genera produce one or more of a range of cyanotoxins, and many are associated with taste and odour problems encountered by water treatment works (Van Ginkel, 2011). Ingesting water containing high concentrations of cyanobacterial toxins presents a risk to human and animal health (Van Ginkel, 2011).

Macrophytes are grouped into submerged, emergent, and floating-leaved, based on the relation of the leaf with the water (Gupta *et al*., 2012). Native macrophyte vegetation plays an important role in maintaining water quality and ecosystem functioning of water bodies (Dhote, 2007; Gupta *et al*, 2012), traits that were first recognized in the 1960s and 1970s (Gupta *et al*., 2012). These plants improve water quality by absorbing nutrients through their effective root systems but also increase sedimentation (Gupta *et al*, 2012). Where there is an excessive amount of introduced macrophyte biomass, it blocks waterways, impedes access to dams and rivers, clogs drainage systems and contributes to flooding and the destruction of canals (Van Ginkel, 2011). The widespread economic damage is matched by the ecological effects which alter the habitat and displace indigenous flora and fauna (Van Ginkel, 2011).

In South Africa a number of aquatic macrophytes are problematic invasive alien species, among them, water hyacinth, water ferns (*Azolla filiculoides* Lam. and *Azolla cristata*

Kaulf. (Azollaceae)), water lettuce (*Pistia stratiotes* L. (Araceae)), salvinia (*Salvinia molesta* D.S. Mitchell and *Salvinia minima* Baker (Salviniaceae)), hydrilla (*Hydrilla verticillata* (L.f.) Royle Hydrocharitaceae), parrot's feather (*Myriophyllum aquaticum* (Vell.) Verdc. (Haloragaceae)), Brazilian waterweed (*Egeria densa* Planch. (Hydrocharitaceae)), yellow flag (*Iris pseudacorus* L. (Iridaceae), Mexican waterlily (*Nymphaea mexicana* Zucc. (Nymphaeaceae) and Delta arrowhead (*Sagittaria platyphylla* Engelmann (Alismataceae)) (Van Ginkel, 2011). The most problematic of the alien plants that have invaded South African waters are floating macrophytes, adapted to large, slow-flowing lowland waters, open waters and wetlands similar to those that occur in the Amazon Basin (Coetzee *et al*., 2011). However, South Africa does not have natural lakes with these characteristics and, as a result, lacks indigenous floating macrophyte counterparts (Coetzee *et al*., 2011). The construction of dams and impoundments, and high levels of eutrophication have created an ideal environment for invasive floating plants (Coetzee *et al*., 2011).

For more than a century, considerable effort has gone into managing and regulating invasive species in South Africa, with varying degrees of success (Van Wilgen *et al*., 2020). The management of invasions in South Africa has been relatively well studied, because efforts to manage invasive species in natural areas began earlier than in most other parts of the world (Van Wilgen *et al*., 2020). South Africa is one of the few countries which has regulations in place for the control of biological invasions (Van Wilgen *et al*., 2020). The Alien and Invasive Species Regulations were published in 2014 in terms of the National Environmental Management: Biodiversity Act (NEMBA; Act 10 of 2004) (Van Wilgen *et al*., 2020). These regulations place restrictions on the use and management of the invasive alien species which are listed. Research over the past thirty years has helped South Africa establish biological and integrated management programmes for invasive alien plant species which aim to restore access to potable water and to maintain native biodiversity (Hill *et al*., 2020). Currently, 559 invasive taxa are listed in terms of the regulations in four different categories: 1a, 1b, 2 and category 3 species. Category 1a represents species that are targeted for national eradication; Category 1b represents species that must be controlled as part of a national management programme and are not allowed to be traded or spread; Category 2 represents species that are the same as Category 1b species, except that permits can be issued for their usage, while Category 3 represents listed invasive species that can be kept without permits, although these may not be traded or further propagated and must be controlled if they occur in protected areas or riparian zones (Van Wilgen *et al*., 2020). As many as 560 taxa have been listed as prohibited, which means that an import permit will not be considered for these species.

1.3 Water Hyacinth

1.3.1 Taxonomy of *Pontederia crassipes*

Previously water hyacinth was known as *Eichhornia crassipes* (Mart) Solms-Laub, however Pellegrini *et al*., (2018) presented evidence for Pontederiaceae based on plastid and morphological data in order to redescribe *Pontederia* to include *Eichhornia* and *Monochoria*, while providing an identification key for the genera in the family Pontederiaceae. Pontederiaceae is a small aquatic monocot family, placed in Commelinales, an order of flowering plants, as a sister to Haemodoraceae (Pellegrini *et al*., 2018).

1.3.2 Distribution of *Pontederia crassipes*

Pontederia crassipes is native to South America in the Amazon Basin, in Brazil, and Argentina, but has become invasive in many parts of the tropics and subtropics (Barrett & Forno, 1982; Venter *et al*., 2013; Abba & Sankarannair, 2024). Water hyacinth has spread across multiple continents, including Asia, Africa, Europe, Central America, North America and Caribbean (Abba & Sankarannair, 2024). Humans have been the main agent of species spread across the world as the entry of water hyacinth into Africa, Asia, Australia and North America coincided with the arrival of vessels of first explorers, and today, *P. crassipes* appears on every continent except Antarctica and is found in more than 50 countries as a result of this anthropogenic spread (Coetzee *et al*., 2017). In the 19th century, water hyacinth spread from its native range in lowland tropical South America to become the world's most serious aquatic weed (Barrett & Forno, 1982). The plant reached Australia in 1895, India in 1902, Malaysia in 1910, Zimbabwe in 1937 and South Africa in 1908 as an ornamental plant (Gupta *et al*.,2012; Coetzee *et al*., 2014).

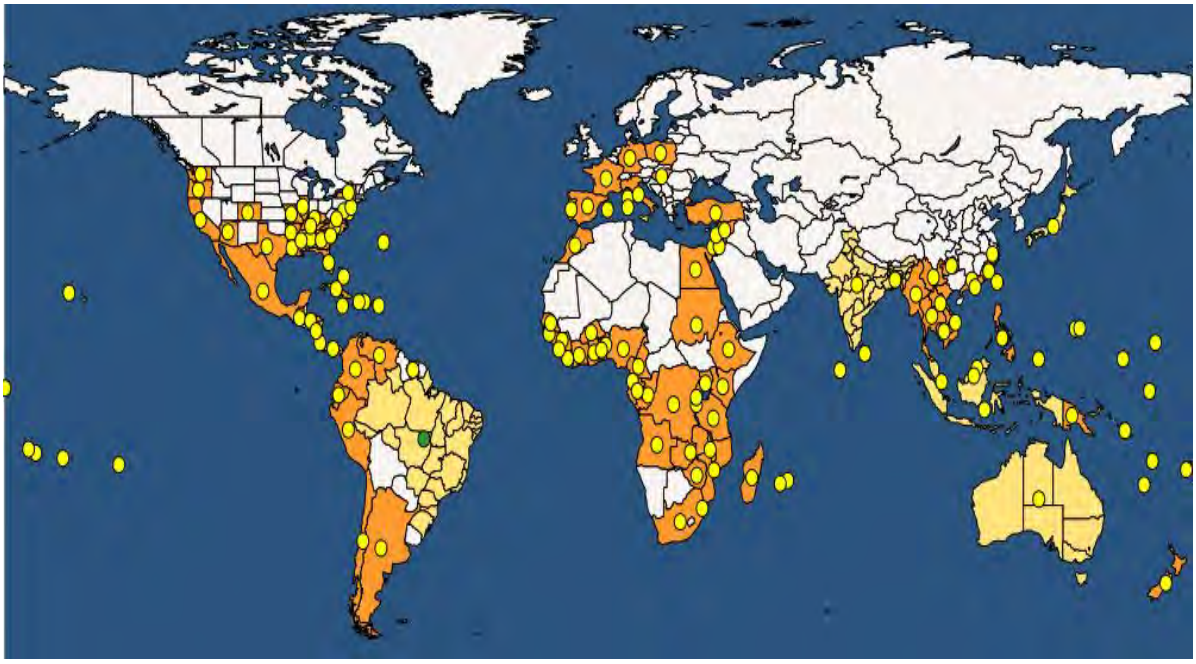

Figure 1.3. Visual representation of *Pontederia crassipes* global distribution ● Invaded range ● Native range (Source: EPPO database https//gd.eppo.int ,2024).

1.3.3 Biology of *Pontederia crassipes*

Water hyacinth possesses prolific powers of clonal propagation which is pivotal for its success as a weed (Barrett & Forno, 1982). Gopal (1987) reviewed the doubling time and showed it to vary from 5.9 to 18.2 days with the doubling time for weight between 3.7 to 57.8 days for plants measured in the open (outside ponds) or in the field (Coetzee *et al*., 2017). At very high densities, self-thinning occurs (Coetzee *et al*., 2017) which serves as a density regulator where density declines and biomass increases. Knowing the growth rate of plants in an area to be controlled and the conditions that encourage growth is important for some control techniques (Coetzee *et al*., 2017). Water hyacinth also replicates sexually through seeds released by the inflorescence (Pérez *et al*., 2011, Faltlhauser *et al*., 2023). A single inflorescence with 20 flowers can produce up to 3000 seeds (van Wyk & van Wilgen, 2002; Pérez *et al*., 2011). Depending on the sampling site and time of the year, Pérez *et al*. (2011) found that the number of seeds per square metre of vegetation ranges from 400 to 3400 (Pérez *et al*., 2011). The seeds are released in capsules of 40 to 300 seeds each that either sink or accumulate in the floating mat (Pérez *et al*., 2011; Degaga, 2018). The fate of the seeds is generally to drop into the adjacent sediment and germinate if the conditions are favourable (i.e., enough oxygen, light and space for growth) (Pérez *et al*., 2011). Germination can occur immediately after seeds are released by the flowers, but the seeds can also remain dormant for years (Coetzee *et al*., 2017); however, germination is encouraged by aerobic conditions and alternating temperatures (Coetzee *et al*., 2017). Seeds remain viable for 20 or more years (Pérez *et al*., 2011; Degaga, 2018; Goode *et al*., 2021; Abba & Sankarannair, 2024).

Seeds survive in wet mud and are long-lived, and flowers can be produced within 10-15 weeks after germination (Coetzee *et al*., 2017). Large populations of seedlings may become established on exposed mud at the edge of the waterbody when the water levels fall (Coetzee *et al*., 2017). Initially, seedlings are rooted in the mud but, after a short period of growth under water, they pop to the surface and float (Coetzee *et al*., 2017) where they become free floating as a result of wave action and rising water levels. Seeds are the source of new infestations or reinvasions, as are vegetative propagules (Pérez *et al*., 2011; Coetzee *et al*., 2017; Faltlhauser *et al*., 2023).

A study by Pérez *et al*. (2011) investigated the role of the seed banks as a source of persistent re-infestations of cleared water bodies and revealed that water hyacinth has a rapid colonization capacity as 80% of the seeds germinate in 3-4 days under ideal environmental conditions (Pérez *et al*., 2011). The study proved the existence of a seedbeds in South African waterbodies with historic water hyacinth infestations. The longer the invasion the higher the number of seeds on the sediment (Pérez *et al*., 2011). Pérez *et al*. (2011) found that the mean seed density of water hyacinth was in line with the seed density of native *Sarcocornia perennis* in South Africa and the invasive *Spartina* in China. Pérez *et al*. (2011) also found that the mean seed density was 2534 seeds/m2 at New Year's Dam in the Eastern Cape, 1494 seeds/m^2 at Kluitjeskraal Dam in the Western Cape, and 4228 seeds/m^2 at Seaview Road in the Eastern Cape.

Water hyacinth's rapid growth rate, ease of propagation and its ability to compete successfully with other aquatic plants gives rise to significant amounts of biomass that cover the water surface of a great variety of habitats, often interfering with the use and management of water resources (Téllez *et al*., 2008). The weed's high adaptability to extreme conditions contributes to its potential for invasion (Sharma *et al*., 2016), and it has evolved traits to survive in its native habitat where desiccation and flooding occur regularly (Coetzee *et al*., 2017). Water hyacinth tolerates desiccation once the water has receded, leaving the plants exposed to mud, and because it is free-floating and mobile, it is capable of surviving and flourishing in variable water levels (Coetzee *et al*., 2017). This pattern of desiccation and flooding also breaks the dormancy of seeds in the sediment (Pérez *et al*., 2011).

A study by Marlin *et al*. (2013b) demonstrated that water hyacinth growth is strongly influenced by water nutrient levels. The plant's prolific growth correlates with high nutrient concentrations, particularly high phosphorus and nitrogen. Plants grown in water with high N and P were healthy, with tall petioles, and they generally produced more leaves and daughter plants than plants grown in water with lower N and P content. Plants grown in low nutrients had short bulbous petioles and did not survive the winter season. *Pontederia crassipes* rhizomes and feathery roots are submerged and respond to changes in nutrient availability; while longer, denser roots are associated with limited phosphorus availability, shorter roots are associated with high concentrations of phosphorus in the water column (Coetzee *et al*., 2017). Water phosphorus content significantly affects growth and nutrient storage by water hyacinth (Coetzee *et al*., 2012), and Haller and Sutton (1973) found that when the phosphorus level falls below 0.1 mg, active growth of water hyacinth is halted; however, concentrations above this level allow for growth as well as the uptake of nutrients in excess of the plant's requirements (Coetzee *et al*., 2017). The water hyacinth problem in South Africa has been exacerbated because the country has adopted a high 1 mg/l Phosphorus standard since the 1970s (Coetzee *et al*., 2012).

An effluent standard of 1 mg/l orthophosphate for wastewater discharge from point sources was promulgated by the Department of Water Affairs and Forestry (DWAF) on 1 August 1980 (Van Ginkel, 2011). In nutrient-rich sites, water hyacinth biomass can increase eightfold as compared to nutrient-poor sites (Coetzee *et al*., 2017). Increasing concentrations of nitrogen and phosphorus result in increased ramet production, shoot: root ratio, and plant height (Reddy *et al.*, 1989). Water phosphorus content significantly affects water hyacinth growth and nutrient storage as all measures of plant growth increase with increasing phosphorus, but the rate of increase is not proportional (Reddy *et al.*, 1990). *Pontederia crassipes* growth responds positively to nitrogen concentrations of up to 5.5 mg/l and phosphorus concentrations of 1.06 mg/l, but biomass accumulation does not significantly increase above these levels (Reddy *et al.*, 1989, 1990). Nitrogen storage in the plant increases to a maximum at 50.5 mg/l, while phosphorus storage in the plant increases indefinitely as the water phosphorus concentration in water increases (Reddy *et al.*, 1989, 1990). The net nitrogen storage within the plant is at a maximum when the water phosphorus concentration reaches 2.56 mg (Reddy *et al.*, 1989). Singh *et al*. (1984), Sastroutomo *et al*. (1987) and Reddy *et al*. (1989) have proved that biomass accumulation, ramet production, shoot: root ratio and plant height increase in accordance with increases in concentration of nitrogen and phosphorus. Thus, the rate of infestation is closely correlated to the nitrogen and phosphorus concentrations (Sharma *et al*., 2016).

1.3.4 Impact of Water Hyacinth on Water Bodies

South Africa's most limiting natural resource is freshwater, thus the provision of safe and sufficient drinking water in South Africa relies on maintaining freshwater ecosystem services (Van Ginkel, 2011); a reduction in water quantity and quality will have major negative environmental and social impacts (Fraser *et al*., 2016). After the implementation of the National Eutrophication Monitoring Programme in 2002, it was very clear that South Africa faces wide-spread problems of water provision, chiefly in the larger metropolitan areas and the dams on which these areas rely for their water supplies (Van Ginkel, 2011).

South Africa is a water-scarce country; compared to the average global annual rainfall of 860 mm, South Africa receives an average of 450 mm of rain, and IAPs affect both the quality and quantity of available water (Fraser *et al*., 2016). Sustainable water management must therefore include the control of any additional factors that may aggravate water scarcity (Arp *et al*., 2017).

The presence of water hyacinth mats affects the physiochemical properties of the aquatic ecosystem it has invaded. Dense water hyacinth mats reduce light penetration, dissolved oxygen and other nutrients in the water column, adversely affecting the ecology of the invaded waterbody (Sharma *et al*., 2016). The mats decrease dissolved oxygen concentrations beneath them by preventing the transfer of oxygen from the air to the water's surface. By blocking light necessary for photosynthesis, the water hyacinth mats reduce phytoplankton productivity and prevent photosynthesis in submerged vegetation (Villamagna & Murphy, 2010; Sharma *et al*., 2016, Mironga *et al*., 2012) and the lack of phytoplankton alters the composition of invertebrate communities (Coetzee *et al*., 2017). A study by Masifwa *et al*. (2001) showed an increase in macroinvertebrate abundance at the edges of the *P. crassipes* mats on Lake Victoria, while studies of South African impoundments by Midgley *et al*. (2006) and Coetzee *et al*. (2014) showed that *P. crassipes* mats significantly reduced the diversity and abundance of benthic invertebrates. In Spain, significant reductions were reported in the total density of phytoplankton and zooplankton after invasion by *P. crassipes*, where changes in zooplankton communities were evidenced by the substitution of crustacean species for others (Coetzee *et al*., 2017). The effect of *P. crassipes* infestations on fish abundance and diversity depends on its impact on invertebrates and plankton abundance and diversity which are a crucial link in the tropic ecology of aquatic ecosystems (Coetzee *et al*., 2017). *Pontederia crassipes* also outcompetes a number of aquatic plant species, and elimination of these plant species alters the habitat of aquatic communities effecting changes in aquatic biodiversity

(Coetzee *et al*., 2017). Drifting water hyacinth mats also scour vegetation, destroying native plant and wildlife habitat (Coetzee *et al*., 2017).

Pontederia crassipes not only impacts biodiversity, but it also has socio-economic impacts as the dense impenetrable mats restrict access to water, negatively impacting fisheries and related commercial activities (Coetzee *et al*., 2017). *Pontederia crassipes* impacts the effectiveness of irrigation canals, navigation, transport, hydroelectric programmes and tourism; the plants build up against bridges, fences, and walls, obstructing water flow and increasing flood levels, which can result in damage to property (Coetzee *et al*., 2017). *Pontederia crassipes* alters livelihoods of any rural communities which have a high dependency on the freshwater waterways for food, transport and clean water (Coetzee *et al*., 2017).

Pontederia crassipes is known to absorb heavy metals, organic contaminants and nutrients from the water column (Villamagna & Murphy, 2010) and is referred to as a bioaccumulator (Lissy & Madhu, 2011). Nutrient uptake occurs in three ways: through root absorption, foliar absorption, and adsorption (Lissy & Madhu, 2011). These aquatic macrophytes accumulate contaminants in their tissues and have a high tolerance for contaminants like heavy metals, which they absorb in large quantities by a method called phytoextraction (Lissy & Madhu, 2011). Since the 1940s, *P. crassipes* has been promoted as a relatively cheap and environmentally friendly tool for decontamination of wastewaters because of its rapid growth rate and high rate of heavy metal and nutrient absorption; even today it is used to treat contaminated water, particularly in Asia (Coetzee *et al*., 2017).

Villamagna and Murphy (2010) found that most of the research done on the impact of water hyacinth establishment on water quality focused on the consequences of dense mats formed by the weed; specifically, lower phytoplankton productivity and dissolved oxygen levels below the mats, and an increase in sedimentation rates (Villamagna & Murphy, 2010). The research also revealed higher evapotranspiration rates from the water hyacinth leaves than evaporation rates from open water (Villamagna & Murphy, 2010). Water hyacinth disrupts activities associated with water use and causes substantially increased water losses through evapotranspiration (Sharp, 2014) which is the evaporation of moisture from living cells through the stomata (Timmer & Weldon, 1967). Timmer and Weldon (1967) found that evapotranspiration from water hyacinth was 3.7 times higher than evaporation from open water. The presence of water hyacinth results in unnecessary loss of water, which could have otherwise been used in a more productive manner (Arp *et al*., 2017). The presence of water hyacinth in a system may erode water and irrigation productivity, with a negative impact on irrigation-fed agriculture (Arp *et al*., 2017).

1.4 Control measures for water hyacinth

Research for over thirty years has helped South Africa establish biological and integrated management programmes for invasive alien plant species, with the aim of restoring access to potable water and maintaining native biodiversity in a sustainable manner (Hill *et al*., 2020). However, the complex interactions of invasive plants with their invaded habitats creates significant management challenges (Hinz *et al*., 2019). Manual and mechanical, biological control and chemical control methods have been implemented with varying degrees of success (Van Ginkel, 2011), with an integrated approach being the most promising solution to combat aquatic water weeds. The suitability of a control method depends on site-specific conditions like the size and spatial configuration of the area to be controlled, seasonal weather patterns, and designated use of the waterbody. This is especially true for the management of water hyacinth (van Wyk & van Wilgen, 2002) which has moved from eradication to reducing the plant density levels to ones which minimize economic and ecological impacts, as weed eradication has proved impossible at sites larger than one hectare (Villamagna & Murphy, 2010).

1.4.1 Mechanical Control

Mechanical control opens physical space for boat traffic, recreation, fish and fishing activities. Mechanical control includes harvesting the plants manually or mechanically, and *in situ* cutting. Manual removal of the plant through hand-pulling or using a pitch fork is common in most developing countries like South Africa. It is a labour-intensive method and is only effective for small infestations. However, it is often used as an employment-creation exercise (Hill & Coetzee, 2008).

Zimbabwe initiated a manual removal programme to deal with the infestation on Lake Chivero in the 1980s; however, this failed to reduce the amount of water hyacinth on the lake despite the programme having 500 workers each working eight-hour days (Hill & Coetzee, 2008). After six months of the project, a mechanical control programme was implemented using a bulldozer, boat, conveyor belt and dump trucks. This ensured that two tonnes of water hyacinth plant were removed daily, which nevertheless, did not effectively reduce the water hyacinth coverage of the lake (Hill & Coetzee, 2008). The flaw in mechanical removal is that since water hyacinth is made up of 90% water, it is extremely heavy to transport. It grows too quickly for mechanical control to get on top of the situation, except where the plant grows in cool temperate regions and plant growth ceases in winter. Furthermore, owing to its capacity to absorb contaminants from polluted water, its disposal requires health and ecological considerations.

Mechanical removal has, however, proved to be successful in a programme in Mexico where it was used in combination with chemical control using the herbicide 2,4 dichlorophenoxy-acetic acid (2,4-D) and a mechanical harvester (Hill & Coetzee, 2008).

1.4.2 Chemical Control

After World War II, the main approach to controlling *P. crassipes* was through chemical control (Téllez *et al*., 2008). In the 1960s, various herbicides hit the market exhibiting different degrees of effectiveness and environmental consequences, with amitrol, 2,4-D amine, diquat, glyphosate and paraquat being the herbicides most often used (Téllez *et al*., 2008; Villamagna and Murphy, 2010). Water hyacinth has proved to be susceptible to herbicides such as 2,4-D, diquat, paraquat and glyphosate (Hill & Coetzee, 2008). Herbicide application has the advantage of being fast acting, but herbicides are less selective than mechanical control and can kill non-target species with far-reaching ecological impacts, including deoxygenation of the water as the plants sink *en masse* (Villamagna & Murphy, 2010). The effectiveness of chemical control depends on a long-term commitment of follow-up applications for possibly 20 or more years (Hill & Coetzee, 2008), particularly because, when spraying stops, the water hyacinth plant populations rebound rapidly; thus, the sustainability of such maintenance control is permanently linked to budgets capable of supporting such programmes (Tipping *et al*., 2017). While herbicide application kills plants and reduces populations temporarily, it does not fundamentally change or stress the plant (Tipping *et al*., 2017).

1.4.3 Biological Control

Classic biological control is the use of host-specific natural enemies imported from the native range of *P. crassipes*, which are known to regulate the growth of the plant and result in acceptable levels of plant coverage on water bodies in its native range (van Wyk & van Wilgen, 2002). The initial surveys to find phytophagous natural enemies were limited to the Amazon Basin, where *P. crassipes* has the largest number of co-evolved herbivores. However, thirty years later, surveys conducted in 1999 and 2000 by the USDA, CABi and ARC-PPRI (South Africa) near Iquitos, Peru at the confluence of Maranon and Ucayuli Rivers (04°19’29’’S 73°18’ 11’’W) found a greater abundance and diversity of natural enemies previously known to be associated with water hyacinth than anywhere on the South American continent (Coetzee *et al*., 2017).

In the initial study, Perkins (1974) identified 43 herbivorous insects associated with water hyacinth, 19 of which inflicted sufficient damage and exhibited potential host-specificity to be considered for use as biological control agents (Coetzee *et al*., 2017). Perkins divided the herbivorous insects into four categories based on the damage they inflicted on the water hyacinth plants: (1) defoliators and external leaf feeders, such as the grasshopper (*Cornops aquaticum (*Brüner) (Orthoptera: Acrididae), and the weevils (*Neochetina eichhorniae* Warner (Coleoptera: Erirhinidae) and *Neochetina bruchi* Hustache (Coleoptera: Erirhinidae) which are the most widely used biological control agents throughout the tropics and subtropical areas of the world; (2) petiole borers, considered to be the most destructive herbivores as the result of subsequent waterlogging, such as the moth larvae *(Niphograpta albiguttalis* Warren (Lepidoptera: Crambidae) as well as the boring by *Neochetina* larvae; (3) leaf tunnellers, with a single representative, the mite *Orthogalumna terebrantis* Wallwork (Acarina: Galumnidae); (4) sap-suckers, including *Megamelus scuttelaris* Berg (Hemiptera: Delphacidae), *Eccritotarsus catarinensis* (Carvalho) (Hemiptera: Miridae) and *Eccritotarsus eichhorniae* Henry (Hemiptera: Miridae) (Coetzee *et al*., 2017).

Sixty fungal species were found to be associated with *P. crassipes*, with 10 being virulent and known to cause disease in the plant. They are: *Acremonium zonatum* (Sawada) W. Gams, *Alternaria alternata* (Fr.) Keissler, *Alternaria eichhorniae* Nag Raj & Ponnappa, *Bipolaris* spp., *Cercospora piaropi* Tharp. (Mycosphaerellales: Mycosphaerellaceae) (=*Cercospora rodmanii* Conway), *Fusarium chlamydosporum* Wollenw & Reinking, *Helminthosporium* spp., *Myrothecium roridum* Tode ex Fr., *Rhizoctonia solani* Kühn and *Uredo eichhorniae* Gonz.-Frag. & Cif (Coetzee *et al*., 2017).

Researchers in Florida (USA) pursued classical biological control as a control mechanism in an attempt to transform or permanently weaken the plants. They identified suitable biological control agents and developed mass-rearing programmes of these herbivorous insects (Tipping *et al*.,2017). Damage by these co-evolved herbivorous insects leads to reduced biomass, vegetative reproduction, and limited population growth. These results are observed in infested water bodies under low nutrient conditions and in tropical to subtropical climates. However, in eutrophic systems, especially those prone to cold winter temperatures, results from biological control programmes around the world have shown a reduced impact of herbivory on plants (Coetzee *et al*., 2017).

Classical biological control has proved to be the most cost-effective and sustainable control method for exotic invasive plants since its introduction more than 150 years ago, and it has resulted in some spectacular successes in a variety of environments (Hinz *et al*., 2019). In

South Africa, the biological control programme against water hyacinth was initiated in 1973 (Hill & Olckers, 2000), with *N. eichhorniae* released in 1974. Since then, several other agents have been released against the weed, including *N. bruchi* in 1983, the moth *Niphograpta albiguttalis* in 1990; the mirid *E. catarinesis* in 1996, and *E. eichhorniae* in 2007 (Paterson *et al*., 2016), the water hyacinth grasshopper (*Cornops aquaticum*) in 2010 (but this species did not establish), the water hyacinth planthopper, *M. scutellaris* in 2013 (Hill & Olckers, 2000; Sutton *et al*., 2016) and the pathogen *C. piaropi* recorded in 1987, while the mite, *O. terebrantis* was observed in 1989 (Hill & Olckers, 2000).

Although South Africa has the highest number of biological control agents released against water hyacinth, it has, however, not achieved the success observed in Uganda with Lake Victoria where the weed is under control (Hill & Olckers, 2000). In South Africa, biological control has proved to be effective in the coastal and subtropical climatic conditions of the Eastern Cape and KwaZulu-Natal, but has been less effective in the Western Cape which has coastal, Mediterranean climatic conditions (Hill & Olckers, 2000).

Hill and Olckers (2000) assessed the factors that affect the efficacy of biological control agents in controlling water hyacinth. These include the impact of cold winters, which vastly increase the time that it takes to control the weed, while hyper-eutrophic waters allow the weed to thrive, despite herbivory (Hill & Olckers, 2000). In the high elevation areas of the highveld, the plants and the insects remain dormant for up to five months in a year (May–September).

Hill and Olckers (2000) observed that plant populations increased rapidly with the onset of spring (late September–October), whereas the resurging insect populations which regenerate from considerably low numbers because of the cold-induced mortality and low reproductive output, struggle to reach damaging levels until the end of summer (March–April) only to crash again during winter (Hill & Olckers, 2000). Population dynamics studies by Byrne *et al*. (2010) on *Neochetina* weevils, Maseko *et al*. (2021) on *E. catarinensis* and Miller *et al*. (2021) on *M. scutellaris*, found that biological control agents lagged two months behind the plants following regrowth in spring. These studies all recommended that post-winter augmentative insect releases should be initiated in order to reduce the long recovery phase of biocontrol agents, as the cold winters prevent the biological agent populations from reaching population densities required to severely stress the weed (Hill & Olckers, 2000, Maseko *et al*., 2021; Miller *et al.*, 2021).

It is therefore not surprising that the most severe water hyacinth infestations in South Africa occur in water bodies that are nutrient enriched and at high altitudes (Cilliers, 1990; Byrne *et al*., 2010). The Hill and Olckers (2000) study concluded that additional natural enemies that can be effective in cooler areas need to be identified and introduced into the biological control strategies. The low temperatures and winter frosts at high elevations render biological control as a single method of control less effective (Byrne *et al*, 2010). An integrated management approach which entails a combination of control methods to achieve acceptable levels of control would therefore be the most appropriate approach (Hill & Olckers, 2000; Hill & Coetzee, 2008).

Van Wilgen *et al*. (2004) stated that the most commonly used approach in determining the feasibility of a control programme is a benefit-cost analysis which involves valuing and comparing the cost and benefits of different control programmes to ensure that scarce resources are allocated efficiently among competing projects (Arp *et al*., 2017). Economic valuation thus plays a crucial role in measuring the relative success of invasive species control programmes needed to justify continued funding for such programmes (Arp *et al*., 2017). For example, in 1999, *Neochetina eichhorniae* adults were introduced to New Year's Dam in the Eastern Cape, which at the time was almost completely covered by water hyacinth and reduced the cover to less than 5% (Fraser *et al*., 2016). The biocontrol programme saved approximately 2 million m^3 of water at an estimated value of R8 million over a 22-year period (Fraser *et al*., 2016). Van Wyk and Van Wilgen (2002) used an average evapotranspiration rate of 5mm/day to estimate the annual cost of water loss accruing to water hyacinth infestation in the Hartbeespoort Dam, estimated to be about 37 million m^3 at a cost of R3.7 million (van Wyk & van Wilgen 2002; Arp *et al*., 2017).

1.4.4 Integrated Management of *Pontederia crassipes*

The global agreement amongst scientists and water managers is that an integrated management programme is the best option to control *P. crassipes* (Téllez *et al*., 2008). Biological control is perceived as a slow-acting process, despite its successes (Hill & Coetzee, 2008). This is particularly true for areas that experience frost during the colder months of the year, leading to high mortality of biological control agents while the plants are able to regrow after winter from the crown, which is unaffected by frost. In these areas, there has been a shift from purely biological control measures to an integrated management approach which includes aspects of biological control, herbicide application and manual removal, and importantly, the management of nutrients entering the aquatic ecosystem (Hill & Coetzee, 2008).

A report by Center *et al*. (1982) found that the water hyacinth (*Neochetina* spp.) weevils were more effective in controlling water hyacinth when used in combination with a growth retardant. For a chemical control to be used in conjunction with biological control, the concentration of the herbicide must be sufficiently low to leave the plant alive but with reduced vigour, and the substance used must not adversely affect the insects (Téllez *et al*., 2008). Studies have shown that active integration of the two control mechanisms is possible by modifying patterns and timing of herbicide application in an attempt to enhance the impact of *Neochetina* spp. herbivory (Haag, 1986; Haag & Habeck, 1991; Haag *et al*., 1998). These modifications included varying the herbicide spray coverage and treating small areas sequentially allowing for the untreated patches of *P. crassipes* to act as refugia for the insects, thus maintaining their populations at levels that could significantly impact the remaining, untreated plants and impede growth (Goode *et al*., 2021). Tipping *et al*. (2017) found that herbivory by biocontrol agents significantly boosted the overall effectiveness of the herbicide (Tipping *et al*., 2017), with the presence of the biological control agents more than quadrupling the effectiveness of a reduced dose of 2,4-D and doubling the operational rate of 2,4 D's effectiveness of reducing *P. crassipes* biomass (Tipping *et al*., 2017). Herbivory by insects likely weakens the plants to the point that the reduced dose of herbicide was as effective as the higher operational or full dose of the herbicide (Tipping *et al*., 2017). The logistics model of Tipping *et al*. (2017) showed that the suppressive activities of the insects reduced the number of herbicide retreatments from five to two, thus, a reduction of 60% in reapplications was achieved. Furthermore, Tipping *et al*. (2017) found that having two biological agents present on a water hyacinth infested freshwater sytem increased the efficacy of the herbicide, as they observed that plants attacked by *N. eichhorniae* and *M. scutellaris* were unable to regrow readily following 2,4-D applications even at a reduced dose (Tipping *et al*.,2017).

An integrated management programme for water hyacinth was initiated by Jones and Cilliers (1999) and Jones (2001) for the Nseleni River system in the subtropical region of KwaZulu-Natal Province in South Africa (Hill & Coetzee, 2008). In the case of the Nseleni River, 5% coverage was attained and maintained by the introduction of an integrated management programme (Hill & Coetzee, 2008). The river was divided into management units, together with the implementation of appropriate control methods for each of the management units (Hill & Coetzee, 2008). The key elements of the approach included the appointment of one individual or an organization to drive the control programme and the involvement of all interested and affected parties on the river system (Hill & Coetzee, 2008). Further, engagement with communities who live around or along the shoreline of an infested waterbody is important for the success of the biocontrol programme because integrated control of water hyacinth requires long-term commitment to implementation, monitoring, evaluation, and constant feedback from affected communities (Hill & Coetzee, 2008).

Eradication of water hyacinth is deemed to be impossible once the weed establishes in a river, lake or dam, and thus an acceptable level of control must be determined (Hill & Coetzee, 2008). The rule of thumb for South Africa has been that an acceptable level of control for a waterbody which had 100% coverage by water hyacinth, would be coverage of no more than 20% coverage following weed management measures (Hill & Coetzee, 2008).

A cost/benefit analysis by van Wyk and van Wilgen (2002) for three separate control approaches in South Africa determined that biological control was the cheapest form of control for water hyacinth, however, it took 3–5 years to achieve control while herbicide application was the most expensive control option at USD 210/ha. The cost for biological control ranged between USD 0.51/ ha and USD 44/ha, depending on the extent of the follow-up programme (Hill & Coetzee, 2008). An integrated control programme gave the best return on investment at a cost of USD 39/ha for an implementation period that achieved control in a shorter time frame of 12–16 months (Hill & Coetzee, 2008).

1.5 Impact of Control of *Pontederia crassipes*

Determining the consequences of controlling an established water hyacinth infestation depends on our ability to understand how water hyacinth affects the system that it inhabits (Villamagna & Murphy, 2010). Villamagna and Murphy (2010) found that most literature and research focused on the management of water hyacinth by looking at the removal of the weed, but little was done to understand or assess the ecological changes (abiotic and biotic) that occur in response to the establishment or management of a non-native invasive species. Each of the *P. crassipes* control methods that have been studied has characteristics of time, effort, cost, environmental consequences and efficacy. The proposed control method with acceptable efficacy against the weed is a combination of various methods (Téllez *et al.*,2008).

1.6 Aims of the Study

The main aim of this study was to develop an integrated management programme for *P. crassipes* on the Hartbeespoort Dam which is a cool temperate, hypertrophic freshwater reservoir plagued with water hyacinth infestations since the 1970s. A moratorium on the use of herbicides as a control measure has left physical removal and biological control as the only options available for controlling the weed. Owing to the trophic status of the dam, the suite of biological control agents previously released on the dam and interference from herbicide operations struggled to bring the weed under control. This research involves the introduction of a new biological control agent, *Megamelus scutellaris* to Hartbeespoort Dam and the development of a release programme that would assist the agent in overcoming the limitations caused by the cold winters and the high nutrient state of the water. The cold winters often led to frosting of the water hyacinth plants, which in turn reduced the food available for biological control agent, while the eutrophic state of the water allows the plants to compensate for herbivory with increased leaf turnover.

1.7 Outline of the Thesis

1. Chapter 1 of the thesis is a literature review on the introduction of alien invasive species to South Africa via the increase in global travel with a special focus on water hyacinth, the biology of the plant, and the possible control mechanisms for this aquatic weed.
2. Chapter 2 of the thesis focuses on a site description for the Hartbeespoort Dam and the water hyacinth control measures that have been carried out on the dam. It also considers the biological control agents that established on the dam at the onset of the project, their biology and the impact they have on the host plant.
3. Chapter 3 investigates the introduction of a new biocontrol agent, *Megamelus scutellaris,* on the dam. This biological control agent was introduced into South Africa in 2013, but had not been introduced to the dam. The cool temperate conditions and the hypereutrophic nutrient state of the dam allowed the water hyacinth plants to compensate for insect herbivory, thus no control was achieved, despite the establishment of a suite of biological control agents on the site. The chapter also investigates the impact of abiotic factors on the establishment and effectiveness of the biological control agent.
4. Chapter 4 examines the consequences of controlling an established water hyacinth population by examining the ecosystem services provided by the invading water

hyacinth plants to the aquatic ecosystem of the Hartbeespoort Dam and assessing the impact the complete removal of the weed would have on biodiversity and the perceived ecosystem services. This is compared to the impact on a control site where biological control is used to manage the weed.

5. Chapter 5 investigates the perceptions of residents and visitors to the dam of whether the weed is under control. It also deals with the residents' willingness to pay to achieve the desired control level. This chapter determines the impact on the property prices of the colonization of the dam by water hyacinth and subsequent control of the weed.
6. Chapter 6 is a general discussion of the findings of the research and the development of an integrated management programme for water hyacinth-infested water bodies in cool temperate regions prone to frosting during the cold winter months where *M. scutellaris* was introduced and makes recommendations for future studies.

Chapter 2: A Review of the Study System

2.1 Historical Background on Hartbeespoort Dam

Hartbeespoort Dam (25°44′51″S 27°52′01″E) is located in the North West Province of South Africa. (Figure 2.1). Hartbeespoort Dam was initially constructed in 1921 as an irrigation dam (Harding *et al*., 2004, Botha, 2013), and the Hartbeespoort Irrigation Board is one of the oldest irrigation schemes in South Africa (DWR, 2013). In 1971, the sluice gates of the dam were raised by 2.44 m, increasing the gross capacity of the dam to 211 Mm^3 (Ashton et al, 1979, Botha, 2013). Today, the scheme consists of Hartbeespoort Dam, 205 Mm^3 on the Crocodile River and approximately 135 km main canals and 405 km of branch canals (DRW, 2013). Water is delivered to farmers through sluices, which are adjusted by hand every 12 hours (DWR, 2013)

Figure 2.1. Hartbeespoort Dam in the North West Province of South Africa. A) Crocodile River inlet B) Magalies River inlet C) Swartspruit inlet D) Crocodile River outlet. Sentinel-2 satellite image obtained from: https://davidkinsler123.users.earthengine.app/view/macrophyte-monitoring-tool

The dam has a catchment of 4112 km^2 (DWR, 2013) and is divided into five sub-catchments:

- The Magalies River catchment

- The Upper Crocodile River catchment
- The Juskei River catchment
- The Hennops River catchment, and
- The incremental Crocodile River catchment between the Upper Crocodile River catchment and the dam (including the area around the dam and the Swartspruit) (Botha, 2013) (Figure 2.2).

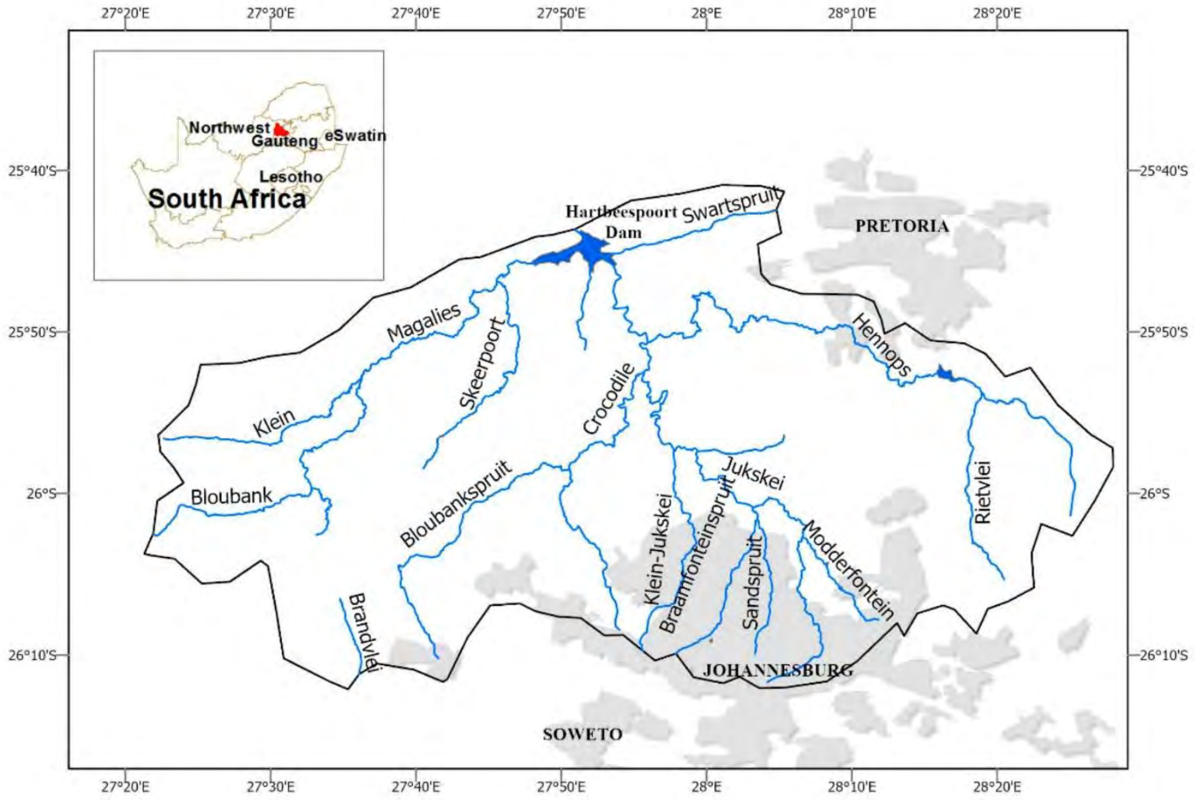

Figure 2.2. Hartbeespoort Dam catchment area extracted from Ali *et al*., (2022).

Hartbeespoort Dam is a eutrophic, fresh waterbody that suffers water hyacinth infestation because it is located downstream of urban and agricultural activities. High levels of urbanisation and dysfunctional wastewater treatment works have led to the dam becoming eutrophic (Carroll, 2019). When conducting algal bioassays, Steyn *et al*. (1975) showed that the algal growth potential was more than 100 mg/l, confirming that the eutrophic state of the water was attributed to urbanisation and industrialisation in the dam's catchment area. Water researcher, Prof. Anthony Turton (University of the Free State, South Africa), described Hartbeespoort Dam as the most eutrophic dam on the continent (Carroll, 2019).

Hartbeespoort Dam is one of the seven hypertrophic dams in the Crocodile West Marico Water Management Area (Seymore, 2007). As early as 1975, it was noted that the dam was highly eutrophic (Steyn & Toerien, 1975). The eutrophic state of a freshwater reservoir or lake is determined by the total phosphorus (TP) concentration in the water column. A total phosphorus concentration of between 0.0035-0.1 mg/l is evident in eutrophic reservoirs, while those with total phosphorus concentrations above 0.1 mg/l are classified as hypertrophic (Hart & Harding, 2015). Atta *et al*. (2020) confirmed the hypertrophic state of the dam as the phosphorus concentration in Hartbeespoort Dam was 0.2 mg/l. The dominant source of total phosphorus is wastewater effluent (Hart & Harding, 2015), the result of high nutrient input from wastewater treatment works (WWTW), leaking sewers, and urban and agricultural run-off (Carroll & Curtis, 2021). The dam receives approximately 700 million litres of purified sewage effluent daily, resulting in an addition of 280 tons of phosphates per annum (Seymore 2007). The Crocodile River contributes more than 99% of the nutrient influx into the Hartbeespoort Dam as documented by the NIWR (National Institute for Water Research) report, *The Limnology of the Hartbeespoort Dam* in 1985 (Roux *et al*., 2010; Botha, 2015; Mitchell & Crafford, 2016; Carroll & Curtis, 2021). The Crocodile River is the largest river that sustains the dam, delivering 90% of the annual inflow into the dam, and bringing waste effluent from three metropolitan areas: Johannesburg, Ekurhuleni, and Tshwane (Harding *et al*., 2004; Seymore, 2007; Carroll, 2019). The current sources of eutrophication include sewage spills and litter washed into the dam by storm water (Seymore, 2007). Greywater also washes into the Crocodile River owing to inadequate infrastructure, while the natural purification capacity of the riverbanks, riverbeds and wetlands has been compromised by modification due to urbanization (Seymore, 2007).

Situated in one of the most economically active areas of South Africa, Hartbeespoort Dam is one of the most significant dams on the economic hub of the North West Province. It is a tourism attraction that offers a variety of water activities to three million tourists a year (Seymore, 2007; Carroll & Curtis, 2021), who generate approximately R1.4 billion for the North West Province (Mokoena *et al*., 2017). Although the dam was initially built for irrigation and as a source of drinking water, it is currently used for recreation (van Wyk & van Wilgen, 2002; Carroll, 2019), and the pristine state of the water is essential for the dam's tourism attraction status. In reviewing the impact of the bioremediation efforts on Hartbeespoort Dam, Hart and Matthews (2018) noted that the proposal of biomanipulation as a method of dealing with the hypertrophic state of the dam and the consequences (macrophyte infestation and algal blooms) thereof, was owing to strong vested public interest (recreational boating and carp angling, high-capital shoreline property investment, adventure tourism, and as a source of irrigation and limited potable water supply) and socio-political pressures.

In 2005, the Department of Water Affairs and Forestry initiated an integrated biological remediation programme, Harties: Metsi A Me (translated - My Water) which aimed to find solutions for the eutrophication and deal with the invasive aquatic weeds (Seymore, 2007). The Metsi A Me programme ran from 2006 until 2016 and was aimed at rehabilitating the dam using a strategy to reduce nutrient stocks and associated nutrient cycling by harvesting plant and animal biomass (Carroll, 2019; Carroll & Curtis, 2021). The multi-pronged, strong food-web restructuring approach involved fish removal, algal and water hyacinth biomass harvesting, sediment dredging, construction of floating wetlands and composting the harvested water hyacinth (Carroll, 2019; Carroll & Curtis, 2021). Food-web management (biomanipulation) is well-known as a prospective remedial tool to ameliorate in-lake impacts of eutrophication, relying on one or both mechanisms; first ‘top-down’ enhancements of predatory interactions to maximize grazing pressure on autotrophs and thereby reduce their biomass stimulated by nutrient enrichment (Hart & Harding, 2015); second, ‘bottom-up’ resource-based interventions to reduce biotic recycling of internal nutrients, through biomass harvesting, specifically and exclusively for fish (Hart & Harding, 2015).

The Metsi A Me management plans cited biomanipulation as a strategy against eutrophication at the Hartbeespoort Dam (Carroll, 2019). The multi-pronged Hartbeespoort Dam Bioremediation Programme (HDBP) incorporated an explicit biomass harvesting approach, where water hyacinth and algae were removed. It also included a food-web restructuring of the fish population to achieve a balanced ecosystem by removing the taxa responsible for the resuspension of nutrients into the water column by virtue of their benthic feeding behaviour (Hart & Harding, 2015). This consisted of the removal of three species of undesirable fish, the common carp (*Cyprinus carpi*), sharp tooth catfish (*Clarras gariepnus*) and the canary kurper (*Chetia flaviventralus*) (Hart and Harding, 2015). Lastly, it aimed to restore natural filters in the form of wetlands while regulating water use in the larger catchment (http://harties.net/articles/676/latest-phase-2-metsi-a-me-and-foreshore-leases.php).

The HDRP was developed as a result of a joint effort between the National Department of Water Affairs (DWA) and the North West Department of Agriculture, Conservation and Environment (NWDACE) and was meant to be carried out in two phases where Phase 1 consisted of the development of a project framework, implementation of pilot projects and testing the outcomes of these pilot programmes. Phase 2 of the programme would be a full-scale implementation (Seymore, 2007; Harties.net). Two governing structures were put in place to deal with the implementation of the Harties, Metsi A Me Programme (Harties.net): the Hartbeespoort Dam Steering Committee, which had been formed with the principle aim of coordinating and integrating stakeholder interest in the programme at a strategic level, and the Hartbeespoort Dam Implementing Task Team (Hartbeespoort Dam Coordinating Committee-HDCC), which comprised the members from the implementing agent, Rand Water, tasked with coordinating all activities related to the implementation of the remediation programme (Harties.net). The Project's governance structure, that is, management roles, functions and responsibilities, formed part of the implementation agent's brief (Harties.net). In 2012, Phase 1 of the programme was halted to ensure that a new implementing agent was secured to carry out Phase 2 of the programme, but the programme stopped completely in 2016 due to inconsistent results of chemical control and in-situ nutrient managament (Chikodza *et al*., 2025).

Studies have shown that the current 0.2 mg/l total phosphorus concentration in the Dam would need to be reduced to 0.05 mg/l in order to curb algal growth (Chutter & Rossouw, 1992; Mitchell & Crafford, 2016; Atta *et al*., 2020). This would require preventative control measures, where the discharge requirement standards for purified wastewater effluents are adhered to, to ensure a lower inflow of phosphorus into the dam (Hart & Harding, 2015). However, the lack of technical experts, lax and lenient enforcement of the effluent standards, coupled with poor performance of many municipal wastewater treatment plants led to the discharge from these plants often contributing further to the eutrophication of water bodies (Hart & Harding, 2015; Atta *et al*., 2020). Declining 'preventative' control increased interest in curative in-lake options to reduce phosphorus levels in an attempt to remedy the resulting impacts of eutrophication on reservoir ecosystem health and concomitant human health threats arising from the use of the reservoir or lake as a primary source of potable water (Hart & Harding, 2015).

Hart (2006) found that prospects of applying classical biomanipulation as a management tool to ameliorate consequences of eutrophication in local reservoirs were weak as the reservoirs typically receive high external nutrient loads from large volumes of water carried by influent rivers draining relatively large catchment areas or highly urbanized watersheds with short hydraulic retention times (Hart & Harding, 2015; Carroll, 2019). Further studies supported the idea that biomanipulation was an inefficient method of reducing nutrient stocks in the Hartbeespoort Dam and concluded that the trophic state of the dam was too high for biomanipulation to have a significant effect on nutrient stocks (Hart & Harding, 2015; Hart & Matthews, 2018; Carroll, 2019; Carroll & Curtis, 2021). Even as early as 1985, the NWIR revealed that the removal of water hyacinth and algae from the dam was purely for aesthetic purposes and would be unlikely to improve the impacts of eutrophication (Carroll, 2019). In addition, Chislock *et al*. (2013) noted that fish-centric biomanipulation is most effective in small, easily managed systems such as ponds, and only has an effect on water quality in the time-range of weeks to months (Carroll, 2019).

Carroll (2019) found that upgrading wastewater treatment works in the catchment and refurbishing leaking and overflowing sewers would be the most likely long-term solution to the eutrophication problem at the Hartbeespoort Dam as the Dam will continue to receive large amounts of waste water effluents from the cities of Johannesburg, Midrand and Krugersdorp for the foreseeable future and the eutrophic state of the Dam would be unlikely to change anytime soon (Harding *et al*., 2004).

2.1.1 First Appearance of Water Hyacinth on Hartbeespoort Dam and Management Process

According to unpublished records of the Department of Water Affairs, water hyacinth first appeared on the Hartbeespoort Dam in 1959. The highest coverage the Dam recorded was in a 1976 study to determine the impact of the chemical control of water hyacinth on Hartbeespoort Dam which showed that 55-60% of the dam surface was covered; that is, approximately 1100–1200 hectares of water hyacinth (Ashton *et al*, 1979). In the same year, a socio-economic survey conducted to assess the impact of the severe infestation revealed that water-related recreational activities (angling, yachting, power-boating, water-skiing) generated 691,000 visitor-days annually with an estimated turnover of R13 million, and that this income would be adversely impacted by the water hyacinth which covered the water surface (Ashton *et al*., 1979).

During the 1976 infestation, the Department of Water Affairs discussed control strategies for the water hyacinth. At the time, mechanical harvesting was the most attractive control strategy for managing water hyacinth infestations of the Hartbeespoort Dam as it would have minimal ecological impact; however, it was considered technically and economically unfeasible because of the difficulty of access, high transport costs and the rapid growth of the plant (Ashton *et al*, 1979). Biological control of water hyacinth on the Hartbeespoort Dam was considered inappropriate as there was insufficient preliminary research on biological control in South Africa and because the crisis water hyacinth infestation prevalent on the Dam at that time warranted an immediate solution (Ashton *et al*, 1979).

An investigation into the cost of mechanical removal in 1976 found that chemical control by herbicide would be half the cost of the mechanical removal of water hyacinth, where mechanical harvesting was expected to cost R600 000 to harvest 1200 hectares of the plant growth at a rate of 6% per day (Ashton *et al*., 1979). The Department of Water Affairs carried out a small-scale trial to establish the effectiveness of the chemical control (Ashton *et al*., 1979) and sprayed the registered herbicide, Clarosan 500FW (Terbutryn), on approximately 20 hectares of water hyacinth on the Dam. Following on this trial, herbicides were used to control water hyacinth on the Hartbeespoort Dam for 24 years (van Wyk & Wilgen, 2002).

The global agreement amongst scientists and managers is that no single method is effective in eradicating *P. crassipes,* hence an integrated management of the weed is the best option (Téllez *et al*., 2008). However, in many developing countries, freshwater bodies, such as Hartbeespoort Dam, that have water hyacinth infestations are used for drinking water, and the contamination of the water bodies by herbicide can have an adverse impact on human health (Hill & Coetzee, 2008). Therefore, chemical control of water hyacinth in developing countries is not a suitable control measure (Hill & Coetzee, 2008). The Department of Environmental Affairs put a moratorium on herbicide use on the Hartbeespoort Dam in 2016, since then, the only control mechanisms available for the management of water hyacinth on the Dam have been physical control (both manual and mechanical removal) and biological control. Classical biological control has been less successful in temperate regions than in warmer tropical and subtropical regions (Maseko *et al*., 2021) because mortality of biological control agents is high during winter in temperate areas, not only owing to cold-induced mortality but because the quality of the host plants is poorer, which reduces agent populations (Maseko *et al*., 2021).

2.1.2. Biological Control Agent Interactions

Understanding the potential synergistic or antagonistic interactions between a suite of agents released for the control of a single species is necessary to predict the outcomes of a multi-agent biocontrol programme. In its native range, *Pontederia crassipes* occurs in low densities as the various natural enemies of the plant are present; these herbivores have co-evolved with the weed, meaning that they complete their entire life cycle on the plant. Host-specific natural enemies are introduced to an invaded habitat with the aim of establishing self-sustaining natural enemies, and so leading to a reduction in weed population density (Falthauser *et al*., 2023). A proliferation of the weed in the native range may occur as a result of changes in the hydrological regime of the waterbody altered by human activities, where the level of nutrients in the water has increased or where flushing of the plant and its natural enemies occurs, and the plant population recovers faster than the population of its natural enemies (Coetzee *et al*., 2017).

Eventually, the balance is restored as the populations of the natural enemies increase to reduce plant populations (Coetzee *et al*., 2017).

The aim of biological control is to reduce weed populations to manageable levels through a balance between populations of the host plant and that of its host-specific natural enemies (Coetzee & Hill, 2008b). Goode *et al*. (2020) found that releasing multiple biological control agents can increase the success of a biological control programme through niche partitioning.The level of interactions by multiple biological control agents released against the same weed can be classified as (i) synergistic, where the interactions cause a significantly greater reduction in the plant variables than when one agent feeds on the weed; (ii) additive, where the interaction causes the same reduction in a plant variable as would the combined damage of agents (Hatcher 1995); however, the definition of an additive interaction was adjusted by Turner *et al.* (2010) to one where the impact of multiple agents is greater than that of the most damaging agent acting alone, but less than or equal to the added impact of each agent acting alone; (iii) equivalent interactions that occur when the damage caused on the plant is equivalent to when each of the agents act alone; (iv) inhibitory interactions that occur when a significantly lower reduction of a plant variable than would be observed if damage was caused by the weaker of the two agents (Hatcher, 1995).

Ajounu *et al*. (2007, 2009) examined the interactions among the mirid, *E. catarensis* and two *Neochetina* spp. weevils and found that although the mirid was compatible with the weevils, *N. eichhorniae* fed less when combined with the mirid, while Delfosse (1977, 1978) examined the interaction between *N. eichhorniae* with the mite, *Orthogalumna terebrantis* and found that *N. eichhorniae* laid more eggs in the presence of the mite. The weevil also exhibited increased feeding in the presence of the mite (Marlin *et al*., 2013a). Marlin *et al*. (2013a) examined the paired interactions of *O. terebrantis*, *N. eichhorniae* and *E. catarensis* and found that the three species can co-exist with little negative interaction. Their co-existence is neither additive nor synergistic. Although the combined treatment of the mirid and the mite caused the most leaf damage, this combination did not translate into an impact on plant growth, that is, ramet production, or a reduction in biomass.

Goode *et al*. (2020) found that plants exposed to *Neochetina* spp. weevils and *M. scutellaris* had a higher mortality rate than those exposed to either type of insect individually. This finding indicates that there is at least an additive effect of the biological control insects on *P. crassipes* mortality (Goode *et al*., 2020). *Megamelus scutellaris* feeds by piercing the tissues of its host plant using a needle-like rostrum (Sosa *et al.*, 2005), while adult *Neochetina* sp. weevils feed on the leaves and the larvae tunnel through the petioles and the crown, causing significant damage to the plant (Coetzee & Hill, 2008b). Additionally, the tunnelling of the crown by weevil larvae in the lower petioles results in water entering the plant. This water-logging and introduction of secondary fungi causes the plant tissue to rot, contributing to the eventual sinking of the plant (Coetzee & Hill, 2008b). Larval tunnelling of the *N. albuguttalis* through the petioles also causes heavy but sporadic damage to the water hyacinth plants (Coetzee & Hill, 2008b).

Herbivory only leads to the death of plants when the leaf dynamics of the water hyacinth plant are disrupted, when leaf mortality surpasses leaf production, thus reducing the plant's ability to stay afloat (Coetzee & Hill, 2008b). The combination of these feeding mechanisms by all of the water hyacinth control agents ultimately leads to death of the plants through sinking, reducing the population density, and resulting in control. This thesis investigates the contribution of *M. scutellaris,* the most recently released agent, to the existing biocontrol programme on Hartbeespoort Dam, in the face of eutrophication, temperate winters, and in the absence of chemical control.

2.1.3 Study Organisms: The Biology and Impact of Biological Control agents used against *Pontederia crassipes* in South Africa

The successful biological control of invasive weeds requires detailed knowledge of the ecology of the biological control agents being used and of their impact on the weed (Wilson *et al*., 2006). Understanding the biology of the agent and its requirements in the introduced range will significantly improve the success of long-term, self-sustaining biocontrol programmes (Maseko, 2021). Of all the biotic and abiotic factors that impact the biological control of water hyacinth, the following are the most important in limiting the effectiveness of the control programme (Hopper *et al*., 2021): (i) cooler temperatures, (ii) intense flooding and drought periods that lead to the removal of both plant and biological control agents, (iii) heavy use of chemicals and herbicides and (iv) highly eutrophic conditions.

To assess the impact of biological control agents on the host plant, information is required on (i) what controls the dynamics of the insects, (ii) the rate at which the insects damage the plant, and (iii) how these relationships vary with environmental conditions. To date, nine biological control agents, eight arthropods and one fungal pathogen have been released against water hyacinth in South Africa; however, water hyacinth still covers many sites at unacceptable levels (Miller *et al*., 2023). During the 1990s, a classical biological control programme was implemented for water hyacinth on the Hartbeespoort Dam (Coetzee *et al*., 2022a). The *Neochetina* weevils, *N. eichhorniae* and *N. bruchi,* the moth *Niphograpta* *albiguttalis,* and the mite *Orthogolumna terebrantis* were released in the early 1990s, and the mirid, *Eccritotarsus catarensis,* was released in 1997 (Coetzee *et al*., 2022a). Despite the establishment of the suite of biocontrol agents, biological control was limited by a combination of cold winter temperatures, eutrophic water and the application of herbicides which continued until 2017.

2.1.3.1 *Neochetina eichhorniae* Warner and *Neochetina bruchi* Hustache (Coleoptera: Curculionidae)

Classical biological control agents used against water hyacinth are the *Neochetina* weevils, *Neochetina eichhornae* Warner (Coleoptera: Curculionidae) and *Neochetina bruchi* Hustache (Heard and Winterton, 2000). *Neochetina eichhorniae* and *N. bruchi* adults are 4–5 mm and feed nocturnally (Jadhav *et al*., 2008). The weevils exhibit preferential feeding on the youngest leaves on the plant, forming characteristic small, sub-circular scars (Jadhav *et al*., 2008). The *N. bruchi* females lay eggs in batches or singly, inserted below the epidermal layer of older petioles (Jadhav *et al*., 2008, Firehun *et al*., 2015). However, *N. eichhorniae* prefers to oviposit on the three youngest leaves (Wilson *et al*., 2006). Firehun *et al*. (2015) found that first eggs were laid one day after emergence, whereas Deloach and Cordo (1976) found that *N. bruchi* oviposited during the first three days after emergence. The eggs are white when first laid but change to pale orange as they approach hatching (Deloach & Cordo, 1976). Firehun *et al*., (2015) observed the egg-hatching period for *N. bruchi* ranged from 4 to 10 days, while for *N. eichhorniae*, it ranged from 8 to 12 days at an average temperature of 25 °C.

The larvae develop through three stages and usually feed endophagously, tunnelling through the youngest petioles (Jadhav *et al*., 2008). Larvae of *N. bruchi* take a comparatively shorter period of 32–38 days to complete their developmental stage than *N. eichhorniae* larvae which take 52–60 days (Firehun *et al*., 2015). The fully-grown larvae move to the roots of the plant and use fine rootlets to construct a dark circular cocoon in which they pupate (Jadhav *et al*., 2008). The pupal stage takes between 28-30 days for the two weevils (Firehun *et al*., 2015). Adult longevity for both sexes ranged from 80 to 130 days for *N. bruchi* and 90 to 160 days for *N. eichhorniae* (Firehun *et al*., 2015). A study conducted in Kenya indicated that the adults of the two weevils lived for about 112 days on average (Firehun *et al*., 2015).

The release of *N. bruchi* and *N. eichhorniae* from their native range in South America began in the early 1970s (Hopper *et al*., 2021). *Neochetina bruchi* was released in 30 countries, while *N. eichhorniae* was released in 32 countries (Hopper *et al*., 2021). The weevils had a medium to high impact on water hyacinth populations in 18 of the countries; reducing water hyacinth infestations by 95% (Wilson *et al*., 2006). In South Africa, *N. eichhorniae* was introduced into quarantine in 1973 and released at water hyacinth infested sites in 1974 (Cilliers, 1991).

Weevil effectiveness against water hyacinth varies with plant quality, and the two weevil species show a differential preference for plants with different phenologies (Wilson *et al*., 2006). Heard and Winterton (2000) found that *N. bruchi* was more sensitive to plant quality than *N. eichhorniae,* and a higher proportion of *N. eichhorniae* was found in mature rather than developing plants (Heard & Winterton, 2000). Conversely, *N. bruchi* preferred lush plants growing in nutrient-rich water that were previously unstressed by herbivory (Heard & Winterton, 2000). *Neochetina* spp. larvae are observed to cause more damage to the water hyacinth plant than the adults (Wilson *et al*., 2006).

Wilson *et al*., (2006) observed that *N. eichhorniae* experienced density-dependent mortality at early larval stages because first and second instars did not move from the petioles where they were laid. The later instars were able to move between petioles and plants; this mobility makes them less subject to competition for food and leaf mortality (Wilson *et al*., 2006). Leaf mortality impacted larval densities as the larvae at early stages had a higher probability of being stranded in dead and dying leaves (Wilson *et al*., 2006). This lack of mobility at early larval stages should be a consideration for integrated control programmes where foliar pesticides are used as part of the control measures (Wilson *et al*., 2006). Applying foliar pesticides where there are relatively higher numbers of young larvae would drastically reduce the weevil populations (Wilson *et al*., 2006).

The same can be argued for frosting over of leaves: should the onset of winter begin when. *N. eichhorniae* larvae are in the early stages, the weevil population would be drastically reduced (Wilson *et al*., 2006). Conversely, if foliar herbicides are applied when the weevil population is at later larval stages or adults, then the negative impact of leaf mortality may be reduced (Wilson *et al*., 2006). A similar mitigating effect against the negative impact of leaf mortality can be achieved by using sub-lethal doses of herbicides, or leaving some areas unsprayed to provide a reserve for the biological control agent (Wilson *et al*., 2006).

Wilson *et al*. (2006) noted that high-nutrient leaves tended to have broader petioles, thus allowing for higher larval densities (Wilson *et al*., 2006). Towards the end of their study, Wilson *et al*. (2006) observed that the large larvae were feeding on the meristem and rootstock. Wilson *et al*.'s (2006) investigation of the *N. eichhorniae* larval densities on larval development under low and high nutrients found that their results supported Heard and Winterton's (2002) findings where *N. eichhorniae* larvae developed faster at higher water nutrient concentrations, and the larvae of particular instars in high nutrients were bigger than those in low nutrient plants (Wilson *et al*., 2006).

Heard and Winterton (2000) found that *N. bruchi* can reduce plant biomass to very low levels, even at higher nutrient concentrations, but *N. eichhorniae* was not as effective at high-nutrient levels. They also noted that water hyacinth plants grown in higher water nutrient concentrations were superior hosts for *N. bruchi* than for plants grown in a medium nutrient concentration.

Herbivory by biological control agents, particularly *Neochetina* weevils whose larvae mine the petioles and root stock (Figure 2.3), leads to stunted growth of water hyacinth plants and, because they are water-logged, the plants sit lower in the water column (Jones *et al*., 2018; Faltlhauser et al., 2023). The water-logged plant mats then require wind or wave action to break up and sink, reducing the water hyacinth plant coverage of the water surface (Jones *et al*., 2018).

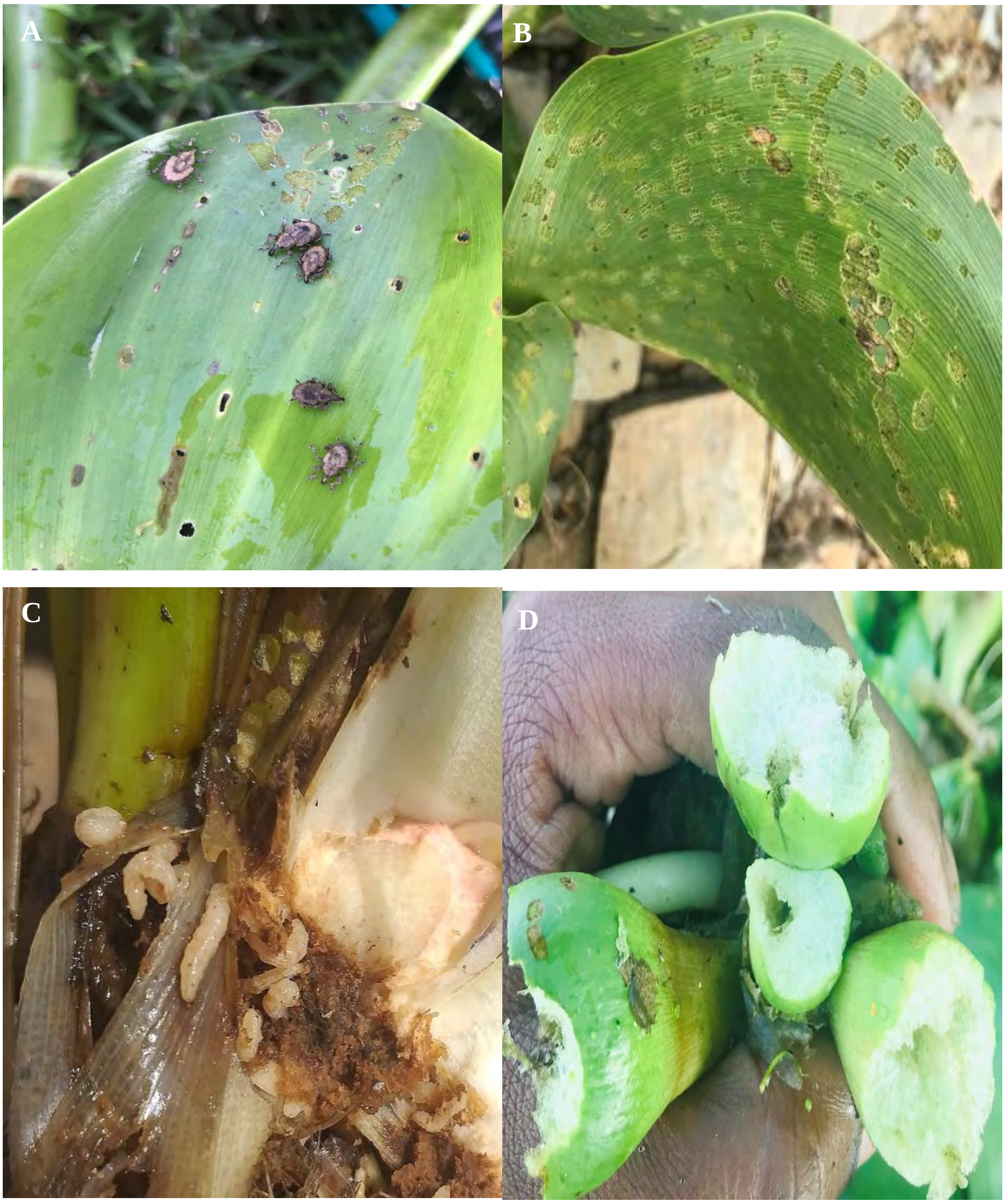

Figure 2.3. A) Adult *Neochetina* spp; B) Feeding scars of adult *Neochetina* spp; C) *Neochetina* spp larvae feeding on the meristem and rootstock of a water hyacinth plant; D) Water hyacinth petioles mined by *Neochetina* spp larvae

2.1.3.2 *Niphograpta albiguttalis* Warren *(*Lepidoptera: Pyralidae*)*.

The South American moth, *Niphograpta albiguttalis* Warren (Lepidoptera: Pyralidae)., was released in South Africa in 1990 as a biological control agent against water hyacinth (Canavan *et al*, 2014). *Niphograpta albiguttalis* was discovered in South America in 1968 and, after testing, was found to be a suitable biological control agent as it was able to disperse over long distances (up to 4 km a day), to tolerate variable climates, generate rapidly (approximately 35 days from egg to egg) with high fecundity (up to 300 eggs per adult female) and most importantly, to be host specific to water hyacinth (Canavan *et al.*, 2014).

Adult females oviposit on the leaves of water hyacinth, primarily in areas where the epidermis has been damaged (Canavan *et al.*, 2014). Larvae develop through five instars, tunnelling into petioles and feeding below the epidermis, resulting in damage 'windows'; older larvae feed down towards the central rosette, eventually leading to the plant becoming water-logged and sinking (Canavan *et al.*, 2014). The moth was first released in South Africa at only a few locations, but has since established under a wide range of climatic conditions from tropical KwaZulu-Natal to the cold, high-altitude Vaal River catchment (Canavan *et al*., 2014).

Canavan *et al*. (2014) aimed to predict the establishment patterns of *N. albiguttalis* in various water systems in South Africa by assessing its effectiveness as a biocontrol agent against water hyacinth in different nutrient conditions typical of South African water bodies by examining the damage done by the moth to water hyacinth plants grown at three different nutrient levels: low-, medium- and high-nutrient concentrations (Canavan *et al*, 2014). The study showed that *N. albiguttalis* significantly damages water hyacinth plants grown at high-nutrient levels; however, its damage did not result in acceptable levels of control because of the high productivity of the plants under eutrophic conditions (Canavan *et al*., 2014). The study proposed that *N. albiguttalis* be used in conjunction with other biological control agents and included an integrated management programme involving herbicidal control (Canavan *et al*., 2014).

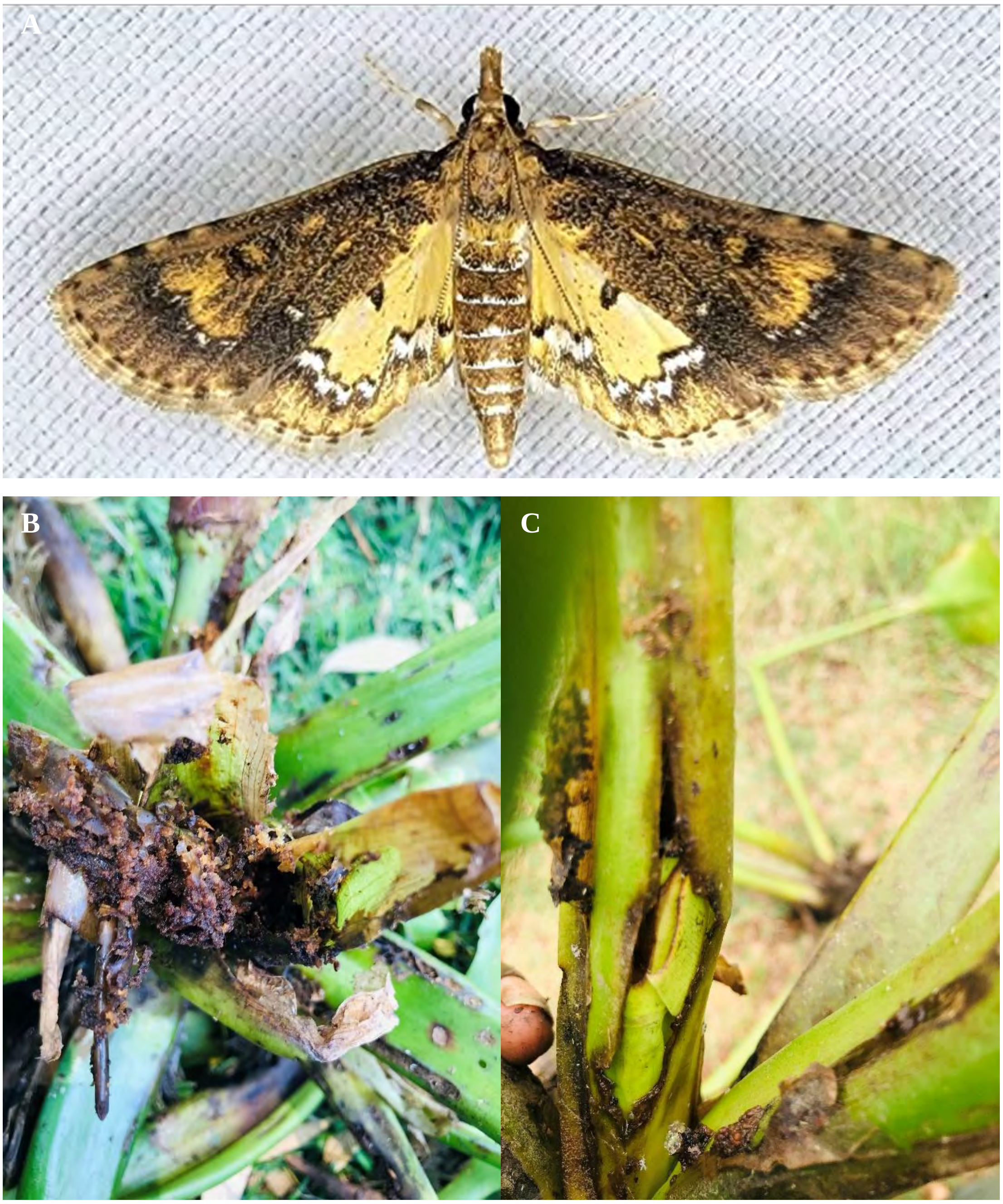

Figure 2.4. A) *Niphograpta albiguttalis* adult, Image from GBIF (www.gbif.org/occurence/4936526100); B) Feeding damage cause by the *N. albiguttalis*; C) Feeding damage and exit point for *N. albiguttalis* moth.

2.1.3.3 *Orthogalumna terebrantis* Wallwork (Acari: Galumnidae)

The South American mite, *Orthogalumna terebrantis* Wallwork *(Acari: Galumnidae)* is one of the seven biocontrol agents on water hyacinth. established in South Africa in the late 1980s, and recorded from 17 out of 66 sites surveyed across the country (Marlin *et al*., 2013b). The impact of its herbivory had not been evaluated until the work of Marlin *et al*. (2013b). Female *O. terebrantis* oviposit on the youngest water hyacinth laminae underneath the cuticle in small perforations made with their mandibles, in the middle layer of the parenchyma. As the larvae and nymphs develop, they feed on the tissue inside the lamina, creating distinctive yellowish linear markings known as galleries. The galleries become more visible with time as they elongate, reaching a length of approximately 4 mm before adults emerge.

Field observations in South Africa indicate that during summer, mite herbivory may damage more than 50% of the leaf surface area in certain water hyacinth infestations (Marlin *et al*., 2013b). Water hyacinth growth was affected more by nutrient levels than the mite herbivory. Unlike the nutrients, mite herbivory had little impact on plant parameters.

Although water nutrient content had a great impact on plant growth, growth was unaffected by mite herbivory at all levels of nutrients tested (Marlin *et al*., 2013b). Feeding by *O. terebrantis* decreased water hyacinth photosynthetic rate and light reaction even at relatively low mite densities. Marlin *et al*. (2013b) showed that the impact of this biological control agent on its host plant may not be obvious at a plant growth level, but may nonetheless affect the plant at a physiological level because herbivory may reduce the photosynthetic ability of a plant more so than simply reducing the photosynthetic surface area (Marlin *et al*., 2013b).

Figure 2.5. A) *Orthogalumna terebrantis*, Image from the National Bureau of Agricultural Insect Resources, India (www.lsuagcentre.com)**;** B) Feeding galleries made by mites on water hyacinth leaf at Hartbeespoort Dam

2.1.3.4 *Eccritotarsus catarinensis* (Carvalho) (Hemiptera: Miridae)

A leaf-feeding, sap-sucking mirid, *Eccritotarsus catarinensis* Carvalho was collected in Rio de Janeiro in 1989 and released in South Africa in 1996 (Hill *et al.*, 1999). The insect has a short generation time so the population can increase rapidly (Hill & Oberholzer, 2004). Hill *et al*. (1999) described the biology of this agent as follows: the duration of immature stages (from egg to nymphs) is approximately 23 days; the females insert their eggs horizontally and singly into water hyacinth leaf tissue, mainly on the undersurface of the leaves; the mean incubation time for the eggs is about nine days; there are four nymphal instars that are creamy white and nearly transparent, with conspicuous red eyes; the nymphs vary in length from about 0.96 mm in the first instar to about 2.83 mm in the fourth instar; the duration of the nymphal development is approximately 15 days. Adult *E. catarinensis* survive ~50 days.

The adults and nymphs feed gregariously on the leaves of water hyacinth, causing severe chlorosis and stunting of the plant (Hill & Oberholzer, 2004), producing shiny black frass marks on both surfaces of the leaves (Hill *et al.*, 1999). The adults are typically slender with a black exoskeleton, pale legs with reddish eyes, and hyaline patches on the wings (Hill *et al.*, 1999). The sexes are easily distinguishable (Hill *et al.*, 1999). The male abdomen is slender with a yellow tip and the female's abdomen is rounded and entirely black (Hill *et al.*, 1999). The females are slightly bigger than the males (Hill *et al.*, 1999).

A study by Hill *et al*. (2000) showed a higher chance of establishment of the insect when eggs, nymphs and adults of the insect are released onto plants. The nymphs feed gregariously, mainly on the undersurface of the water hyacinth leaves, often in the presence of the adults (Hill *et al.*, 1999). The adults and the nymphs feed on the leaf tissue of water hyacinth, causing yellowing and browning, or chlorosis of the lamina due to the extraction of chlorophyll from the palisade parenchyma, which ultimately leads to the premature death of the leaf (Hill *et al.*, 1999).

Mirid populations are negatively affected by environmental factors such as wind and rainfall; however, may be effective in tropical and subtropical regions, especially when used in conjunction with the other natural enemy species released on water hyacinth in South Africa (Hill & Oberholzer, 2004). For example, the mirid was successful at a subtropical site near Durban in KwaZulu-Natal where it reduced water hyacinth cover of 10 hectares from 100% to 10% in 18 months (Hill & Oberholzer, 2004). However, both eutrophication and cold winter temperatures reduce the degree of control of water hyacinth by *E. catarinensis* (Coetzee *et al*., 2007a, b; Maseko *et al*., 2021).

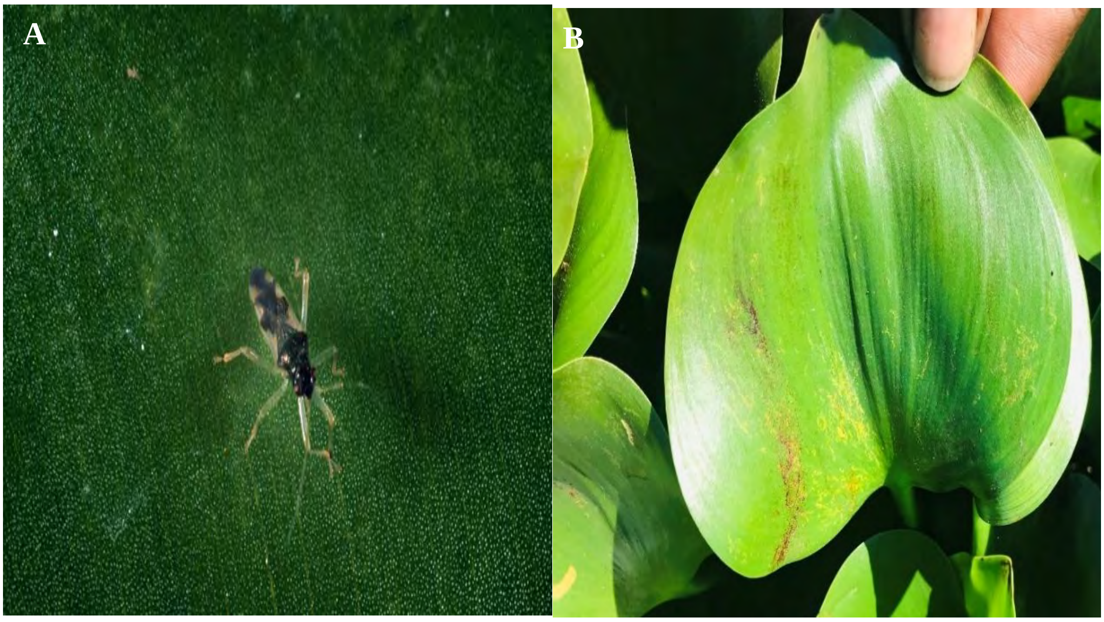

Figure 2.6. A) *Eccritotarsus catarinensis*, Image by Martin P. Hill, ARC - Plant Protection Research Institute, Bugwood.org; B) Chlorosis scars made by *Eccritotarsus catarensis* feeding.

2.1.3.5 *Megamelus scutellaris* Berg (Hemiptera: Delphacidae)

Megamelus scutellaris is a delphacid planthopper, native to Peru, Brazil, Uruguay, and Argentina where it is found associated with *P. crassipes* (Sosa *et al*.,2005; Goode *et al*., 2021). It has been released for the control of water hyacinth in the USA (Tipping *et al*. 2015), South Africa (Miller *et al*., 2019) and Zimbabwe (Coetzee, J.A. pers, comm.). This sap-sucking planthopper feeds by piercing the tissues of its host plant using a needle-like rostrum. The small size of these mouth parts makes it difficult to detect the damage done to plant tissues even though photosynthetic damage may have occurred. Photosynthetic damage is expected when a planthopper is present, as planthoppers typically feed directly on photosynthates (Miller *et al*., 2019). *Megamelus scutellaris* reaches high population densities in its native range and thus was considered as a biological control agent candidate in the management of water hyacinth where the aquatic plant is invasive (Sosa *et al*., 2005).

Megamelus scutellaris' life history, as described by Sosa *et al*. (2005), is summarized as follows: mating occurs close to the water level, and one to four eggs are laid in the apical portion of the petiole and pseudolaminae. Females predominantly oviposit on the isthmus between the petiole and the lamina of *P. crassipes,* and eggs can continue to develop even in plant senescence or herbicide mortality (Goode *et al*., 2021). Ovipositional scars are characterised by three parallel marks which turn brown after approximately three days. The eggs are aligned with the shortest central mark. Following oviposition, nymphs emerge 1-2 weeks later and are mobile enough to move between plants, which allows them to abandon sprayed, dying plants and disperse to healthier ones (Sosa *et al*., 2005; Goode *et al*., 2021). The first instars feed in groups near the water hyacinth pseudolaminae. Sosa *et al*. (2005) observed that the entire immature stage lasts approximately 15 days under controlled conditions; however, in outdoor conditions, the immature stages may take up to 25 days. Host-specific testing by Grodowitz *et al.*, 2017 showed that *M. scutellaris* had a short developmental time of <25 days from egg to adult at 25 °C.

From May to August in localities in Argentina, water hyacinth decays due to frost, but the base of the plant remains protected by leaf litter where the planthopper resides. The immature stages of *M. scutellaris* represent by far the most abundant stage collected overwintering. This suggests that the planthopper could overwinter as nymphs at least in a protected area. *Megamelus scutellaris* has wing dimorphic adults whereby adults can either be macropterous (flighted) or brachypterous (non-flighted) (Goode *et al*., 2021). The production of macropterous forms allows for escape from deteriorating local conditions and the colonization of new habitats (Denno *et al*.,1991). Males are the first to be winged at low densities for mating purposes, followed by dispersal (Denno *et al*.,1991).

Denno *et al*. (1991) found that the levels of migration (% macroptery) in field populations decreased significantly as the persistence of their habitats increased (Denno *et al*.,1991). Macropterous (winged) forms were triggered at low densities for species inhabiting temporary rather than persistent habitats (Denno *et al*., 1991). In persistent habitats, wings are less necessary for habitat escape, and they are rarely required for mate location (Denno *et al*.,1991). Wing development imposes a reproductive penalty, thus most dimorphic species prefer flightlessness (Denno *et al*.,1991). For species in temporary habitats, wings are favoured in males to locate females at low densities, and are favoured by all sexes at high densities to escape the habitat (Denno *et al*.,1991). The advantage of flightlessness in female planthoppers is that brachyptera are both more fecund and reproduce earlier in life than the long-winged counterparts (Denno *et al*., 1991).

Roff (1984) and Denno *et al*. (1989) argued that the reproductive delay and reduced fecundity observed in the macropterous form of many dimorphic insects supports the hypothesis that there are phenotypic trade-offs between flight and reproduction (Denno *et al*., 1991). Wing form in planthoppers is determined by a developmental switch that responds to various environmental cues (Denno *et al*., 1991) such as crowding, host plant condition, temperature, and photoperiod which are all known to trigger developmental switch and influence wing form (Denno *et al.*, 1991). Of all environmental factors, population density is the most influential factor known to affect wing form in plant hoppers (Denno *et al*., 1991). In most species, the production of the migratory forms (macropters) is density-dependent, is associated with crowded conditions, and is intensified by nutritionally inadequate host plants (Denno *et al*., 1991).

Megamelus scutellaris was first brought into quarantine in 2008, at the United States Department of Agriculture (USDA), Agricultural Research Service (ARS), Invasive Plant Research Lab (IPRL) in Fort Lauderdale, Florida where it was evaluated and tested (Freedman and Harms, 2015). The water hyacinth planthopper was released in the Sacramento Delta and its tributaries by scientists with the California Department of Food and Agriculture (CDFA) in 2011 (Hopper *et al*., 2021). In 2013, *M. scutellaris* was approved for release in South Africa, and the first was made on the Kubusi River in the Eastern Cape, South Africa (Miller *et al*., 2021). The easily detectable oviposition marks on *P. crassipes*, the efficient rearing in captivity and the high survivorship (Sosa *et al*., 2005), were important attributes for the mass-rearing of the insect for release on water hyacinth-infested water bodies (Miller *et al*., 2021).

Figure 2.7. A) *Megamelus scutellaris* at diffent life stages, nymphs, adult and winged individuals; B) Feeding damage caused by *Megamelus scutellaris*.

This chapter has summarised the suite of biological control agents that were present on Hartbeespoort Dam at the onset of the project. Hill *et al.* (1999) noted that 24 years after the intentional release of *Neochetina eichhorniae*., it was apparent that no single natural enemy would achieve sufficient control of the weed and that it was more likely that a suite of herbivorous insects and pathogens would ultimately result in the effective biological control of water hyacinth. Releasing multiple biological control agents can increase the success of a biological control programme through niche partitioning (Goode *et al*., 2020) which is the process by which natural selection drives competing species into different patterns of resource use or different niches (Goode *et al*., 2020).

Despite the release of this suite of natural enemies, control of water hyacinth in South Africa is variable, and has largely been ascribed to eutrophication and cooler temperatures experienced in temperate regions of South Africa (Coetzee *et al*., 2022). Despite these limitations, a decision was made to release the planthopper, *M. scutellaris*, at Hartbeespoort Dam, but to adapt the management strategy that would allow populations of the hopper to build up through frequent and inundative releases from mass rearing facilities (Moffat *et al*., 2024).

Chapter 3: Post-release Evaluation of *Megamelus scutellaris* at a Cool Temperate, Eutrophic, Urban Impoundment

3.1 Introduction

Biological control programmes comprise two phases: the pre-release phase which includes surveys for potential agents in the indigenous range and host-specificity tests, followed by the post-release phase that includes mass-rearing, redistribution of agents and post-release monitoring and evaluation of success (Paterson *et al*., 2023). Post-release evaluations measure the success of a biological control programme by assessing changes in the invasive alien plant community following the introduction of a biocontrol agent (Miller *et al*., 2019; Maseko *et al*., 2021; Paterson *et al*., 2023). Several studies (Schaffner *et al*., 2020; Falthauser *et al*., 2023; Paterson *et al*., 2023) have noted that of all the aspects of biological control of weeds, post-release monitoring remains most neglected and underfunded, and, despite their presumed importance, there are even fewer assessments of ecosystem responses to biocontrol (Carson *et al*., 2008).

Post-release evaluations can be carried out at different scales, ranging from monitoring physiological changes within the target weed, to changes in individual plant parameters, population level and landscape level changes (Paterson *et al*., 2023). Post-release monitoring entails researching the population dynamics of the biological control agents and the target weed, weed resurgence, the efficacy of the biocontrol agents, and the need to introduce the same or other biological control agents (Falthauser *et al*., 2023).

A reduction in the percentage water hyacinth cover of the water surface is the main goal and measure for the efficacy of biological control of the weed. However, this is regarded as an arbitrary metric to measure the success of the weed's control programme as floating macrophytes are prone to dispersion (Jones *et al*., 2018). Herbivory and its impact on the weed, however, provide better insight into the physiological changes in the target weed that led to a decline in coverage. Herbivory by biological agents will reduce petiole length, as well as above- and below-surface biomass of water hyacinth plants due to physical damage (Jones *et al*., 2018). For example, measurements of the longest petiole length and number of feeding scars on leaf 2, the second youngest leaf on a water hyacinth plant, which is preferentially fed upon by adult *Neochetina* weevils and reflects the most recent feeding activity, are recorded for each plant in the assessment of the impact of weevil herbivory and efficacy of the biological control agent (Jones *et al*., 2018). These parameters are standard measurements used in water hyacinth biological control programmes throughout South Africa (Jones *et al*., 2018).

Biological control has been highly effective in controlling invasive aquatic weeds such as water hyacinth but has suffered from a lack of empirical post-release evaluation that links the cause and effect (Jones *et al*., 2018). Therefore, quantitative post-release monitoring is necessary to account for differences in biological control outcomes across spatial and temporal scales (Hinz *et al*., 2020). Paterson *et al*. (2023) separated post-release evaluation studies into six categories as detailed below:

3.1.1 Weed Physiology Assessments

Weed cover changes can be attributed to a variety of factors, such as seasonal fluctuations, nutrient availability, and drought cycles. Herbivory impacts the photosynthetic ability of the plants as the surface area of the water hyacinth leaves is reduced. To ascertain the impact of herbivory by *Megamelus scutellaris* on water hyacinth, Miller *et al*. (2019) used chlorophyll fluorometry to assess photosynthetic activity in the presence of a biological control agent, where a reduction in photosynthetic activity was correlated with feeding.

3.1.2 Weed Growth Analysis

Herbivory is expected to have an impact on the growth parameters of the plants. A study by Jones *et al*. (2018) showed that water hyacinth plants subjected to herbivory had significantly lower biomass both above and below water. The plant petioles were also shorter than those of insect-free plants (Paterson *et al*., 2023).

3.1.3 Weed Population Dynamic Assessments

Herbivory by natural enemies reduces plant coverage on the water surface. Hoffmann *et al*. (2019) recommended documenting outcomes of biological weed control at a population level through the quantification of four invasion parameters: (i) weed density, (ii) area occupied by the weed, (iii) biomass of the weed, and (iv) the number of propagules. Sites invaded by water hyacinth require long-term monitoring as the sites are prone to resurgence of infestations owing to the seedbed.

3.1.4 Landscape Level Impact Assessments

In contrast to Paterson *et al*. (2023), Carson *et al*. (2008) described landscape scale monitoring of an invaded habitat as (i) the abundance of the biological control agent, (ii) the impact of the biological control agent on the target plant species, (iii) the potential for non-target effects, and

(iv) the response of native species and community to a reduction in the invasive species. Changes in weed coverage at landscape level is difficult to assess; however, development in drone and satellite technologies have made visualization in coverage changes possible, particularly for water bodies which are easy to delineate. A study by Coetzee *et al*. (2022) measured plant coverage of the weed over time, following the release of *M. scutellaris* on Hartbeespoort Dam, using Sentinel-2 MultiSpectral Instrument (MSI) satellite imagery at a 10m ground resolution.

3.1.5 Socioeconomic Returns Analysis

Pontederia crassipes infestations and the rapid spread of the weed has an adverse economic impact on agriculture, fishing and navigation on the waterbody it has invaded, imposing significant cost on local economies and livelihoods (Abba & Sankarannair, 2024). The high levels of evapotranspiration which occur in water hyacinth-infested water bodies result in losses of economically productive water resources (Arp *et al*., 2017). For a water-scarce country like South Africa, IAPs affect both the quality and quantity of available water (Fraser *et al*., 2016). A reduction in water quantity and quality has major economic implications in view of the fact that water is regarded as an important "economic good" (Fraser *et al*., 2016). Irrigation water contributes roughly 30% towards the country's total agricultural output (Arp *et al*, 2017). Water saving benefit refers to the prevention of water loss through evapotranspiration as a result of implementing a biological control programme against the weed. Water savings are measured by estimating the value of the water lost by evapotranspiration (Arp *et al*, 2017). Arp *et al*. (2017) estimated the average value of irrigation water for the Vaalharts Irrigation Scheme as a whole was R38.71/m^3 based on the crops through the scheme. With the implementation of a biological control programme, the water-saving benefit of water hyacinth control had a conservative benefit value of R54 million (Arp *et al.*, 2017).

The economic returns of controlling water hyacinth are not only limited to water savings. A study by De Groote *et al*. (2003) found a reduction of water hyacinth coverage caused by the implementation of a biological control programme, which introduced three natural enemies, undertaken between 1991 and 1993 in southern Benin led to an increase in income for the fishermen of R524,42 million (30 million USD) per year. Van Wyk and van Wilgen (2002) noted that the investment in property around Hartbeespoort Dam became the most vibrant in South Africa with the Dam being water hyacinth-free. At the time, a 500 m^2 shoreline plot was worth R2 million. Khatri *et al*. (2018) noted that water hyacinth infestations in lakes lead to plummeting tourism revenues from boating and other recreational activities, while also impacting people whose livelihood depends on the lake and surrounding businesses. The clearing of the infestation would improve revenue for areas such as Hartbeespoort which is reliant on tourism.

Wyk and van Wilgen (2002) conceded that although an integrated management programme for water hyacinth was the most cost-effective programme at R 227/ha at the time, they did note that biological control has the potential of being even cheaper if implemented over the long term. The study found that biological control costs R309/ha and offers a long-term solution that will also become cheaper the longer it is implemented, with a potential cost of R3.60/ha. They also found that herbicidal control was a short-term solution that costs R1 481/ha, which is five times less cost effective than biological control and an integrated control programme.

A widely used method of determining the feasibility of biological control programmes is a benefit-cost analysis (Fraser *et al*., 2016). Benefit-cost studies involve quantifying the effects of biological control measures by comparing the benefits with the cost of the control programmes (Fraser *et al*., 2016). The cost of the biological control programmes takes into account costs associated with research and technologies of the programmes, such as researcher salaries based to the time dedicated to the research, costs associated with the use of vehicles, administrative expenses and complementary services (Fraser *et al*., 2016). The De Groote *et al*. (2003) study of the southern Benin biological control programme was the first attempt at estimating the socio-economic impact of water hyacinth and its biological control in Africa. The total cost of the control programme for water hyacinth was estimated at 2.09 Million US dollars (De Groote *et al*., 2003). This resulted in a benefit:cost ratio of 124:1.

3.1.6 Ecosystem Returns Analysis

Biodiversity recovery and improved ecosystem functioning is often the goal of a biological control programme. In South Africa, ecosystem recovery after biocontrol has been quantified at a community level using aquatic macroinvertebrates as biological indicators **(**Paterson *et al*., 2023). Coetzee *et al*. (2020) and Motitsoe *et al*. (2020) demonstrated that aquatic macroinvertebrate diversity increased following the biological control of *Pistia stratiotes* and *Salvinia molesta*. Motitsoe *et al*. (2020) found that not only did aquatic macroinvertebrates communities recover following biocontrol, but there was an improvement in aquatic ecosystem processes, structure, and functioning. Whereas Misteli *et al*. (2023) found that mechanical/ physical removal of macrophytes in five sites across the world which experienced vegetative mass development, had an overall negative impact on biodiversity. The removal of macrophytes negatively impacted zooplankton and macroinvertebrate assemblages, while having a positive effect on phytoplankton assemblages (Misteli *et al*., 2023). Motitsoe *et al*. (2020) found that there was a marked difference in ecosystem structure for sites controlled by biological control when contrasted with sites control by conventional control methods. The noted differences were of resource abundance, trophic diversity, and food web complexity.

The aim of weed management programmes is to reduce weed densities, however a reduction in weed density does not always result in improvements in terms of ecosystem services or recovery of indigenous biodiversity (Paterson *et al*., 2023). Shen *et al*. (2023) found that following the biological control of terrestrial weed *Ambrosia artemisiifolia* (common ragweed) over two consecutive years was followed by a proliferation of non-target invaders which co-occurred with the target weed. Similarly, Coetzee *et al*. (2022b) found that following the biological control of *Pontederia crassipes* on the Hartbeespoort Dam in the autumn of 2021, there was a rapid growth of another invader, *Salvinia minima* Baker (Salviniaceae) common salvinia. Up until this, the invasive fern had been observed and limited to ponds in residential estates around the Dam. The same trend was observed by Chikodza *et al*. (2025) on the Dam the following year. This process of a co-occurring invaders suddenly proliferating following the control of a target weed is known as secondary invasion. This is due to the removal of a targeted invasive plant creating empty niches where co-occurring subdominant invaders proliferate and continue to threaten native communities (Shen *et al*., 2023).

3.1.6.1 Secondary Invasion on the Hartbeespoort Dam

Secondary invasions tend to correlate with the declines in targeted invaders, often becoming a barrier for native biodiversity restoration (Chikodza *et al*., 2025). Secondary invaders take advantage of the altered environmental conditions created by the eradication of the dominant invader and may respond more quickly than native species, thus receiving the most benefit from the altered state (Shen *et al*., 2023; Chikodza *et al*., 2025).

Secondary invasions are common in environments with multiple invasive species. Since most ecosystems have multiple established invaders, the likelihood of a secondary invasion when one or more target invaders are controlled increases.

Salvinia minima was recorded by a retired entomologist and biocontrol scientist, Dr Carina Cilliers, while undertaking zooplankton studies of water samples from the Hartbeespoort Dam in 2011 (Coetzee *et al*., 2022b). Though classified as an invasive alien plant in South Africa ***S.*** *minima* is not yet a target for eradication due to the small size of the plant and the low extent of infestation in freshwater systems across the country (Coetzee *et al*., 2022b). Coetzee *et al*. (2022b) confirmed the presence of ***S.*** *minima* at four sites in South Africa's highveld region. Surveys in the region confirmed the presence of *S. minima* in an impoundment of the Crocodile River downstream of the Hartbeespoort Dam, in the Roodekopies Dam and two unconnected systems, Bon Accord Dam and Roodeplaat Dam (Coetzee *et al*., 2022b). This makes it a candidate for biological control. *Cyrtobagous salviniae* Calder and Sands (Coleoptera:Curculionidae), a highly effective biological control agent for S. *minima* in Florida, is currently in quarantine to undergo host-specificity tests before being released onto *S. minima* (Coetzee et al., 2022b, Chikodza *et al*., 2025).

The Chikodza *et al*. (2025) study shows evidence of an emerging issue of secondary invasion, a concern in weed management, where suppressing targeted invasive species may promote the growth of non-target invaders. Shen *et al*. (2023) demonstrated that some biological control programmes have reduced impacts on system recovery because the removal of a targeted invasive plant creates empty niches where co-occurring subdominant invaders proliferate. Therefore, giving credence to the recommendation by Motitsoe (2020) that biological control of free-floating IAPs in freshwater ecosystems should be followed by the active introduction of native macrophyte propagules particularly for a hypertrophic system such as Hartbeespoort Dam.

The main revenue-generation sectors for the Hartbeespoort Dam are tourism and property development, therefore a secondary invasion for the colder months of the year means further limitations for recreational water use (Coetzee *et al*., 2022b). Furthermore, the pristine state of the Dam is important for revenue generation.

3.1.6.2 Biology of *Salvinia minima* Baker (Salviniaceae)

Salvinia minima Baker (Salviniaceae) common salvinia is native to Mexico, Central and South America and Northern Argentina. It is a highly invasive and damaging aquatic macrophyte and has been recorded for the first time in Africa (Coetzee *et al*., 2022b; Chikodza *et al*., 2025).

Salvinia minima is a small, rootless aquatic fern with round floating leaves approximately 0.5-2cm in diameter and a distinctive rib creating bowl-shaped appearance (Coetzee *et al*., 2022b). The adaxial leaf surface contains trichome hairs with a single stalk that divides the four branches, a diagnostic feature of the plant (Coetzee *et al*., 2022b). Below the water surface, leaves are modified to act as a root system for the plant (Coetzee *et al*., 2022b). The plant reproduces via fragmentation from attachment nodes, with up to five lateral buds per node, while the spores are sterile (Coetzee *et al*., 2022b). Rapid expansion has been recorded with population doubling every two weeks in the wild while under greenhouse conditions the plant doubles every 5-6 days depending on the nutrient load (Coetzee *et al*., 2022b). *Salvinia minima* thrives in slightly acidic, high nutrient, slow-moving freshwater. It is also resistant to periods of low temperatures, water stress and elevated pH levels (Olguin *et al*., 2002).

Figure 3.1. *Salvinia minima* Baker (Salviniaceae) common salvinia.

3.1.6.3 Impact of secondary invasion on *Pontederia crassipes* population dynamics on Hartbeespoort Dam

In South Africa, impoundments have been constructed on the majority of river systems to meet the country's water supply needs as it is a water scarce country (Chikodza *et al*., 2025). Due to most impoundments being situated downstream of urban areas, pollution has led to the impoundments become eutrophic. This state of eutrophication allows for the proliferation of invasive macrophytes (Chikodza *et al*., 2025). Hartbeespoort Dam receives substantial nutrient loads from its tributaries, The Crocodile, Hennops and Magalies rivers (Chikodza *et al*., 2025). The Dam has had an infestation of *Pontederia crassipes* since the 1970s and often experienced algal blooms. The implementation of inundative releases of biological control agents against *P*. *crassipes* significantly reduces *P*. *crassipes* populations and in 2021, the temporal absence of *P*. *crassipes* as a result of biological control facilitated the expansion and invasion of *Salvinia minima* (Chikodza *et al*., 2025). This occurrence suggests that *S*. *minima* takes advantage of reduced competition, space and available resources followed by the removal of targeted species as observed in other studies whereby the removal of the dominant species allows other invaders to proliferate (Chikodza *et al*., 2025).

Salvinia minima coverage rapidly increases following the reduction in *P*. *crassipes* coverage in late autumn (Coetzee *et al*., 2022b). Coverage by *S*. *minima* fluctuated following the onset of spring (September-November) with *P*. *crassipes* becoming the dominant macrophyte in late spring as a result of seedling-driven resurgence (Coetzee *et al*., 2022b). Following the biological control of *Pontederia crassipes* in 2021, the dam underwent secondary invasion by *Salvinia minima* thereby reducing the open surface water period experienced in previous year through the autumn and winter months.

Chikodza *et al*. (2025) explored the population dynamics between these two invaders on the Hartbeespoort Dam and found that herbivory by water hyacinth host-specific natural enemies reduced the competitiveness of water hyacinth when compared to common salvinia. Chikodza *et al*. (2025) found that *S*. *minima* was the weaker competitor than *P*. *crassipes* when grown together. However, with herbivory by *M*. *scutellaris* the competitive ability of *P*. *crassipes* was reduced (Chikodza *et al*., 2025). Furthermore, in the absence of herbivory water hyacinth has a competitiveness index 4 times high than common salvinia.

The aim of this chapter was to link the establishment and proliferation of the newly released biocontrol agent, *M. scutellaris,* on the dam to the decline of water hyacinth coverage and to assess the impact the herbivore has on the individual plants. This study looks at the unintended consequence of a successful biological control programme in the form of a second invasion by common salvinia. This study therefore, takes into account three of the stages of a post-release evaluation, evaluations at the individual plant level, the population level, as well as the landscape level.

3.2 Materials and Methods

3.2.1 Inundative Releases of *Megamelus scutellaris* at Hartbeespoort Dam

Classical biological control historically relied on the release of a small founder population of a biological control agent species that then increased in the field. However, given the environment of Hartbeespoort Dam, and the need for an urgent solution to the extensive water hyacinth population in the absence of herbicide application, an inundative approach to the release of *M. scutellaris* was taken. The benefit of this approach was that high number of the insects could be introduced in early spring when regrowth of the water hyacinth plants occurred, whilst the field population of the agent was still low owing to winter. *Megamelus scutellaris* was mass reared at the Centre for Biological Control Mass Rearing Facility (Makhanda/Grahamstown, South Africa) then sent to Gauteng via a courier in ice-boxes fitted with ice packs. At the onset of the release programme, high insect mortality was experienced, and thus a mini-experiment was carried out where temperature probes were placed in the iceboxes to determine the internal temperature of the package as it travelled from Grahamstown to Johannesburg, Gauteng. The outcome was that iceboxes would have to be fitted with an ice pack or frozen water bottle to ensure the survival of the insects.

Megamelus scutellaris was first released on the Hartbeespoort Dam in 2018. In 2019, the inundative release programme was embarked upon. Over 197 000 insects were released at various points around the Dam between 2018 and 2020. A release cycle of three consecutive weeks was carried out at each of the selected release sites. An average of 6000 insects was released weekly for the three weeks at each of the selected sites to ensure a cumulative effect on the population density of the insects, as the females oviposited soon after being released and the life cycle of *M. scutellaris* from egg to adult is less than 25 days. By the last release at a site, the eggs oviposited from the first release would be adults. A visual investigation nearest to the site of release was performed to look for signs of *M. scutellaris* establishement

3.2.3 Environmental Conditions Data

To assess the impact of temperature on the macrophyte coverage over the dam, data were collected from the South African Weather Services station. The minimum and maximum temperatures obtained at 8 a.m. daily were used to determine the mean temperatures for the month. Coetzee *et al* (2012), Miller *et al*. (2020) and Maseko *et al*. (2021) found that weather station temperatue reading from across South Africa were a reliable predictor of ambient temperature within the water hyacinth mat by doing comparative studies.

3.2.2 Macrophyte Coverage Time Series

Satellite imagery, using the macrophyte viewer, Macrophyte Monitoring Tool (earthengine.app), established the percentage cover over the dam. Satellite imagery data was recorded for each month from 2015 (several years prior to the moratorium on herbicide use for the control of water hyacinth) to October 2022, four years after the introduction of *M. scutellaris* as an additional biocontrol agent. The macrophyte viewer generates total macrophyte coverage plots which do not differentiate between the types of macrophytes present on the dam; however, the downloaded point data gave different coverage reading for water hyacinth, *Salvinia minima* and algae.

3.2.4 Plant Parameters

Monthly assessments of plant parameters were taken at three sites around the Hartbeespoort Dam for 24 months from October 2020 to October 2022. The sample sites were Kuper Oord (25°44’57’’S, 27°49’60’’E), The Kurz (25°45'46"S, 27°47'14"E), Lakeland (25°45’45’’S, 27°48’48’’ E), Ifafi (25°44'59"S, 27°53'24"E), Estate D' Afrique (25°46’35’’S, 27°54’17’’E) and Schoemansville Resort (25°44'11"S, 27°52'25"E).

The sample period for the project was October 2020 to October 2022, due to the Covid-19 lockdown restrictions that limited cross-province travel and human contact, thus access to the dam was restricted to property owners around the dam.

At each site, 10 randomly selected individual plants from the water hyacinth mat were selected and assessed by measuring the root length, longest petiole, length for leaf 2 petiole, area of leaf 2, and number of ramets, leaves and flowers. Plant height (length of the longest petiole) and root length were recorded from these plants were used to obtain the shoot:root ratio, which is used as an indicator of plant health (Maseko *et al*., 2021). Ten plants are considered a suitable number to sample owing to the uniformity of water hyacinth populations (Miller et al., 2020, Maseko *et al*, 2021). Petiole length was measured as the distance from the point of attachment at the rhizome to the base of the lamina (Heard & Winterton, 2000). A ramet, or daughter plant, is defined as a plant with one open leaf (excluding the primary leaf) and adventitious root initials (Heard & Winterton, 2000).

To determine biomass, three quadrats (0.25 m^2) were randomly placed on the water hyacinth mat and the plants removed from the mat, counted, and separated into biomass above the water, biomass below the water, and dead biomass (Maseko *et al*., 2021, Damtie *et al*., 2022).

3.2.6 Insect Parameters

***Neochetina* spp. counts**

Adult *Neochetina* spp. weevil-feeding scars were counted on the second youngest leaf of each of the 10 selected plants, which is preferentially fed upon by the adult weevils and therefore reflects the most recent feeding activity by the weevil population (Heard & Winterton, 2000). The plants were then taken apart to count the individual adult weevils on the plant, separating them by species, while also capturing the number of larvae present on the plant within the petioles and the crown of the plant.

***Megamelus scutellaris* counts**

Megamelus scutellaris density was measured using a sampler adapted from one used in the USA (Miller *et al*., 2020, Goode *et al*., 2021). The sampler is a 70-litre plastic bin with the bottom cut off and crosswire fitted at the bottom (Miller *et al*., 2020). The sampler is placed over the water hyacinth mat and then pushed down to submerge the plants. This allows for the *M. scutellaris* nymphs and adults to float on the water surface or climb on the sides of the bin where they can be counted (Miller *et al*., 2020). Ten replicates were sampled at each site around Hartbeespoort Dam at 5 m intervals at wadable depth (Miller *et al*., 2020). Since water hyacinth is a uniform clonal species, the sample size was taken as representative of the population (Miller *et al*., 2020). The data collected was converted to insects per m^2 by equating the circular area of the base of the sampler to a square metre, yielding a conversion of:

$$\frac{\bar{X} \text{ insect number per sample}}{0.093} = \text{insects/m}^2$$

This conversion allows for a comparative analysis with the plant density.

The presence of the mite, mirid, moth and pathogen were noted as part of the monthly surveys; however, their feeding scars were not analysed for this study.

3.3 Data Analyses

TIBCO Statistica 14.0.1 (2022) was used to plot plant parameter data; to assess the impact of insects on water hyacinth coverage and plant parameters RStudio statistical software v 4.4.1 (R Core Team 2024) was used for Generalised Linear Models (Gaussian and Binomial regression), linear regressions, ANOVAs and ANCOVAS of the factors that influence insect densities for *M. scutellaris*, *N. eichhorniae* and *N. bruchi*.

3.4 Results

Hartbeespoort Dam is located in the North West Province in what is commonly referred to as the highveld of South Africa. The region has temperate weather conditions and is prone to frosting over the winter months (June–August). The data confirm that the highveld experiences wet summers and sometimes below-freezing temperatures in the middle of winter, as observed in July 2021 at -1,7 °C. The highest monthly rainfall observed was in April 2021 at 188 mm. Very little rainfall occurs during the winter months (June–August) (Figure 3.2).

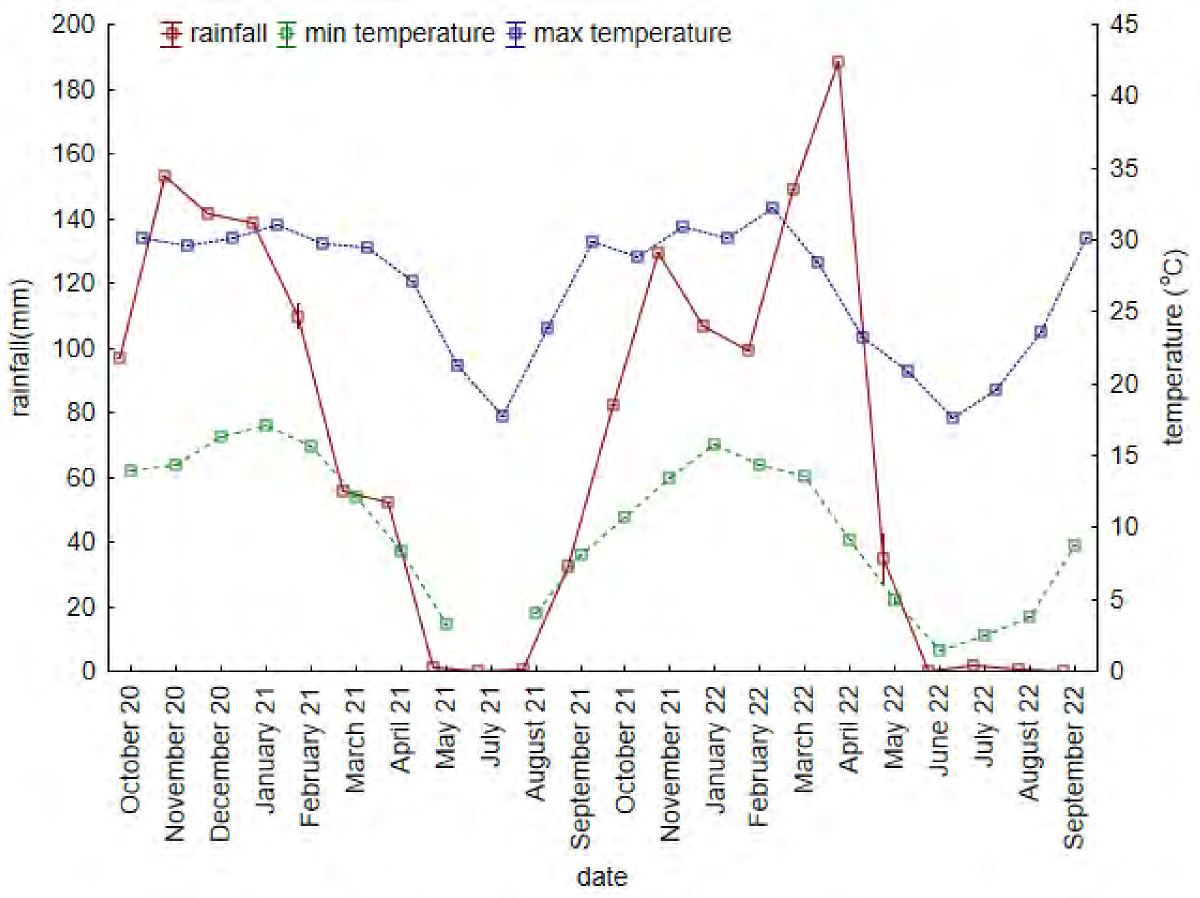

Figure 3.2. Temperature and rainfall patterns over the 24 months sample period (October 2020-October 2022) with a mean minimum temperature of 10.63 °C and a mean maximum temperature of 27.96 °C

Satellite imagery was obtained using the macrophyte viewer, [Macrophyte Monitoring Tool (earthengine.app)](), which allowed assessment of macrophyte coverage on Hartbeespoort Dam.

The macrophyte viewer was used to collect population growth data for water hyacinth from August 2015 to date to include the years where herbicides were used to control the weed (Figure 3.3).

There were higher overall macrophyte coverage levels for the 2021 winter season than in the preceding years. This was due to the proliferation of *Salvinia minima* which was a secondary invader (Figure 3.3).

From 2015 to 2016, water hyacinth coverage remained below 5% for most months of the year, peaking at levels below 20% due to herbicide application. The highest water hyacinth coverage was observed in July 2017 at 40.49% following the moratorium on herbicide use (Figure S1). In the absence of herbicide control, the water hyacinth coverage remained above 10% from April 2017 until December 2019, despite seasonal fluctuations. The first non-herbicide induced reduction in water hyacinth coverage to below 5% occurred in January 2020, following inundative releases of *M. scutellaris*. Coverage remained below that 5% mark until October 2020 when reinfestation occurred from the long-lived seed bank, in the absence or extremely low levels of *M. scutellaris*. Water hyacinth coverage peaked in January 2021 at 38.6% and reduced to 6.2% in March 2021 following another inundative release cycle for *M. scutellaris*. The coverage further reduced to 3.9% by April 2021 (Figure S1), but the Dam remained covered by *S. minima*. The Dam was once again reinfested with water hyacinth from October 2021 and coverage peaked twice, first in December 2021 at 31.4%, followed by a second peak in February 2022 at 38.6% (Figure S1) with the Dam having a total macrophyte coverage of 41.96% (Figure 3.3, Figure S1). This coverage was reduced to 4.7% by April 2022 following another cycle of inundative releases (Figure S1). Water hyacinth coverage remained low until September 2022 when it reached 6.4 % and was at 23.4% when the observation period ended in October 2022 (Figure 3.3).

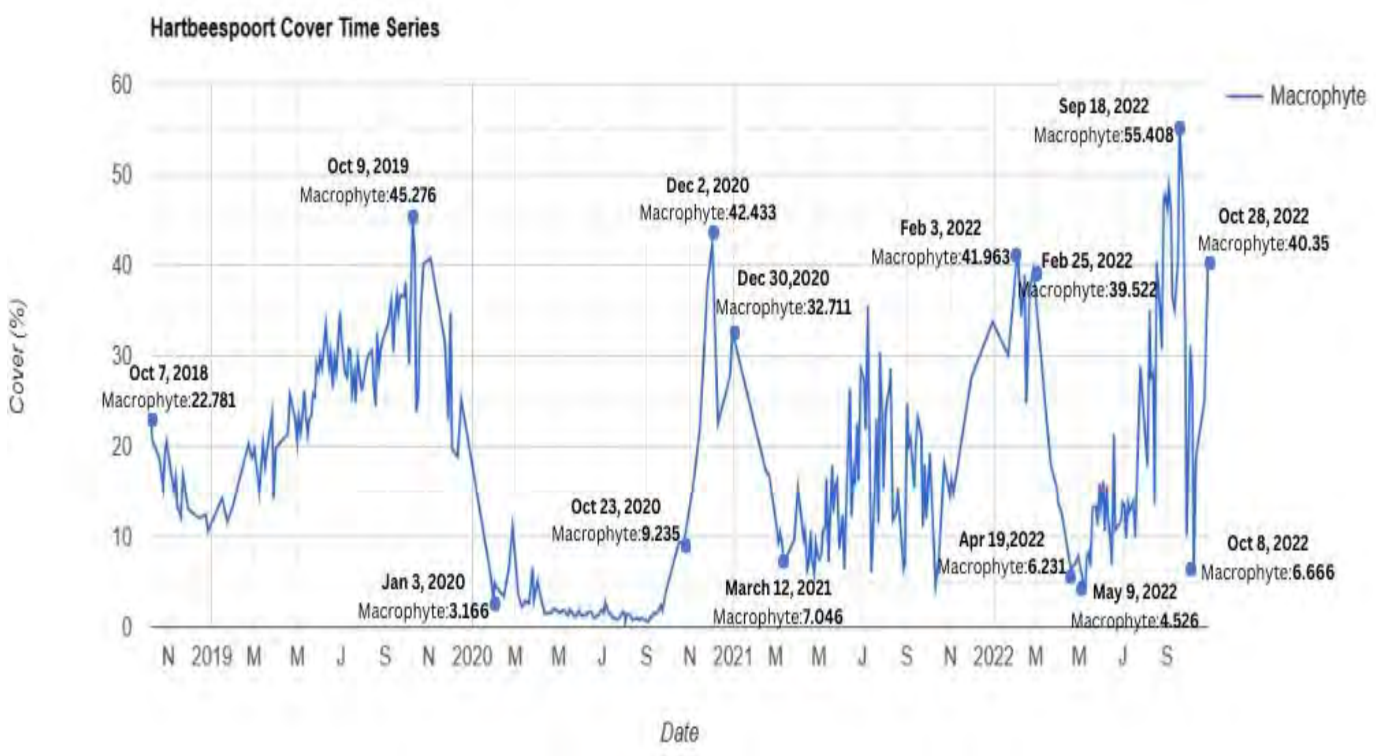

Figure 3.3. Total macrophyte coverage on the Hartbeespoort Dam over the duration of the project (October 2018-October 2022) with coverage including *Salvinia minima* from 2021 autumn months

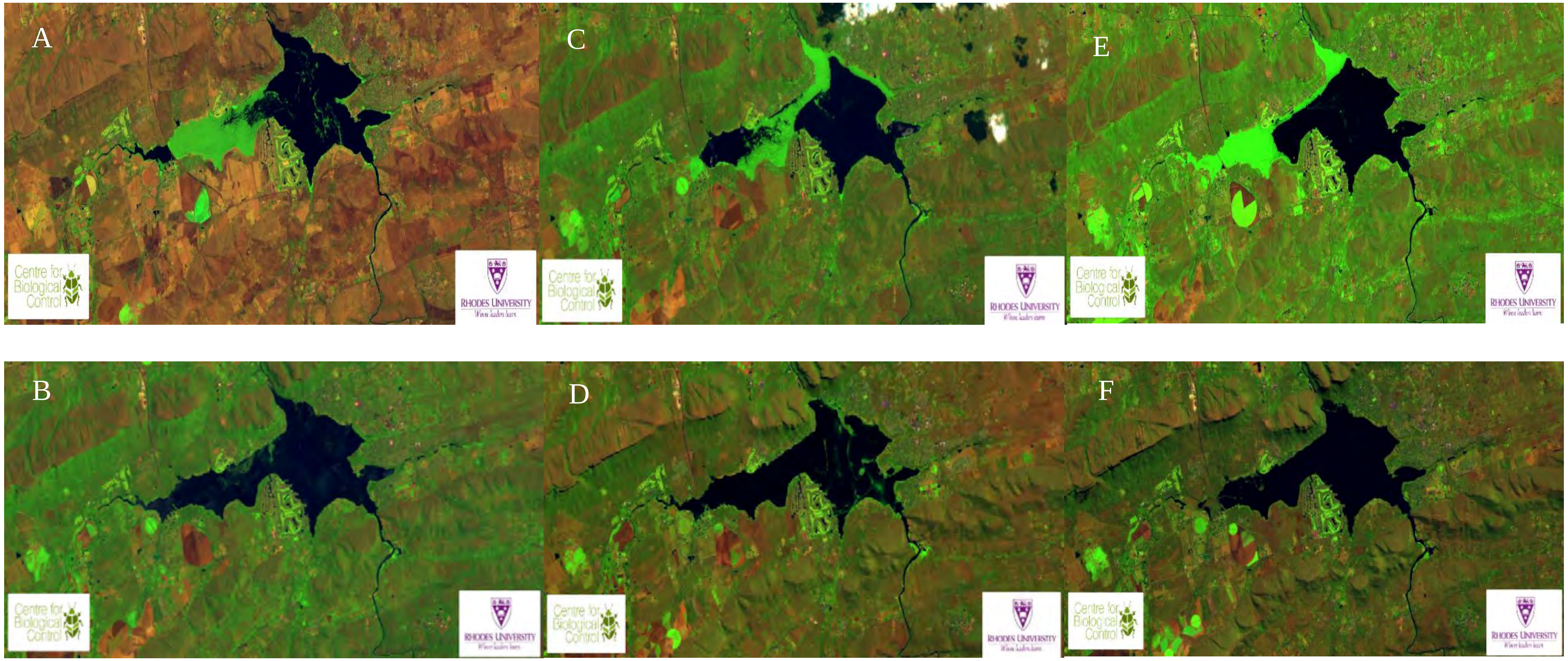

Figure 3.4. The annual reinfestation and clearance patterns from October 2019-April 2022. A) Water hyacinth coverage peak in October 2019 at 45.3%; B) January 2020 clearance level with coverage at 3.2%; C) Water hyacinth coverage peak in December 2020 at 42.4%; D) clearance level with coverage at 7% in March 2021; E) Water hyacinth coverage peak in February 2022 at 41.9%; F) Clearance level with coverage at 6.2% in April 2022. Images obtained from Macrophyte Monitoring Tool (earthengine.app).

Water hyacinth cover increased with increasing temperature but decreased before the onset of autumn. Annually, the coverage remained below 5% of Hartbeespoort Dam surface area between mid-autumn (April) to mid-winter (July) (Figure 3.5). In August the coverage began to increase as the minimum temperature increased above 5°C and a rapid increase was observed from the onset of spring (September) until it peaked in the summer months, December to February each year. In 2020, the coverage peaked at just below 25% in November, plateaued until December, resulting in a twin peak. In 2021, the highest coverage peaked at just above 35% coverage of the dam in February 2022 at the end of the summer season. A rapid increase of coverage was observed from September to October in 2022, where coverage went from 6% to 21%, respectively (Figure 3.5).

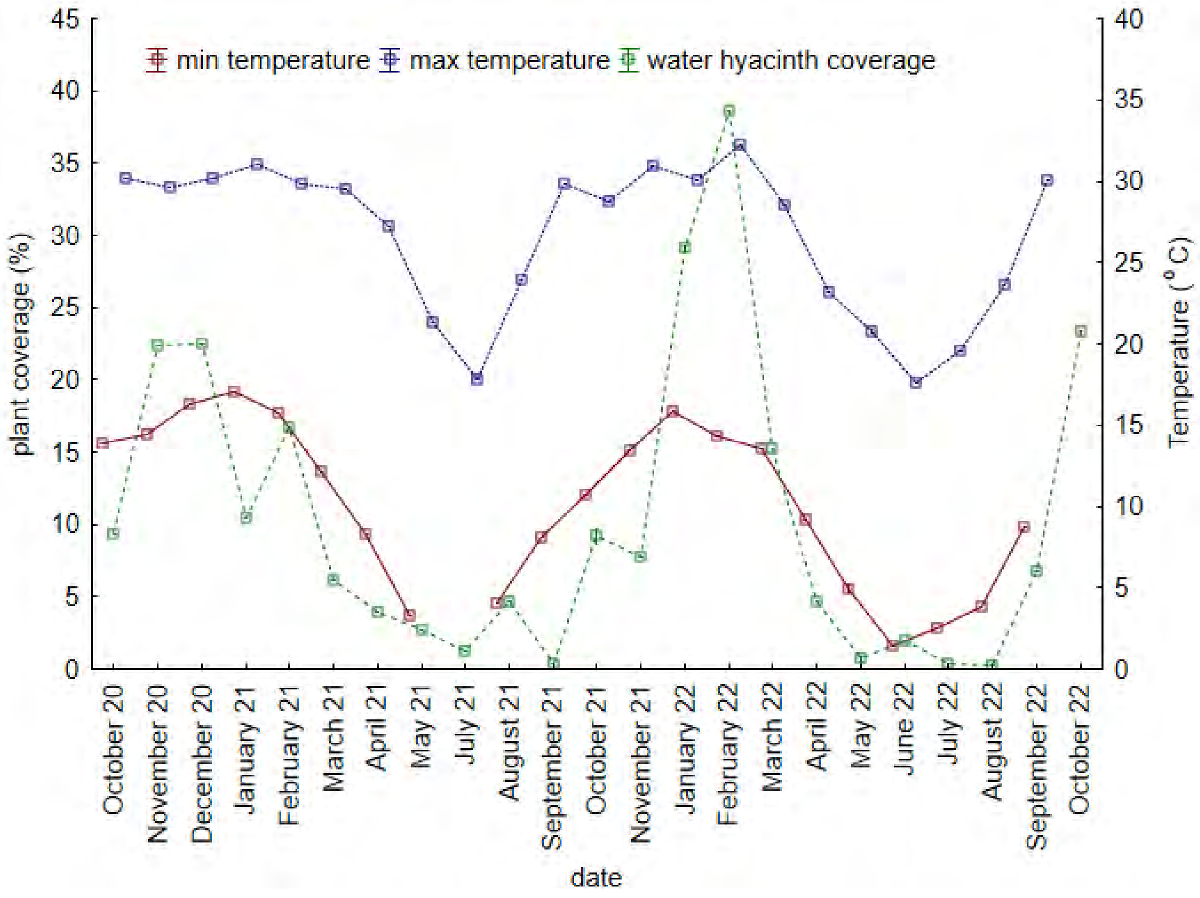

Figure 3.5. Patterns of temperature and water hyacinth coverage of Hartbeespoort Dam

Plant parameters, such as the length of the petiole, the length of roots, the number of ramets and the number of leaves were assessed for ten plants at each site, monthly. The longest petioles were observed in March 2022 with a mean length of 52.2±2.59 cm, while the shortest petioles were observed in August 2021 and August 2022 with mean lengths of 8.13±0.80 cm and 8.45±0.54 cm, respectively (Figure 3.6). The rise in temperatures in August allowed for a reinfestation of the dam from seedlings with short bulbous petioles.

The longest roots were observed in February 2022 at a mean length of 36.65±1.91 cm which then decreased from March 2022 and peaked again in July 2022 with a mean length of 25.90±2.49 cm (Figure 3.6). The shortest roots were observed in October 2021, with a mean length of 15.59±0.62 cm and October 2022, with a mean length of 13.82± 0.63 cm.

Plants had the highest number of leaves in February 2022, with a mean average of 9.5±0.36 per plant, while the least number of leaves were observed in August 2021 where the mean number of leaves was 1.95±0.19, while in 2022, the lowest number of leaves observed on a plant was in June, with a mean of 2.2±0.39 leaves per plant (Figure 3.6).

Plants with the highest number of ramets were observed in August 2021, with a mean of 4.95±0.99 which coincides with a rise in minimum temperatures and a rapid growth period when biological control levels are low from late autumn until late winter (Figure 3.6). The lowest number of ramets was observed in April 2022 at a mean of 0.38±0.14 daughter plants per plant. This also peaked again in August 2022, with a mean of 3.4±0.34 ramets per plant.

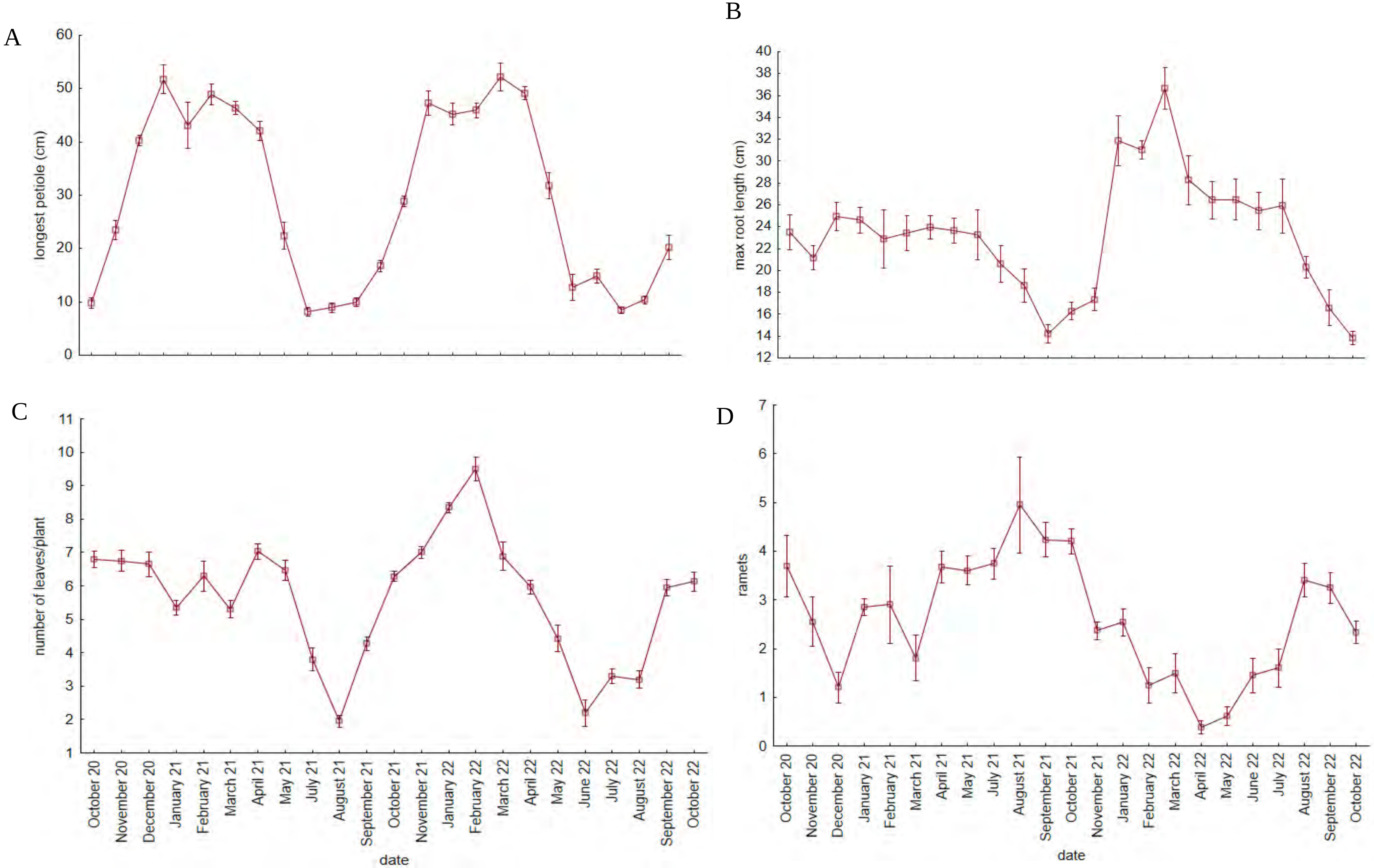

Figure 3.6. Mean of (A) longest petiole (cm); (B) maximum root length (cm); (C) number of leaves per plant; (D) the number of ramets per plant on Hartbeespoort Dam between October 2020 and October 2022. Error bars = ± SE

The plant density fluctuations and biomass were assessed using a 0.25m^2 quadrat. The number of plants per quadrat were counted and then separated into above-water biomass which included the petioles and the leaves, below-water biomass, and dead biomass. The plant density was highest in August 2021 at 130±7.33 plants/m^2 with the lowest destiny observed in July 2021 with 14±3.33 plants/m^2 (Figure 3.7). The heaviest above-water biomass was observed in December 2020, with a mean weight of 5.39±0.33 kg/m^2 which decreased to 0.88±0.28 kg/m^2 by July 2021 (Figure 3.7). The above-water biomass peaked again in September 2021 to 4.66±0.86 kg/m^2 and reduced drastically to 1.71±0.50 kg/m^2 in October 2021 in the presence of *S. minima,* which competed for nutrients. The heaviest roots were observed in November 2021 at mean weight of 4.94±3.63 kg/m^2, while the lowest mean weight was observed in July 2021 at 0.64±0.34 kg/m^2 (Figure 3.7). The greatest weight for dead biomass was observed in September 2021, which was a drastic increase from the mean weight of 0.211±0.10 kg/m^2 (Figure 3.7). In 2022, the mean dead weight peaked in July at 1.61±0 kg/m^2.

July 2021 saw a below zero minimum temperature of -1.7 °C (Figure 3.5) which led to increased frosting of the water hyacinth plants, leading to a low above-water biomass, below-water biomass, and reduced plant density, as *Salvinia minima* proliferated from mid-autumn (April) to the beginning of the summer (December) of 2021.

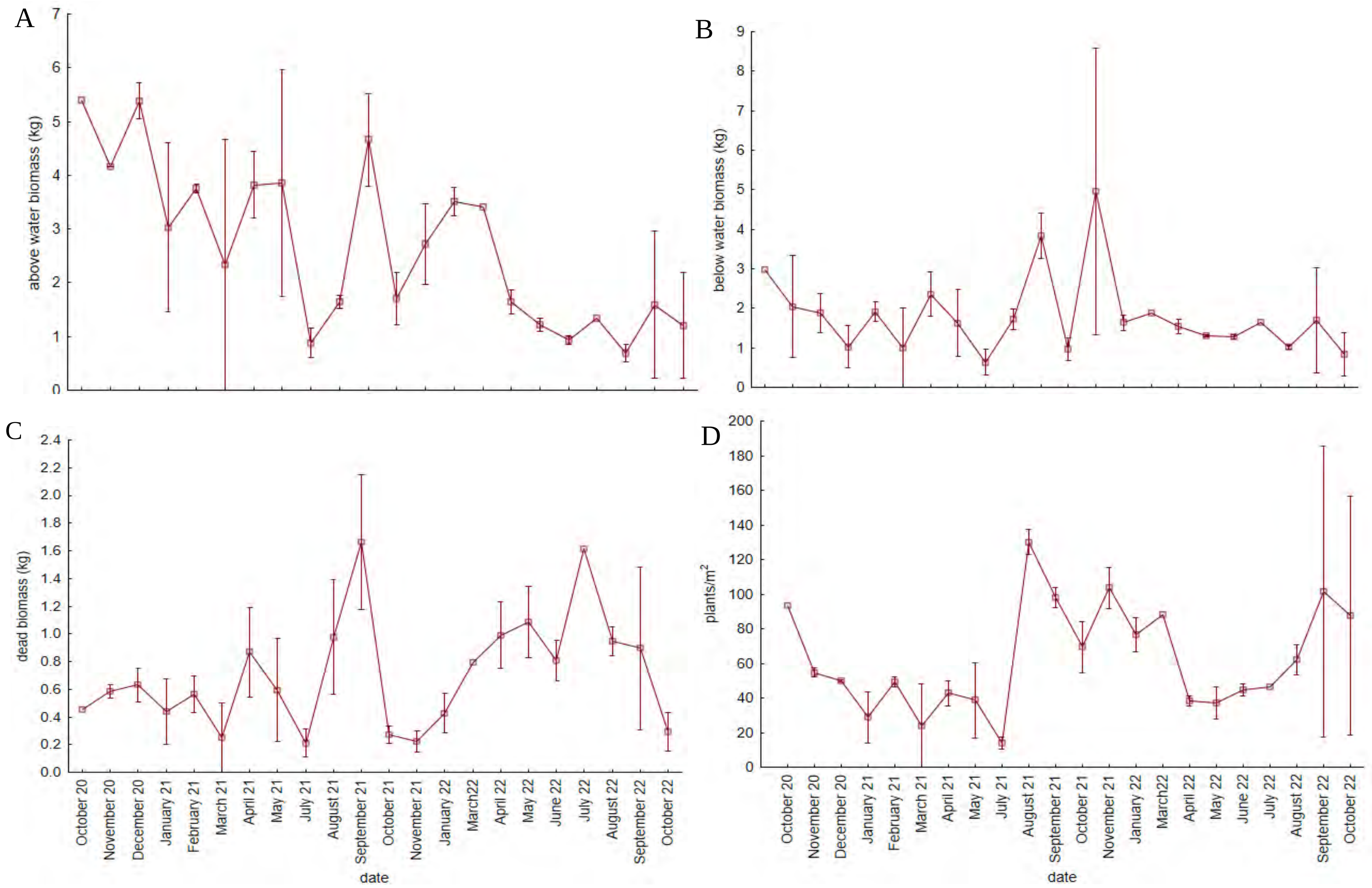

Figure 3. 7. Mean of (A) the above water biomass (kg/m^2); (B) the below water biomass (kg/m^2); (C) the dead biomass (kg/m^2), and (D) the number of plants/ m^2 of water hyacinth plants on Hartbeespoort Dam between October 2020 and October 2022. Error bars = ± SE

The root:shoot ratio changed seasonally too (Figure 3.8). For the winter months, there was a strong positive correlation between the above-water biomass and the below-water biomass (y=0.73x+0.19; R^2=0.7; $F_{1,7}$= 16.17; *P*=0.005). A similar positive correlation was observed for the autumn months (y=1.63x+0.07; R^2=0.51; $F_{1,12}$= 12.73; *P*<0.005), and the summer months (y=1.67x+1.15; R^2=0.5; $F_{1,9}$= 8.882; *P*=0.015). For the spring months there is a less supported linear model (y=0.25x+2.14; R^2=0.15; $F_{1,16}$= 2.816; *P*=0.1128).

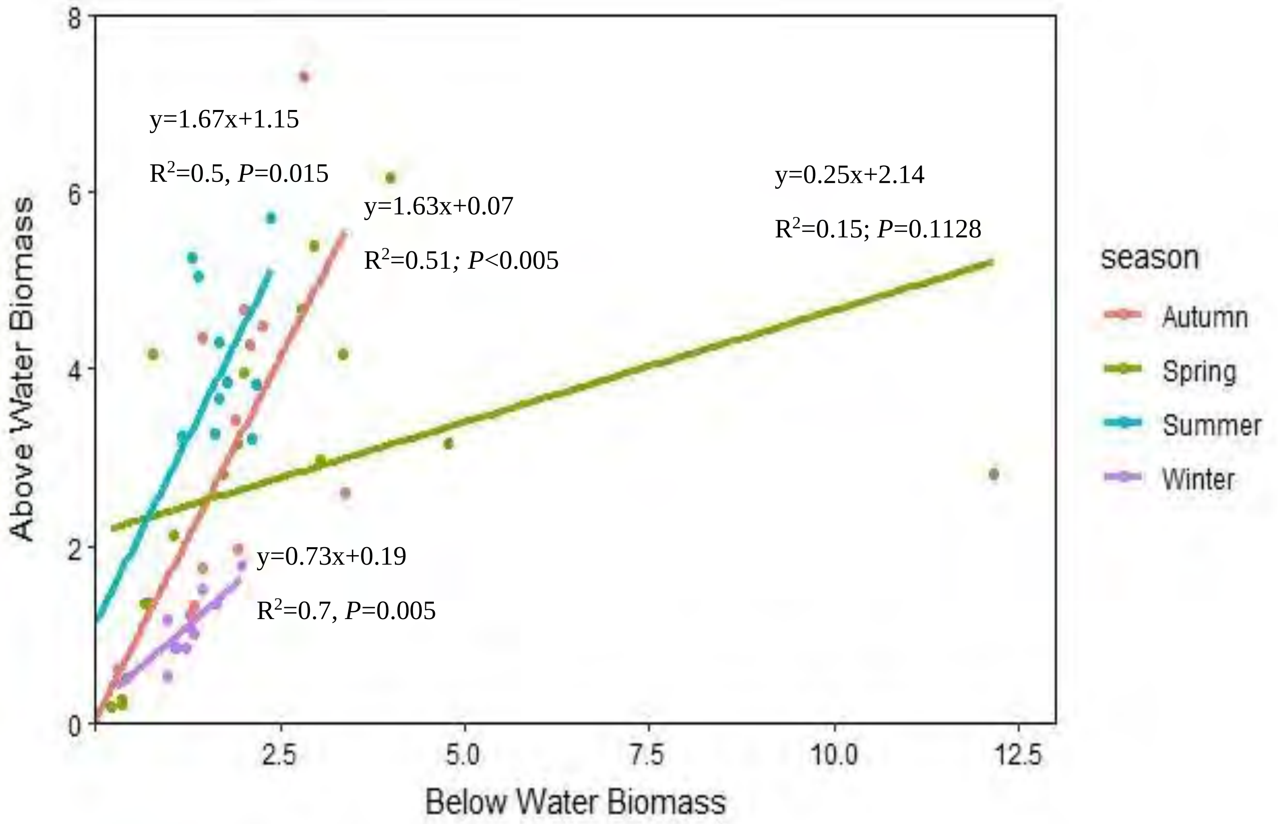

Figure 3.8. Root:Shoot ratio of water hyacinth plants on Hartbeespoort Dam between October 2020 and October 2022. The trend lines indicate the best fit linear models according to seasons.

There was a significant but weak positive correlation between minimum temperature and above water biomass (y=0.13+1.44; R^2=0.13; $F_{1,50}$= 7.314; *P*=0.009); The low R^2 value indicates that other factors, other than minimum temperature influences water hyancinth plant biomass (Figure 3.9).

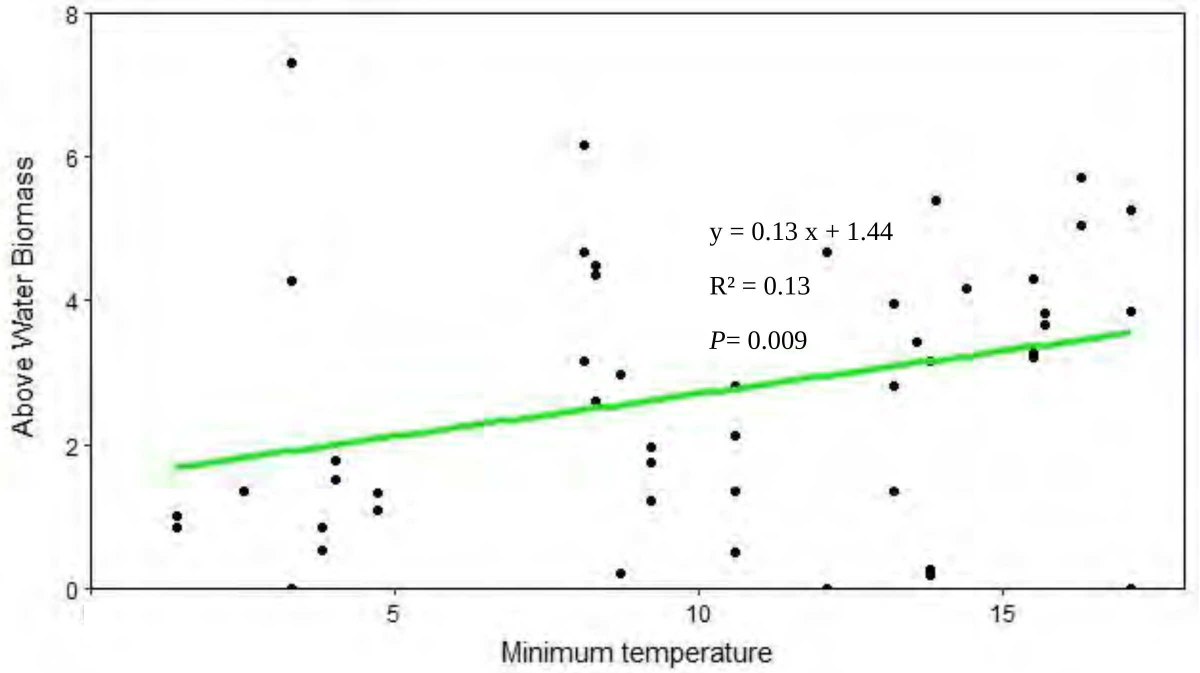

Figure 3.9. Correlation between increasing minimum temperature and above water hyacinth biomass (kg/m^2)

There was a constant presence of *Neochetina* spp. throughout the four seasons of the year with the highest numbers observed in autumn, while *M. scutellaris* numbers were the highest in summer (3411.74±235.49 per m^2) and the lowest numbers observed in winter (0.36±0.27 per m^2_ (Figure 3.10). *Neochetina bruchi* numbers were higher than *N. eichhorniae* in summer (1.89±0.28 and 1.02±0.13per plant), while *N. eichhorniae* had higher numbers in autumn (3.6±0.41 per plant) than *N. bruchi* (2.84±0.30 per plant) (Figure 3.10).

The highest weevil scars were counted during autumn with a mean of 133.02±8.38 scars per plant, while the lowest weevil scars were observed in spring at 20.92±1.9 scars per plant (Figure 3.10).

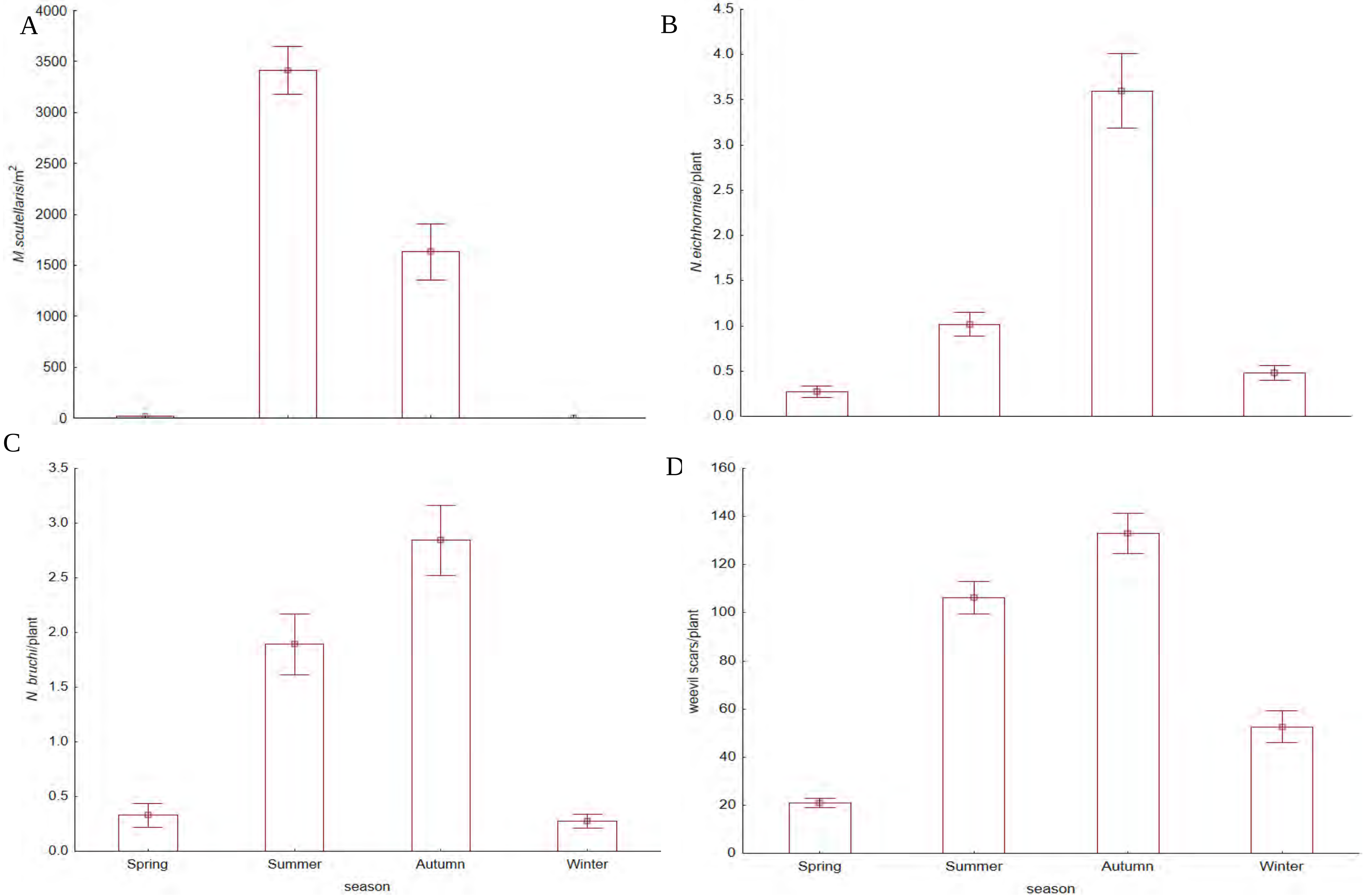

Figure 3.10. Mean of (A) *M. scutellaris* density (insects/m^2); (B) number of *N. eichhorniae* per plant; (C) the number of *N. bruchi* per plant; (D) the number on weevil scars per plant on Hartbeespoort Dam between October 2020 and October 2022. Error bars = ± SE

There was a significant positive relationship between increasing temperature and insect density (y=197.42x-768.05; (R^2=0.22; $F_{1,46}$= 12.62; P<0.005) (Figure 3.11). The results suggest that for every 1°C increase in temperature, insect density is increasing by roughly 197 insects.

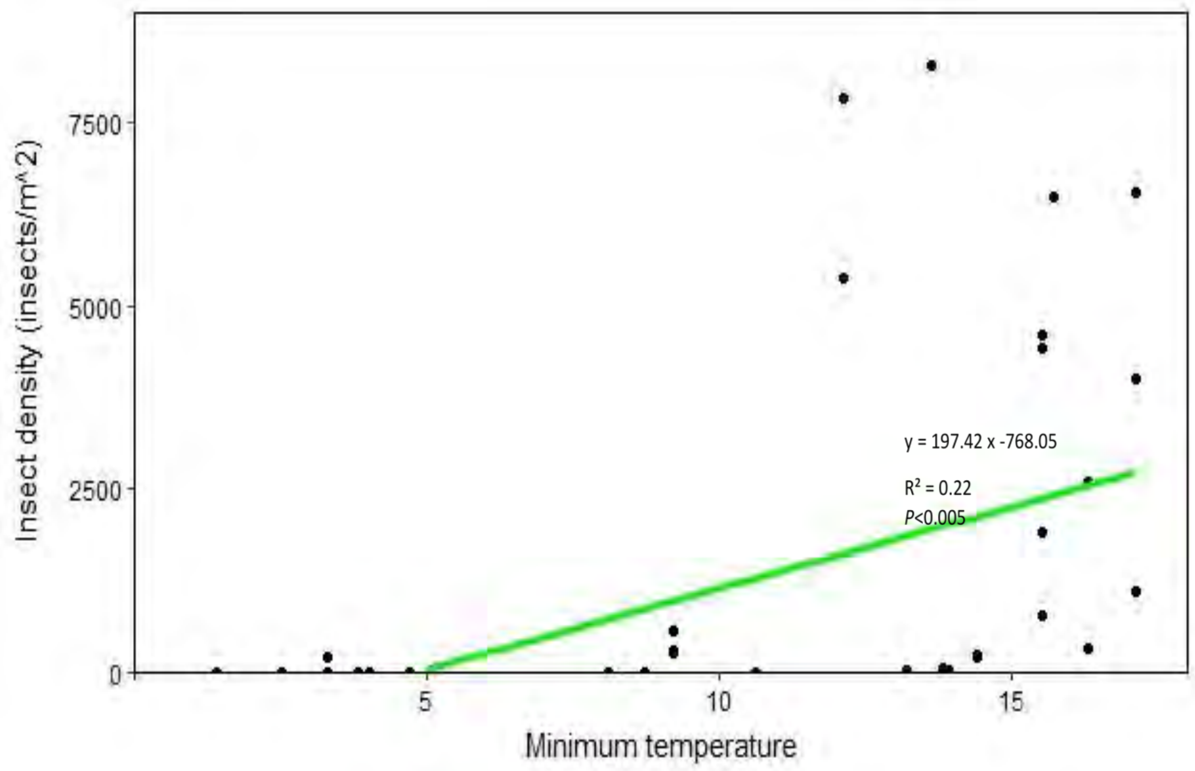

Figure 3.11. The impact of increasing mean minimum temperature (ºC) on *Megamelus scutellaris* density (insect/sm^2)

The highest plant density for *P. crassipes* was measured when *M. scutellaris* density was low, particularly over the colder months of the year from autumn until the onset of summer (Figure 3.12). Plant density decreased as insect density increased. Plant density also decreased rapidly following peak insect density. Once the plant density declined, the insect numbers begin to decrease drastically as their food source declined (Figure 3.12), as observed in April 2021 and April 2022.

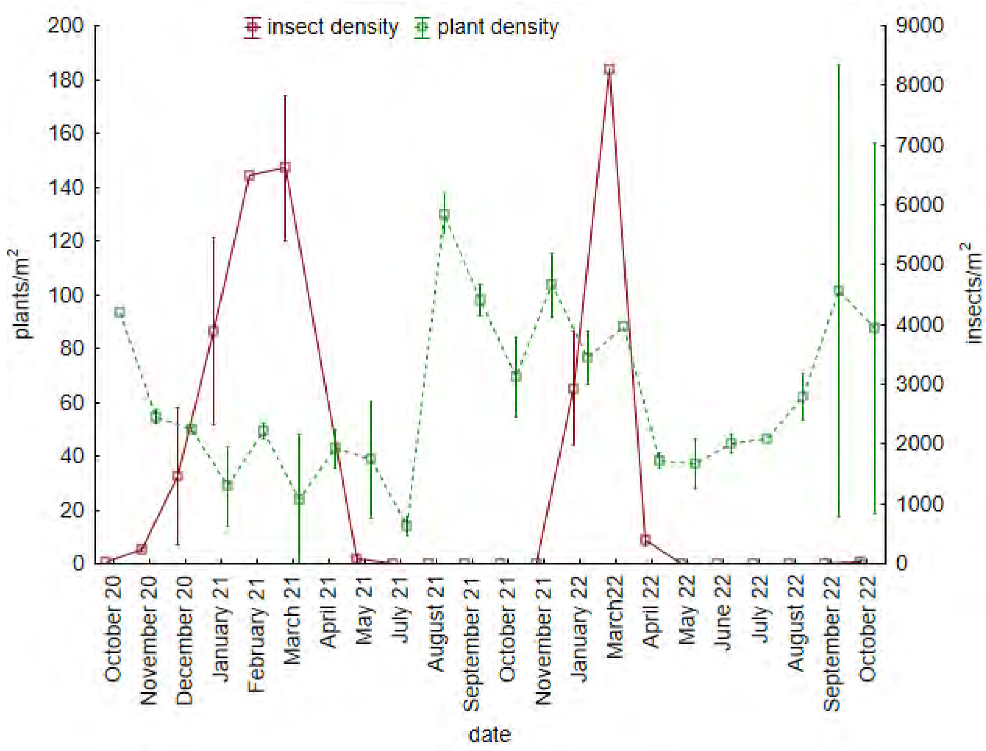

Figure 3.12. Patterns of *Megamelus scutellaris* density (insects/m^2) and water hyacinth density (plants/m^2).

Megtamelus scutellaris density increased with increasing above-water biomass; however, once its density peaked, the above-water biomass declined rapidly (Figure 3.13). The resultant loss of biomass led to a drastic drop in insect density, with insect density remaining negligible over the autumn and winter months. The insect density increased at the onset of summer following the increase of above-water plant biomass.

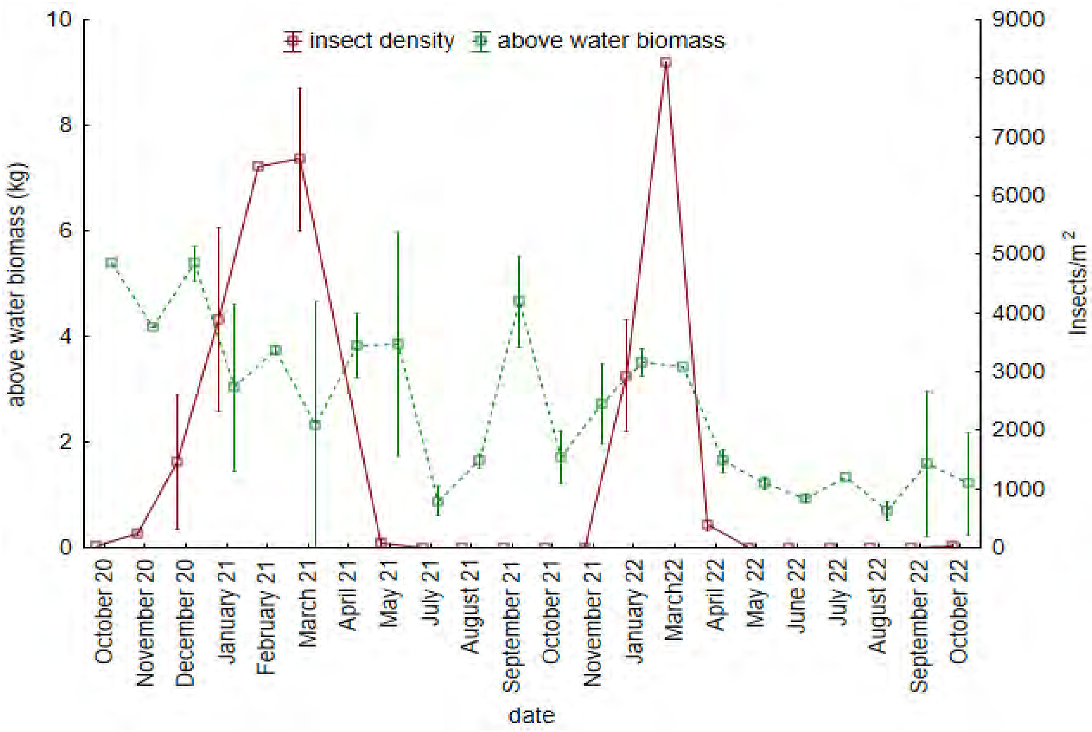

Figure 3.13. Patterns in insect density and above-water *Pontederia crassipes* biomass (kg) over the 24-month observation period (October 2020–October 2022)

Megamelus scutellaris density did not have a significant impact on plant density, although the trendline shows decreasing plant density with increasing insect density (Figure 3.14). This ismodelled by y=0x+67.97 (R^2=0.03; $F_{1,46}$= 1.251; *P*=0.269).

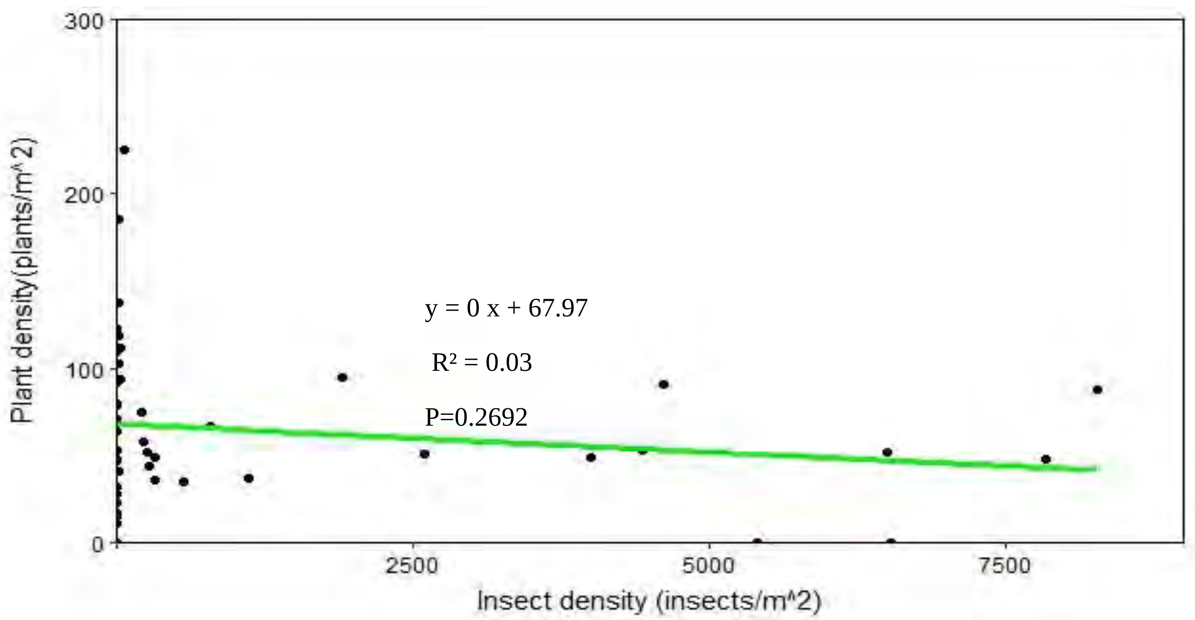

Figure 3.14. The weak negative relationship between *Megamelus scutellaris* density (insects/m^2) on *Pontederia crassipes* density (plants/m^2).

The linear regression analysis confirmed that insect density did not have a significant impact on plant biomass; plant biomass is 67.97 kg/ m^2 when insect density is zero, which is highly significant (P<0.001) (Table 3.1). The negative coefficient indicates a slight decrease in water hyacinth biomass with increasing insect density, but this effect is not statistically significant (P =0.269).

Table 3.1. Linear regression results on the impact of *M. scutellaris* density on water hyacinth plant density

Effect	Estimate	Std. Error	t value	*P*
Intercept	67.970050	7.309795	9.298	**3.9e-12**
Insect density	0.003199	0.002860	-1.118	0.269

ANCOVA analysis investigated the influence of season and plant parameters on *M. scutellaris* density. Water hyacinth petiole length and root length had a significant impact on *M. scutellaris* density (Table 3.2). This is an indication that the host plant health impacts insect densities. The seasons, too, have a highly significant impact on *M. scutellaris* density (F=17.690, P<0.001). The interactions between longest petiole and seasons had a highly significant impact on *M. scutellaris* density, while the interaction between number of leaves and season were significant (Table 3.2)

Table 3.2. ANCOVA results illustrating the effects of various plant parameters and season on *Megamelus scutellaris* density. LP = longest petiole, LR = Maximum root length, and NL = number of leaves. Values in bold indicate significant differences.

Effect	Df	Sum Sq	Mean Sq	F	*P*
Longest petiole (LP)	1	**546,836,598**	**546,836,598**	**154.039**	**< 2e-16**
Maximum root length (LR)	1	**34,732,922**	**34,732,922**	**9.784**	**0.00186**
Number of leaves (NL)	1	3,976,301	3,976,301	1.120	0.29041
Season	3	**188,398,836**	**62,798,836**	**17.690**	**6.26E-11**
LP:LR	1	1,181,095	1,181,095	0.333	0.56433
LP:NL	1	976,573	976,573	0.275	0.60017
LR:NL	1	13,015,288	13,015,288	3.666	0.05609
LP:season	3	**118,486,160**	**39,486,160**	**11.123**	**4.44E-07**
LR:season	3	13,885,388	4,625,388	1.303	0.27275

NL:season	3	**37,261,069**	**12,419,069**	**3.498**	**0.01548**
LP:RL:NL	1	765,348	765,348	0.216	0.64262
LP:LR:season	3	4,288,456	1,429,456	0.403	0.75115
LP:NL:season	3	18,434,757	6,144,757	1.731	0.15968
LR:NL:season	3	26,310,543	8,770,543	2.471	0.06113
LP:LR:NL:season	3	8,896,170	2,965,170	0.835	0.47492
Residuals	502	1,782,000,000	3,549,996		

Bonferroni pairwise comparisons indicated that *M. scutellaris* densities varied significantly with each season (Table 3.3), the most notable variation between autumn and the other seasons. There were no significant differences in insect densities between spring and winter.

Table 3.3. The results of the Bonferroni pairwise t-test function comparing the means of *Megamelus scutellaris* across different seasons

Season Comparison	*P*
Autumn vs Spring	1.1e-11
Autumn vs Summer	3.3e-11
Autumn vs Winter	2.8e-08
Spring vs Summer	< 2e-16
Spring vs Winter	1
Summer vs Winter	< 2e-16

Analysis of the patterns in *M. scutellaris* numbers over the sample period highlighted a peak in February 2021 (6493.55±0 insects/m^2) and a slight increase in March 2021 (6615.59± 1225.27 insects/m^2) (Figure 3.15). Insect numbers plummeted to zero as the minimum temperatures dropped to below 10 °C from April 2021 to November 2021. The highest insect density for the observation period occurred in March 2022 at 8264.52±0 insects/m^2 (Figure 3.15). The insect numbers dropped to a mean density of 381.00± 89.81 insects/m^2 in April 2022 and further declined to zero by May 2022 until the end of the observation period in October 2022. As expected, the insect numbers declined with decreasing temperatures as the developmental threshold of the insect is 11.46 °C (May and Coetzee 2013).

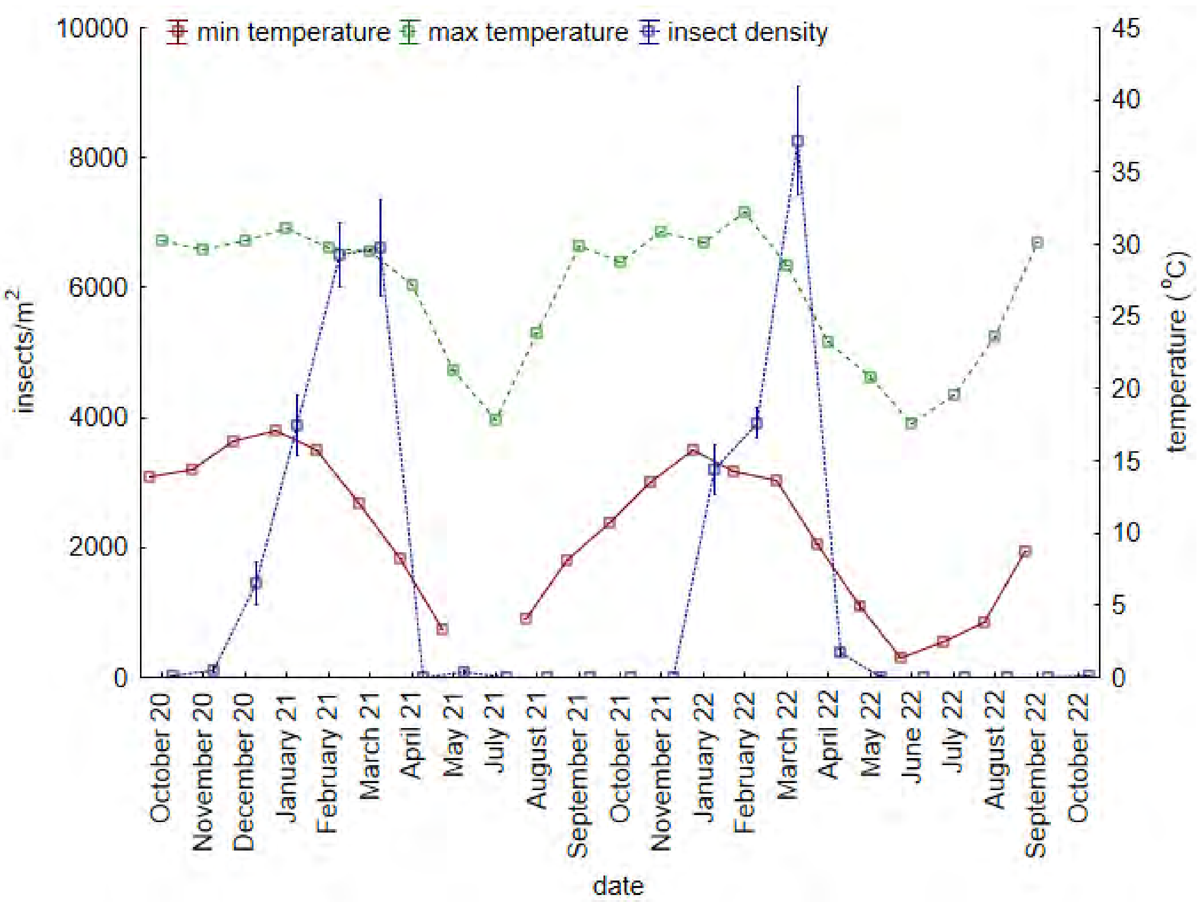

Figure 3.15. Patterns of mean minimum and maximum temperatures and *Megamelus scutellaris* density **(**insects/m^2), over the study period.

The double peaks of water hyacinth cover in October 2020 (22.40%) and December 2020 (22.50%), were mirrored by a double peak in *M. scutellaris* mean density in February 2021 (6493.55± 491.44 per m^2) and March 2021 (6615.59±737.83 insect per m^2) (Figure 3.16). The October 2021 initial coverage peak at 9.2±0.53% was mirrored by the insect density peak of January 2022 at 3193.98± 377.69 insect per m^2. The highest coverage of 38.6% for the observation period was in February 2022 which corresponded with an insect density peak of 8264.52±829.69 insect per m^2 (Figure 3.16).

The insect density and water hyacinth coverage followed a classical biological control graph where the biological control peak trends followed a similar trend as the weed with a lag period between the weed peak point followed by the *M. scutellaris*.

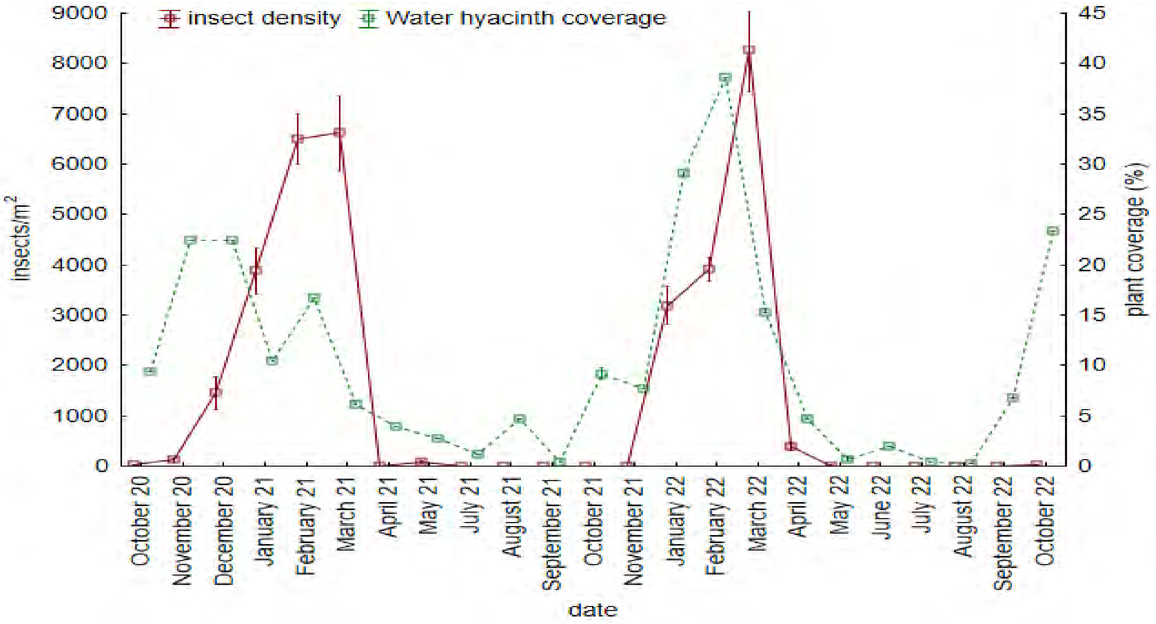

Figure 3.16. Population dynamics of water hyacinth, *Pontederia crassipes* and *Megamelus scutellaris* at Hartbeespoort Dam, over the study period.

The relationship between insect density and water hyacinth coverage was highly significant (Table 3.4). An increase in insect density per square metre is associated with a decrease in water hyacinth cover. Increases in mean minimum temperatures had a highly significant positive impact on water hyacinth coverage. Water hyacinth coverage was significantly lower in spring than in the reference season (autumn), whereas in summer, water hyacinth coverage was significantly higher than in autumn. The interaction between insect density and minimum temperature indicates a highly significant combined effect of the variables on water hyacinth coverage (Table 3.4).

Table 3.4. GLM results of water coverage as affected by insect densities, minimum temperature and season; autumn is the baseline season. Significant values are bold.

Effect	Estimate	Std. Error	t value	*P*
Intercept	0.06447	0.8114	0.079	0.9367
Insect density (m^{-2})	**-0.006361**	**0.001228**	**-5.182**	**3.18e-07**
Minimum temperature	**0.5193**	**0.1122**	**4.630**	**4.66e-06**
Season Spring	**-10.09**	**1.545**	**-6.529**	**1.61e-10**
Season Summer	**235.1**	**14.20**	**16.556**	**< 2e-16**
Season Winter	1.377	0.9241	1.490	0.1370
Insect density: Minimum temperature	**0.0005293**	**9.614e-05**	**5.505**	**5.87e-08**

Insect density: season Spring	-0.1821	0.2284	-0.797	0.4257
Insect density: season Summer	-0.004394	0.003490	-1.259	0.2087
Insect density: season Winter	0.1419	0.1360	1.043	0.2972
Minimum temperature: season Spring	**1.120**	**0.1634**	**6.856**	**2.08e-11**
Minimum temperature: season Summer	**-13.57**	**0.8832**	**-15.363**	**< 2e-16**
Minimum temperature: season Winter	-0.3212	0.1883	-1.706	0.0887
Insect density: Minimum temperature: season Spring	0.01455	0.01587	0.917	0.3596
Insect density: Minimum temperature: season Summer	0.00009891	0.0002237	0.442	0.6585
Insect density: Minimum temperature: season Winter	NA	NA	NA	NA

Neochetina weevil populations were highest in March 2021 with *N. eichhorniae* being the dominant species until November 2021 (Figure 3.17). Thereafter *N. bruchi* became the dominant species. In 2021, when the minimum temperature dropped below 0°C in winter, the weevil population decreased drastically and remained low from July to November 2021. The weevil numbers were lowest between June and August in 2022. *Neochetina bruchi* numbers remained higher than 10 insects per plant from January 2022 to May 2022 (Figure 3.17)

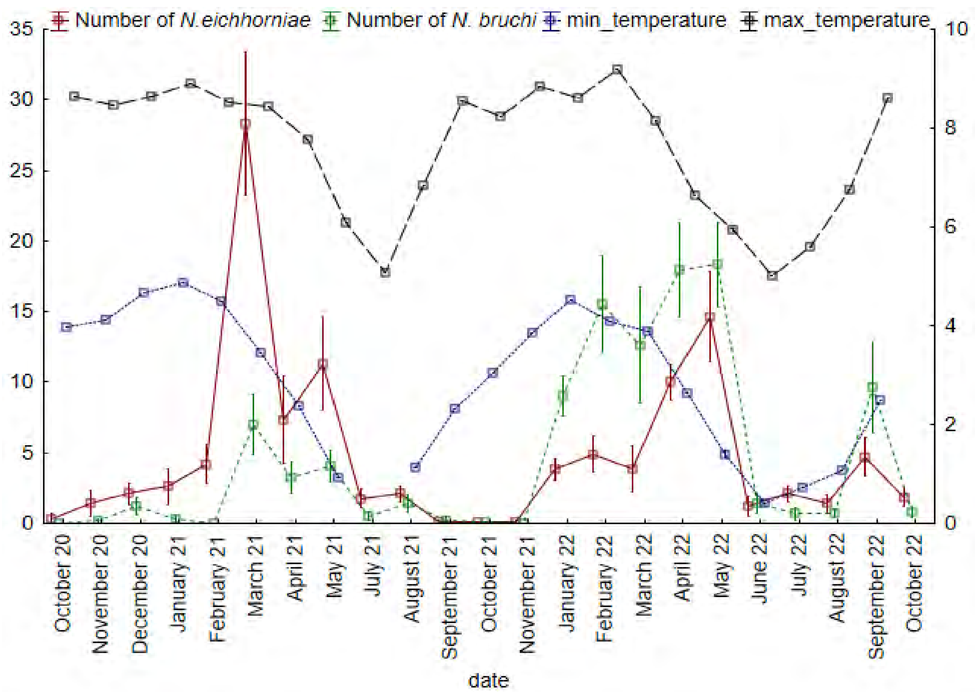

Figure 3.17. Patterns in mean minimum and temperature on *Neochetina spp*. weevils. *Neochetina eichhorniae* was the dominant weevil species from the beginning of the observation period until November 2021 when *Neochetina bruchi* became the dominant species.

Table 3.5. ANCOVA results illustrating the effects of various plant parameters and season on *N. eichhorniae* numbers per plant. LP = longest petiole, LR = Maximum root length, and NL = number of leaves. Values in bold indicate significant differences.

Effect	Df	Sum Sq	Mean Sq	F	*P*
Longest petiole (LP)	**1**	**343.0**	**343.0**	**50.440**	**4.09E-12**
Maximum Root Length (LR)	1	0.3	0.3	0.041	0.839325
Number of leaves (NL)	**1**	**90.9**	**90.9**	**13.363**	**0.000283**
Season	**3**	**600.0**	**200.1**	**29.422**	**< 2e-16**
LP:LR	1	4.0	4.0	0.582	0.445962
LR:NL	1	18.4	18.4	2.702	0.100817
LR:NL	1	4.6	4.6	0.671	0.413191
LP:season	3	12.5	12.5	1.832	0.140308
LR:season	3	0.4	0.4	0.053	0.983717
NL:season	3	12.3	12.3	1.816	0.143279
LP:LR:NL	1	8.5	8.5	1.255	0.263120
LP:LR:season	3	1.0	1.0	0.140	0.935758
LP:NL:season	3	10.5	10.5	1.547	0.201443
LR:NL:season	3	2.9	2.9	0.419	0.739363
LP:LR:NL:season	3	17.8	17.8	2.616	0.050436
Residuals	517	3516.0	6.8		

The petiole size and the number of leaves on a plant have a significant impact on the number of *N. eichhorniae* present on the weed (Table 3.5). Seasons have a very significant effect on the weevil numbers (Table 3.5)

Table 3.6. The results of the Bonferroni pairwise t-test function comparing the means of *N. eichhorniae* across different seasons

Comparison	*P*
Autumn vs. Spring	< 2e-16
Autumn vs. Summer	7.5e-14
Autumn vs. Winter	< 2e-16
Spring vs. Summer	0.087
Spring vs. Winter	1.000
Summer vs. Winter	0.843

Looking at the varied impact of the season on the number of *N. eichhorniae* weevils shows highly significant differences between weevil numbers when comparing autumn to the other seasons indicated by very small *P*-values (Table 3.6). There are significant differences between most pairs of seasons, except between winter and spring.

Table 3.7. ANCOVA results illustrating the effects of various plant parameters and season on *N. bruchi* numbers per plant. LP = longest petiole, LR = Maximum root length, and NL = number of leaves. Values in bold indicate significant differences.

Effect	Df	Sum Sq	Mean Sq	F	*P*
Longest petiole (LP)	**1**	**369.1**	**369.1**	**59.796**	**5.54E-14**
Maximum Root Length (LR)	**1**	**63.4**	**63.4**	**10.272**	**0.001434**
Number of leaves (NL)	1	5.5	5.5	0.898	0.343789
Season	**3**	**279.0**	**92.9**	**15.052**	**2.09E-09**
LP:LR	**1**	**28.0**	**28.0**	**4.544**	**0.033496**
LR:NL	1	7.5	7.5	1.209	0.271993
LR:NL	1	10.0	10.0	1.623	0.203238
LP:season	3	14.0	4.7	0.758	0.518211
LR:season	3	19.0	6.3	1.015	0.385741
NL:season	**3**	**109.0**	**36.4**	**5.904**	**0.000576**
LP:LR:NL	1	12.6	12.6	2.048	0.153042
LP:LR:season	3	9.0	3.1	0.509	0.676557
LP:NL:season	3	13.0	4.5	0.721	0.539620
LR:NL:season	3	14.0	4.6	0.740	0.528331
LP:LR:NL:season	3	18.0	5.8	0.945	0.418438
Residuals	517	3191.0	6.2		

Petiole length and root length are the two plant parameters that have a highly significant impact on *N. bruchi* numbers (Table 3.7). Seasons have a highly significant impact on weevil numbers. The interaction between the number of leaves and seasons had a highly significant impact on the number of *N. bruchi* weevils (Table 3.7).

Table 3.8. The results of the Bonferroni pairwise t-test function comparing the means of *N. bruchi* across different seasons

Season Comparison	P-Value
Autumn vs Spring	< 2e-16
Autumn vs Summer	0.018
Autumn vs Winter	2.8e-12
Spring vs Summer	1.1e-06
Spring vs Winter	1.000
Summer vs Winter	4.6e-05

There are highly significant differences between season pairs autumn and spring, autumn and summer, autumn and winter, spring and summer, and summer and winter; however, there is no significant difference between spring and winter indicated by a high *P*-value of 1.00 (Table 3.8). The *Neochetina* spp. peaked after water hyacinth peaked and followed a similar trend as the water hyacinth coverage peaks. *Neochetina eichhorniae* and *N. bruchi* had comparable peak points. Water hyacinth coverage peaked in November 2020, followed by a peak in *Neochetina* spp. in March 2021 (Figure 3.18). A similar trend was observed in October 2021 when water hyacinth peaked again, followed by weevils peaking in February 2022.

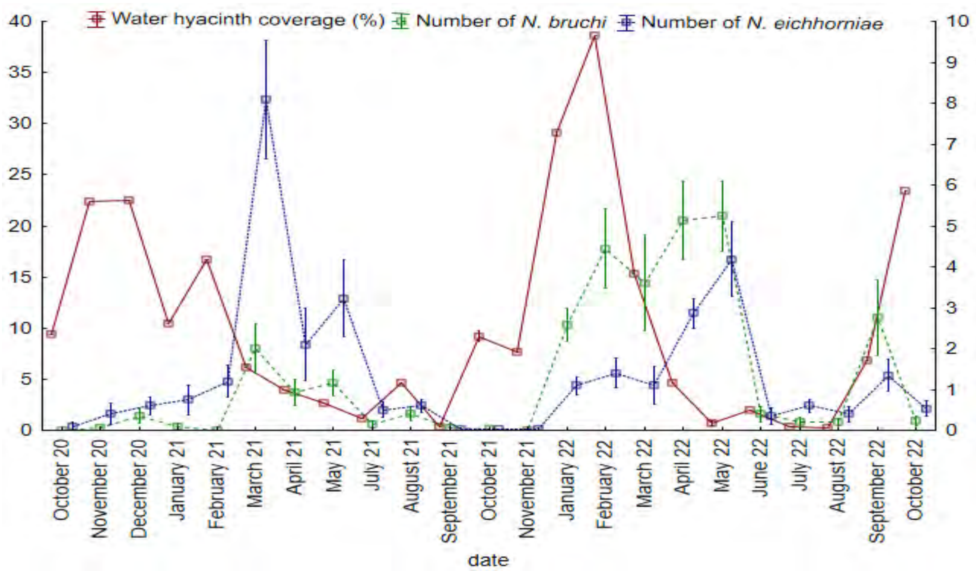

Figure 3.18. Impact of *Neochetina eichhorniae* and *Neochetina bruchi* on water hyacinth coverage over 24 months

Both *M. scutellaris* and *Neochetina spp*. peaked following the water hyacinth coverage peaks, as seen in Figure 3.19. *Megamelus scutellaris* peaked three months after the water hyacinth coverage, while the *Neochetina* spp. weevils peaked four months after the weed peaked. The weevil populations decreased and remained low from June to August in 2022, but the population peaked as the water hyacinth coverage increased (Figure 3.19). The high weevil numbers led to extensive feeding on seedlings by weevils (Figure 3.20). The cold winters and frost kill off the water hyacinth leaves and petioles which the biological control agents rely on for food and oviposition while the crowns of the plants survive the Winter and plant regrowth occurs at the onset of warmer weather; however, the colder weather rapidly depletes insect populations (Coetzee *et al*., 2022a, Miller *et al*., 2023). Water hyacinth recovers rapidly from winter frost damage during the spring, but the control agent population lags behind that of the plant (Coetzee *et al*., 2022a, Miller *et al*., 2023). Insect populations only reach their maximum density by late summer, thus there is a delay in the effectiveness of the biological control agent (Miller *et al*., 2023).

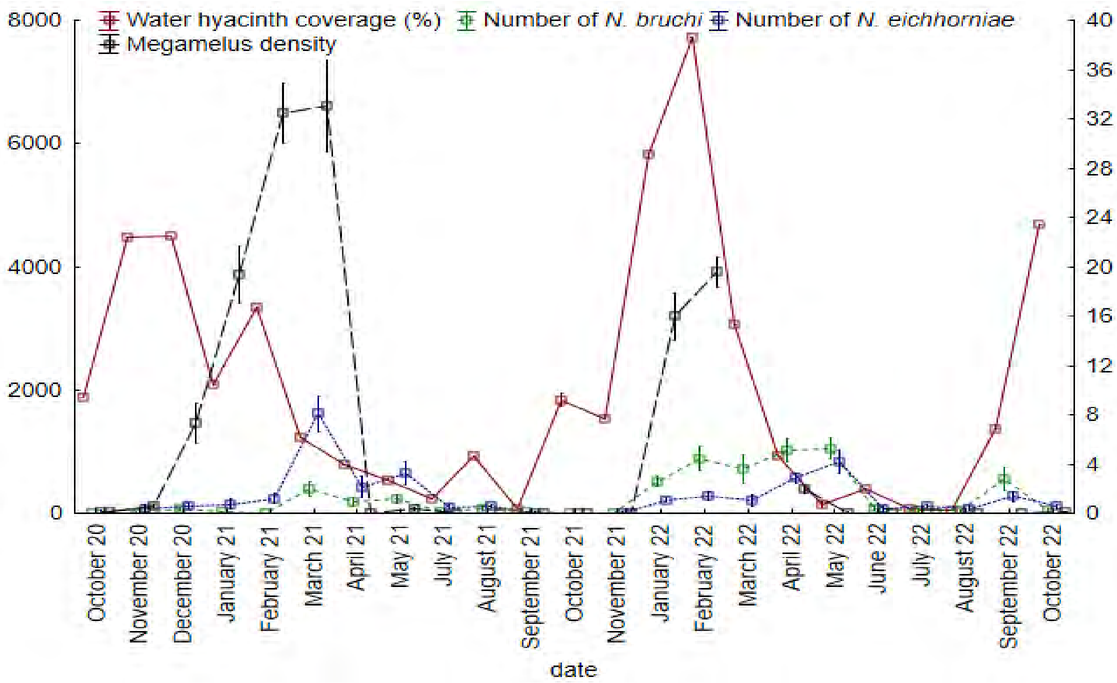

Figure 3.19. The impact of *Megamelus scutellaris* and weevils on water hyacinth coverage. The *M. scutellaris* showed a 3-month lag phase while the *Neochetina* spp. weevils had 4-month lag phase.

Megamelus scutellaris numbers increased with an increase in weevil feeding scars and was not negatively impacted by weevil feeding, as observed by Goode *et al*. (2020).

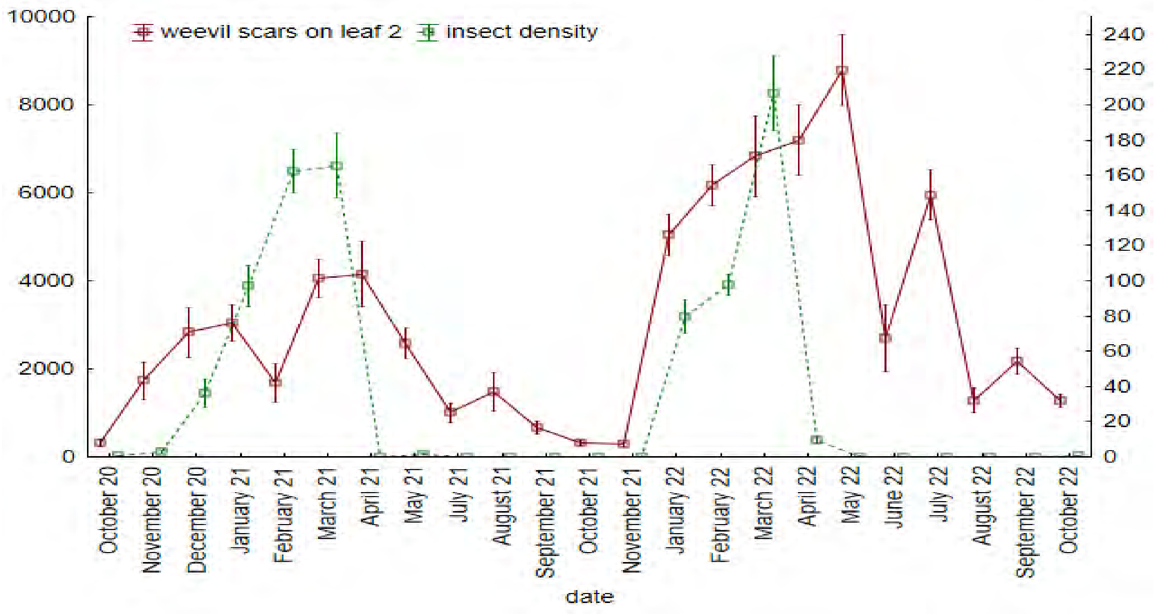

Figure 3.20. Impact of weevils, *Neochetina eichhorniae* and *Neochetina bruchi*, feeding on *Megamelus scutellaris*

Bringing water hyacinth under control freed up nutrients in the water column that allowed for a secondary infestation to occur, where *Salvinia minima* became the dominant macrophyte species in the colder months of 2021 and again in 2022, leading to a delayed peaking of water hyacinth. In October 2022, water hyacinth plants were still small and heavily fed on by *Neochetina* weevil spp. (Figure 3.21).

Figure 3.21. Extensive *Neochetina spp*. feeding on seedlings in October 2022, where *Salvinia minima* was the dominant macrophyte on Hartbeespoort Dam, as water hyacinth regenerated after winter.

The feeding by the biological control agents leads to the browning of plants as seen in Figure 3.22A; this leads to a more diverse macrophyte coverage as shown in Figure 3.22B. Figure 3.22A shows the proliferation of *M. scutellaris* with the nymphs present on the leaves and petioles of the plant. The large-scale clearing of a site following the proliferation on *M. scutellaris* (Figure 3.23), shows the browning of the plant begins in a smaller segment (Figure 3.23A) that expands with time (Figure 3.23 B) as the planthoppers move to healthier plants. This is followed the clearing of water surfaces of macrophyte coverage (Figure 3.23B and 3.23 C) as the plants sinking due to wave action.

Figure 3.22. Impact of feeding by biological control agents on the plants (A) and the infested site (B)

Figure 3.23. Stages of a deteriorating site (The Kurz plot 25°45'46"S, 27°47'14"E) following a proliferation of *Megamelus scutellaris*.

3.5 Discussion

The study examined whether the introduction of an additional biological control agent would reduce water hyacinth coverage on an infested waterbody in a cool temperate region of South Africa which is prone to frosting in winter. Prior to the introduction of the new agent, water hyacinth plants on Hartbeespoort Dam were inspected for the presence of previously released biological control agents. The *Neochetina spp*. weevils, *N. eichhorniae* and *N. bruchi*, the mite, *O. terebrantis*, the mirid, *E. catarensis* and the moth *N. albiguttalis*, were all present on the plants, yet the weed was not under control. At the onset of the project, a moratorium on herbicide use had been in place for close to two years and this had allowed the biological control agents to increase to densities that should have been damaging to the plant, but the hypertrophic state of the dam water had allowed the plants to compensate for the damage caused by herbivory by the biological control agent. The plant hopper, *Megamelus scutellaris*, was initially introduced to the site through a few releases, but in the summer of 2018/2019 an inundative release programme was carried out to increase *M. scutellaris* density numbers during the plant's growing season. In combination with the biological control present on the dam, *M. scutellaris* managed to reduce the water hyacinth coverage of the dam to below 10% by January 2020. Water hyacinth reinfested the dam from the middle of spring from seedlings, and peaked in mid-summer of the year 2020, a similar pattern was observed for the summer of 2021/2022, but coverage peaked late summer on that occasion. This is due to a secondary invasion of the dam by *Salvinia minima* in the cooler months of 2021 as observed by Chikodza *et al*. (2025). The reinfestations by water hyacinth confirmed the presence of a seed bank on Hartbeespoort Dam. Perez *et al*. (2011) concluded that despite efforts to control the weed, the hypertrophic state of South Africa's waterbodies enables the development of adequate seed reserves which contribute to re-infestation of water bodies which were previously successfully managed. Additionally, confirmation of a seed bank supports the findings of Van Wyk and van Wilgen (2002) which found that sites where biological control is used to manage water hyacinth, there will be sporadic resurgence of the weed driven by increased nutrient inputs. It can therefore be concluded that, for a hypertrophic system such as Hartbeespoort Dam, reinfestations would be a common occurrence. Observation confirms that the reinfestation has occurred annually throughout the study. For this reason, Djihouessi *et al*. (2023) recommended that once-off programmes would not be suitable for the control of water hyacinth; rather, continuous action needs to be taken by permanent institutions, and funding for projects should be integrated into annual budgets.

The annual reinfestation and the cold winters have necessitated the annual reintroduction of *M. scutellaris* at the onset on summer in order for the insect to build up damaging densities by the time of the weed's growing season. The temperate conditions and frosting in winter impact the efficiency of biological control agents, with the cold highveld winters reducing *M. scutellaris* density to near zero. Similarly, Miller *et al*. (2020) observed a severe decline in *M. scutellaris* numbers at the onset of winter as the water hyacinth plants experience frost damage. The *Neochetina* spp. weevil numbers were also low during winters however, severe weevil damage was observed on the plants at the onset of spring, supporting the observation by Hill and Olckers (2001) that although *N. eichhorniae* population numbers are not reduced by frost, the life cycle is prolonged over winter. This supports findings by May and Coetzee (2013) that *M. scutellaris* would not fare as well as other biological control agents previously released in the highveld for the control of water hyacinth as a consequence of the cold winters.

Climatic mismatches and low winter temperatures are the limiting factors for the success of biological control programmes for water hyacinth. May and Coetzee (2013) predicted that 0.5 generations of *M. scutellaris* would be produced over the winter months along the Crocodile River, which is the main tributary feeding Hartbeespoort Dam. Therefore, the insect seed culture for the post-winter water hyacinth growth is too low and cannot build up sufficient numbers to effectively stress the plant. The low post-winter insect seed culture results in the insects showing a rapid increase in numbers only in the summer months (May & Coetzee, 2013). Low temperatures have been a limiting abiotic factor for the success of biological control of water hyacinth because the frosting over of the plant reduces the food source for the insects. A linear regression showed a highly significant impact on *M. scutellaris* density which increased with increasing temperature. Minimum temperature has a highly significant impact on biological control agent densities and, as a consequence, the seasons have a significant impact on insect numbers, although these numbers vary between seasons. Understanding the impact that seasons have on insect population dynamics, will assist in determining the opportune time to release biological control agents for inundative insect releases. For *M. scutellaris* and both *Neochetina* weevil spp. there was no significant difference in insect densities between winter and spring, supporting the decision to undertake the inundative releases of *M. scutellaris* in mid- to late spring to allow for a proliferation of the insects at the onset of summer. To bring water hyacinth under control, high insect densities are pivotal; however, if the development of our main biological control agent is limited to the summer months, they will not reach damaging densities at the peak of water hyacinth coverage. Miller *et al*. (2020) found that the maximum insect density was reached at the end of summer on the Kubusi River in the Eastern Cape Province of South Africa.

Minimum temperature not only affects insect densities, but significantly impacts water hyacinth coverage. Lakane *et al*. (2024) observed the influence of water temperature on water hyacinth growth, where water hyacinth coverage increased in spring and the maximum coverage was reached during mid- to late summer, followed by a decrease in cover from autumn as temperatures started to decrease (Lakane *et al*., 2024). Lakane *et al*. (2024) concluded that temperature was the main variable influencing plant growth and water hyacinth coverage, while dissolved inorganic nitrogen and dissolved oxygen were the only abiotic variables influenced by water hyacinth dynamics.

The suite of biological control agents (BCAs) present on the dam, prior to the introduction of *M. scutellaris* were unable to bring the weed under control because the effect of the hypertrophic nutrient status of the water. Eutrophication is another abiotic factor that limits the success of the biological control agents, as the high nutrient levels help the plant compensate for the herbivory of the insect and the growth rate of the plant is faster than that of the insects. Jadhav *et al*. (2008) found that the eutrophication stimulated the growth of plants at a rate which enabled them to outstrip weevil damage, rendering the biological control ineffective. Miller (2020, thesis) concluded that *M. scutellaris* would be an effective biological control agent for water hyacinth growing in water bodies with medium to low nutrient levels, but the herbivory of *M. scutellaris* was not sufficient to cause damage to plants grown in highly eutrophic water which contributed to the inefficiency of the insect as a biological control agent under eutrophic water conditions, contrary to the findings of this study that showed that *M. scutellaris,* coupled with *Neochetina* weevils spp., can be an effective biological control agent even in hypertrophic water bodies in cool temperate regions.

Interestingly, Fitzgerald and Tipping (2013) observed that there was a higher female biomass of *M. scutellaris* on high quality plants grown in high-nutrient water. Eutrophication could possibly be beneficial in attaining higher insect densities for *M. scutellaris* as Hill and Olckers (2001) noted that the eutrophication can lead to the proliferation of biological control agents due to higher quality host plants.

The appearance of a high number of winged *M. scutellaris* individuals is a sign of a deteriorating site and increasingly poor host-plant quality. Miller *et al*. (2023) noted that macropterous (winged) insects are most common when the host-plant quality is poor or where intraspecific competition occurs, while brachpterous (flightless) insects are abundant in a healthy system. The metabolic cost of flight muscles results in reduced fecundity, therefore flightless adults produce more offspring (Miller *et al*., 2023).

The data showed that *M. scutellaris* can thrive in the presence of other biological control agents, creating enhanced damage and stress to the plants. Goode *et al*. (2020) found that plants exposed to *Neochetina* spp. weevils and *M. scutellaris* had higher mortality rates than those exposed to either type of insect individually. Additionally, Marlin *et al*. (2013a) found that a synergistic effect occurs when *O. terebrantis* feeds on water hyacinth plants with either *N. eichhorniae* or *E. catarinensis*. The same study found a synergistic effect when the two *Neochetina* weevils are present at a site together. Marlin *et al*. (2013a) showed that at a plant level, plants exposed to a combination of mites with weevils produced shorter plants with fewer leaves and lower increases in plant biomass than when both weevil species were present at the site in the absence of the mites.

The successful biological control of *Pontederia crassipes* at Hartbeespoort Dam was followed by the invasion of an aquatic fern, *S. minina* supporting the Shen *et al*. (2023) findings that following the eradication of the dominant invader, resource constraints are reduced therefore, subdominant invaders may respond more quickly to the availability of nutrients than native species (Coetzee *et al*., 2022b; Chikodza *et al*., 2025). A Chikodza *et al*. (2025) study looked at the population dynamics of the two invasive species at the Hartbeespoort Dam and examined the impact herbivory on water hyacinth on its competitiveness as an invasive and in the presence of sub-dominant species like *S. minima*. Chikodza *et al*. (2025). Chikodza *et al*. (2025) found that *P. crassipes* being the larger plant is a strong competitor than the smaller *S. minima* under both intra-and interspecific competition, by shading out the smaller *S. minima*, thus limiting its access to light (Chikodza *et al*., 2025). However, when *M. scutellaris* is introduced, *P. crassipes* competitive ability when compared to *S. minima* is reduced by 75% (Chikodza *et al*., 2025).

This study demonstrated that it is essential to mass rear *M. scutellaris* insects throughout the colder months of the year at rearing stations around the Dam in order to attain the desired high densities of insect necessary for damage that would bring the weed under control. Research findings by Hopper *et al*. (2021), Coetzee *et al*. (2011) and Miller *et al*. (2020) found that an augmentative biological control programme complemented with insect mass rearing facilities in the localities of the infested rivers and water bodies would assist in sustaining the control achieved using biological control by providing the insect quantities required to replenish the biological control agent populations following the colder months of the year in the Delta in the US and South Africa after reinfestation occurs. Furthermore, the occurrence of a secondary invasion necessitates the need for another biological control programme against *Salvinia minima* to be carried out in the colder months, as weed is not yet a target for eradication in South Africa (Coetzee *et al*., 2022b).

3.6 Conclusion

The reinfestation of the Hartbeespoort Dam by *Pontederia crassipes* seedlings occurs annually, therefore once-off programmes are not suitable for the control of water hyacinth (Djihouessi *et al*., 2023) because water hyacinth seeds remaining dormant and viable for decades, germinating once the environmental conditions are favourable. The *Neochetina* weevils are more robust than other biological control agent, because their numbers do not dwindle in winter and so they do not need reintroduction to the system. The newly introduced *M. scutellaris* can only be an effective biological control agent for water hyacinth when augmented releases are made annually in highly eutrophic rivers and water system. The releases should be made mid-spring or at the latest at the beginning of summer to reduce the lag phase between the water hyacinth growth peak and the insect density peak, as high insect densities are required to cause significant damage to the plants and reduce plant coverage. The presence of other biological control agents, such as *Neochetina* spp. weevils and the mites, enhanced the damage to the plants, increasing the mortality of the plant. It would be prudent, therefore, to ensure that the *Neochetina* weevils, particularly, form part of the suite of biological control agents in cool temperate regions as they have proved to be more robust, and they overwinter well. Seasons have a significant impact on both the plant growth and the effectiveness of the biological control agents. The hypertrophic state of the Dam facilitated a secondary invasion by *Salvinia minima* during the cold months, therefore, a concurrent release programme should be undertaken to ensure a clear state of the Dam.

This chapter examined the impact of the introduction of *M. scutellaris* as a biological control agent had on the water hyacinth infestation on the Dam. The participation and buy-in of residents for the biological control programme and for maintaining the satellite mass rearing stations around the Dam is pivotal for the success of the biological control of water hyacinth by conducting inundative releases of *M. scutellaris* in order to facilitate the buildup of insect densities that are damaging to the plants and result in a clearance or reduction in water hyacinth coverage.

With the turn of the century, and the increased documentation of the benefits attributed to the presence of waters hyacinth, stakeholders have shown resistance to the total eradication of water hyacinth (Djihouessi *et al*., 2023). Management strategies after the year 2000 have been reorientated towards the restoration of the structure and functioning of the ecosystem with the progressive integration of various sectors (Djihouessi *et al*., 2023). Since there is a moratorium on herbicide use to control water hyacinth on Hartbeespoort Dam, the only available methods of control are biological control and mechanical control, through manual or mechanical removal. Chapter 4 compares the impact of manual removal of the aquatic ecosystem functioning and the "Control site" where biological control agents are being used to control water hyacinth, while Chapter 5 assesses the willingness to pay for the management of the water hyacinth by residents and visitors to the Dam and to establish if the perception people have of the plant as a nuisance influences their willingness to pay, or if other socio-economic factors contribute to their willingness to pay for the weed's management.

Chapter 4: Evaluating Ecosystem Services Impacted by Freshwater Macrophytes: Considerations for Water Managers of Management Programmes

4.1 Introduction

Aquatic macrophyte stands become a nuisance when they exceed a critical density, although canopy-forming and floating vegetation, such as water hyacinth, hinders recreational activities even at relatively low densities (van Nes *et al*., 2002). This weed has serious socioeconomic and ecological effects because its dense mats interfere with fishing, water transportation, recreational use of the waterbody, irrigation, the use of the water for drinking and electric power generation purposes (van Nes *et al*., 2002, Thiemer *et al*., 2021, Harpenslager *et al.*, 2022). The dense mats are detrimental to the biodiversity of the infested ecosystem, owing to reduced light penetration and lower oxygen levels beneath the mats (Groote *et al*., 2003; Hopper *et al*., 2021). A study by Mironga *et al.* (2011) showed that the presence of water hyacinth on Lake Naivasha in Kenya reduced phytoplankton productivity, and the lack of phytoplankton altered the composition of the invertebrate communities within the lake. Conversely, the removal of water hyacinth mats led to a loss of water clarity as phytoplankton grew and cyanobacteria blooms formed (Villamanga & Murphy, 2010; Janssen *et al*., 2021). Water hyacinth mats also restrict oxygen exchange across the air/water interface, leading to reduced dissolved oxygen in the water column and, in extreme cases, the anoxic conditions may lead to massive fish mortality (Yongo *et al*., 2017). McVea and Boyd (1975) and Mironga *et al*. (2011) found that the mean dissolved oxygen concentrations under floating water hyacinth mats were consistently lower than at control sites. Under anoxic conditions, oxygen-sensitive biochemical transformation such as denitrification, methane formation, and the release of iron-bound phosphorus from the sediment take place (Janssen *et al*., 2021) resulting in ammonia (NH_4), iron (Fe), manganese (Mn) and sulphide (S^{2-}) concentrations rising to levels that are harmful to organisms within the aquatic ecosystem (Yongo *et al*., 2017).

4.1.1 Ecosystem Services Provided by Macrophytes

Macrophytes play an important role in aquatic ecosystems and may provide multiple benefits for humans, known as ecosystem services (Thomaz, 2021). The ability of macrophytes to render these ecosystem services depends on the role that macrophytes play in the ecosystem structure and function (Thiemer *et al*., 2021). Hussner *et al*. (2017) argued that if native multispecies macrophyte stands can provide habitats that support biodiversity and can perform key ecosystem services such as nutrient retention, enhanced water clarity and inhibit algal blooms within an aquatic system, then invasive macrophytes could potentially render the same ecosystem services in an infested waterbody. Although mass development of invasive species are generally monocultures that may threaten a more diverse vegetation, the macrophytes are still likely to fulfil important functions within the ecosystem (Thomaz, 2021, Harpenslager *et al*., 2022). These functions are supporting services (habitat provision and nutrient cycling), regulating services (which include water purification, pest and disease control), provision services (environmental monitoring where the presence of macrophytes is an indicator for water quality and community integrity), and cultural services (aesthetics, inspiration for culture, arts and design) (Balvanera *et al*, 2017, Thiemer *et al*., 2021, Thomaz, 2021). Thus, the complete removal of these macrophytes can have adverse impacts on ecosystem structure and function, as their presence alters the food webs of the invaded aquatic ecosystem, possibly hindering the management goals for healthy freshwater ecosystems (He *et al*., 2021, Thiemer *et al*., 2021).

Macrophytes reduce algal growth through at least two other mechanisms: firstly, by providing a habitat for microorganisms, leading to enhanced densities of zooplankton, and secondly, some macrophytes release allelopathic substances which inhibit phytoplankton development (Thomaz, 2021). These mechanisms in temperate lakes contribute to the clear water state (Thomaz, 2021). Free floating plants such as *P. crassipes* prevent light penetration through the water column and rapidly absorb nutrients from the water column, thus preventing phytoplankton and submerged vegetation from absorbing sufficient resources for photosynthesis (Villamanga & Murphy, 2010). McVea and Boyd (1975) found that the shading effect of water hyacinth mats prevents phytoplankton photosynthesis by the algae. Additionally, the microbial breakdown of decaying plant material uses up the available oxygen in the water column (Mironga *et al*., 2011, Yongo *et al*., 2017). Water hyacinth has proved to be a better competitor than phytoplankton for limiting nutrients, as both phosphate and total phosphorus in the water column are rapidly reduced when small stands of floating plants establish. This deprives the phytoplankton of this crucial nutrient and inhibits their growth. Yang *et al*. (1992) found that water hyacinth can exhibit allelopathic effects on algae, by producing algaecidal compounds in its roots and secreting them directly into the water (Mironga *et al*., 2011).

Macrophytes impact nutrient cycling through various physical, chemical, and metabolic processes and interactions with other organisms in an aquatic ecosystem (Thomaz, 2021).

Physical nutrient cycling mechanisms help to reduce nutrients in the water column (Thomaz, 2021). Floating macrophytes, such as water hyacinth, are capable of effectively removing nitrogen and phosphorus from the water because they use dissolved nutrients for their growth (Janssen *et al*., 2021). Therefore, large stands of water hyacinth could cause the rapid removal of nitrogen and phosphorus from the water column (Mironga *et al.,* 2011). Marshall (1997) found that the reduction in water hyacinth coverage led to an increase in nitrogen and phosphorus in the water column following successful biological control of the weed in Lake Chivero during the 1990s. Therefore, there is positive feedback between phosphorus concentrations and floating macrophyte dominance (Janssen *et al*., 2021). Yongo *et al*. (2017) observed slightly higher water temperatures in water hyacinth-infested sites which they attributed to the dense mats blocking the exchange of heat between the water surface, and the decaying organic matter from water hyacinth generating heat that raises the temperature (Yongo *et al*., 2017). Yongo *et al*. (2017) further observed that pH values were generally lower in the hyacinth-infested areas than in the non-infested areas.

The provisioning of habitat, particularly for periphyton, is a key ecosystem service provided by macrophytes as it facilitates a variety of other ecosystem services. Periphyton are microorganisms that are attached to the surface of the macrophyte (Thomaz, 2021). Ecosystem services such as nutrient cycling, capturing and storage of gases, and water purification occur as a result of the activity of macrophytes combined with the activity within their periphyton (Thomaz, 2021).

Dense macrophyte stands lead to an increase in sedimentation and carbon sequestration, thus contributing further to reduce the turbidity of shallow lakes (Harpenslager *et al*., 2022, van Nes *et al*., 2002). Phytoplankton and aquatic macrophytes are key bioindicators for the ecological status of lakes (Swe *et al*., 2021). In the case of eutrophic temperate lakes, Scheffer *et al*. (1993) suggested the existence of two stable states: one being a clear water state, abundant in submerged macrophytes, and the other state being turbid and phytoplankton-dominated (Swe *et al*., 2021). This suggests that in the absence of the macrophytes, the phytoplankton state would dominate. Competition for nutrients by aquatic macrophytes and their periphyton, impacts the abundance of phytoplankton and cyanobacteria, thus creating clear water conditions (Harpenslager *et al*., 2022).

This chapter formed part of a multi-disciplinary and multi-national project known as the Water JPI MadMacs project which set out to develop a ‘cookbook’-tool to assess and balance benefits and drawbacks of aquatic macrophyte removal through harmonized-BACI (Before After Control Impact) studies. The case study sites for the MadMacs project carried out *in situ* experiments in a harmonized BACI design at five case study sites across four countries. The main aim of the MadMacs project is to use the results obtained in this Chapter to develop a decision support system for the management of waterbodies experiencing mass developments of aquatic plants, by looking at the impact on the aquatic ecosystem following the removal of the mass development of an aquatic weed (Schneider *et al*., 2024).

4.2 Materials and Methods

4.2.1 Site Description

Sampling took place at Kuper Oord (25°44’57’’S 27°49’60’’E), a site owned by the Department of Water and Sanitation for the Water JPI MadMacs. Kuper Oord is located in the suburb of Kosmos village on the banks of Hartbeespoort Dam in the North West Province, South Africa. The site is not open to the public, therefore, there is minimal disturbance to the site, making it ideal for tests that require minimal site disturbance. It has a boat launching site located on Site B (Figure 4.1) the jetty of which separates the Impact and Control sites.

Fieldwork was carried out from 11 January to 1 February, 2020. Site A was selected as the control site while site B was selected as the impact site and was cleared by manual removal of the water hyacinth mat on the 22 January 2020 by community members hired by the Harties Foundation, an NPO which was carrying out physical removal of the weed around the Dam, in addition to the work being done by individual estates to keep their shorelines clear of the weed. The area of site B that was cleared was boomed off to prevent water hyacinth mats from floating into the cleared area (Figure 4.2). Apart from the manual removal, Hartbeespoort Dam had a biological control programme, and a new biocontrol agent, *Megamelus scutellaris*, had been introduced to the system 14 months prior to the commencement of the MadMacs sampling (see Chapter 3). Hartbeespoort Dam was the only site with an integrated management programme for the invading macrophyte.

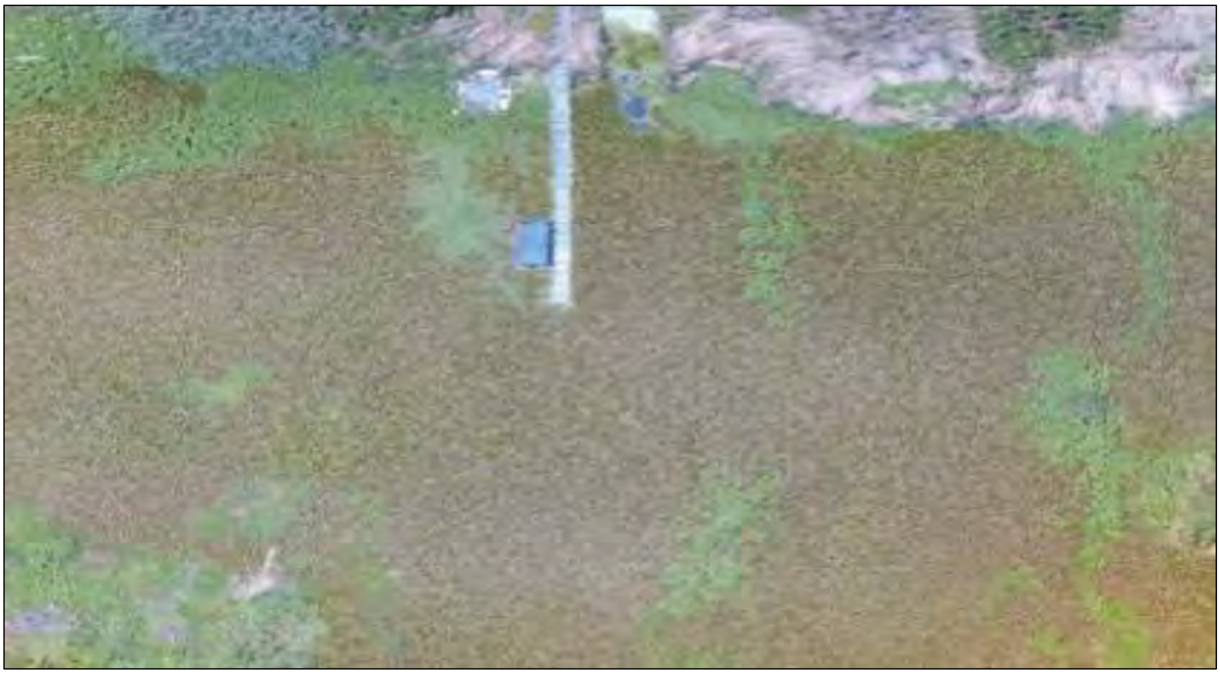

Figure 4.1. Aerial image of Kuper Oord project before the manual removal of water hyacinth

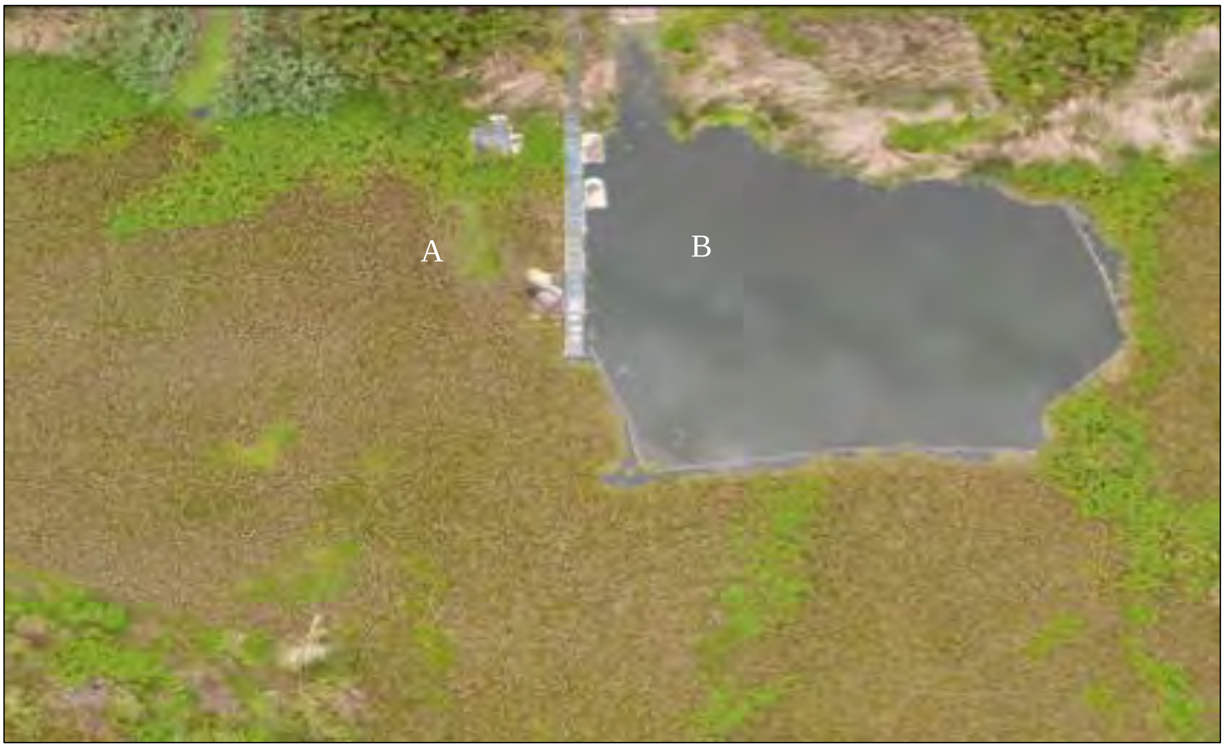

Figure 4.2. The manual removal created a clearing of approximately 625m^2 at the Kuper Oord Project site, Hartbeespoort Dam. A) Control site S25.750633°, E27.830099°); B) Impact site (S25.749192°, E27.833316°), each of the sites has an area of 625 m^2 with a depth range between 1.2-1.8 m

4.2.2 The Role of Macrophytes for the Provision of Habitats

To determine the role of the macrophytes as a habitat, parameters related to ecosystem structure and functions were quantified, including response diversity (Elmqvist et al. 2003) and functional redundancy (Naeem 1998), to determine the susceptibility of the communities to stress. This was done on the 11 January 2020 and again on 15 January before the macrophyte removal. Following the manual removal of macrophytes, the tests were carried out on 28 January 2020, a week after clearing. after macrophyte removal at the control and impact areas.

Biological components measured were phytoplankton (integrated water sampling plus microscopy, chlorophyll quantification, PAM fluorometry), zooplankton (net sampling, microscopy), benthic algae (standardized substrates, microscopy, HPLC pigment signatures), macrophytes (aquascope and grab samples), macroinvertebrates (hand net and Surber net sampling, stereo-microscopy), and fish (electrofishing). Harmonization of methods and taxonomic resolution were monitored by ECOBIO, in tight collaboration with all partners. The indicator species to be assessed were fish, macroinvertebrates, periphyton, phytoplankton, and zooplankton.

4.2.2.1 Macrophyte measures

To determine macrophyte species richness, three parameters were examined: cover of macrophytes, PVI and biomass (gDW m^{-2}) and stoichiometry (dominant species). For the macrophyte coverage, estimations were made for each species present at 10% scale, with the smallest category being <1%. This category noted the presence of the macrophyte even though it covered less than 1% of the area. Estimations of species diversity were conducted one week before removal, a week after removal, and a year after removal. For the PVI, the canopy height was measured several times, and this represented the percentage of the water column that is occupied by the plant t and not the above the water plant coverage of the surface surface for each species. The PVI was calculated from the canopy height and the water depth. To determine the biomass, macrophyte biomass was collected from five random quadrats (0,25 m^2) within the control and impact sites. Measurements of the above-water and below-water biomass (fresh weight) for the dominant species were taken. Subsamples were taken and measured for fresh and dry weight.

4.2.2.2 Electrofishing: Fish species identification and abundance evaluation

To undertake an inventory of the fish within Hartbeespoort Dam, electrofishing was carried out one week ahead of the removal of the macrophyte and again a week after the removal.

Electrofishing uses electricity to catch fish. The electricity is generated by a system whereby a high voltage potential is applied between two electrodes placed in the water (USGS, 2004). Electrofishing is regarded as the most effective single method for sampling fish communities in wadeable streams (Plafkin *et al.*, 1989). The electrofishing assessment was conducted by Approved Signatory Aquatic Biologist with Golder Associates Africa (Pty) Ltd, Warren Aken.

Electrofishing in an open waterbody such as a Dam, is not entirely effective and needs to be combined with other sampling techniques, such as netting. However, due to the dense coverage of water hyacinth at the project site, netting was not possible. Therefore, electrofishing along the margins was conducted to best assess and represent the fish assemblages present within the Dam. Electrofishing was conducted with a Smith-Root LR-24 portable electrofishing device (DC 12V pulsating). Two surveys were conducted, one prior to the clearing on the 14 January 2020, and one after clearing on the 28 January 2020.

4.2.2.3 Macroinvertebrate assessments

Since macroinvertebrates are found in the sediment and on plants, two samples had to be collected: a grab sample for the sediment and a sweep sample for macroinvertebrates found on plants. Five replicates of each sample type were collected in the control and impact sites. Grab samples were taken under the vegetation by avoiding the plants as much as possible. The samples were then cleaned in a 250 µm-mesh-size sieve and stored in bottles in ethanol. Sweep samples were taken with a 250 µm-mesh-size hand net for 30 seconds in a defined area (between 2 m^2). These samples were also stored in plastic bottles in ethanol. All macroinvertebrates were sorted, the samples fixed in 96% ethanol to a final concentration of roughly 75-96%, and sent to Rennes, France, for identification.

4.2.2.4 Periphyton assessment

Eight plastic strips, 2 x 10 cm, were attached to a 2 m aluminium round pole in clusters of four. Four strips 20 cm below the surface of the water were labelled as ‘Up’, and four strips 20 cm above the sediment, labelled as ‘Down’. Holes were punctured at the top of each strip and cable ties were used to fix the strips to the pole. The pole was hammered into the sediment until firmly settled. The strips were exposed one week before sampling removal and collected one week after exposure, allowing for the periphyton to colonize the substrate. Following collection, each of the strips was placed in a 50 ml falcon tube with soda water for 30 s – 1 min to remove invertebrates. Then the strip is placed in another falcon tube containing filtered Dam water.

The invertebrate sample was preserved with ethanol and kept in a cool, dark cooler box. The strips were taken to the on-site laboratory, the periphyton was scraped, using filtered Damwater and a toothbrush. Both sides of the strips were scraped and the toothbrush cleaned using filtered dam water and that was added to the sample. The total volume of the samples was measured and recorded. From the samples, 35-45 ml of periphyton slurry for TP was frozen in a Falcon tube, and 20 ml and was preserved with 5 ml 96% ethanol for identification of diatom species composition. The samples were shaken vigorously and filtered using Whatman filter paper 25 mm; 0.7 µm GF/F. Sharp forceps were used to place filters on pre-labelled foil pieces. Filters were pre-combusted for 4 hrs at 550 °C to remove any organic contaminants, then the filters were weighed before use. For biomass determination, the used filters were dried at 60 °C for 24 hrs, then weighed. The filters were then stored in aluminium foil packages and send to IGB for CN analyses.

4.2.2.5 Phytoplankton assessment

Sub-surface water in different areas was collected in 500 ml glass bottles, taking care not to disturb the environment. The bottles were closed under water with an airtight cap. Lugol was added to a final concentration of maximum 2% to obtain a light brown colour. Extra drops of Lugol were added to samples which became clear as it was important to ensure that the samples remained brown to preserve the integrity of the sample.

4.2.2.6 Zooplankton assessment

Twenty litres of Dam water were filtered in a 60 µm mesh sieve. The volume of water filtered was adjusted to the density of the organisms with at least 400 individuals of the dominant species needing to be counted. The sieve was placed in sparkling water for a few seconds until organisms no longer moved. The bigger the organisms, the longer the delay. The carbonated water was removed, and the sample preserved in a bottle with ethanol to a final concentration of 80%. The tubes were stored at 4 °C in the dark until they could be sent to Rennes, France. In France, all replicates were analysed according to functional groups and species identification was done for pooled samples.

4.2.2.7 Biogeochemistry analysis

Two litres of subsurface water samples were collected at both the control and impact sites one week before, during removal, one week after, and six weeks after. For pH, conductivity, dissolved oxygen (DO) and water temperature, a third site, ‘Open water’ was tested. The time of the day when the samples were taken was recorded.

The geochemistry parameters of the water samples from the control and impact sites were assessed and these included pH, conductivity, nitrate concentrations, phosphates, DOand chlorophyll-*a* content.

Water samples were collected at the impact and control sites one week before and one week after macrophyte removal. Parameters such as pH, conductivity, water temperature and DO concentrations were recorded at the same locations where samples were collected. The water samples were fixed in the field using 2N HCl and transported frozen to the IGB laboratory (Germany) for analysis. Chlorophyll-*a* (chl-*a*) content was determined by filtering a known amount over a GF/F (Whatman; 0.7 µm) filter. The filters were kept at -80 °C until chl-*a* content was analysed using high-performance liquid chromatographic (Harpenslager et al., 2022). MiniDOTs (MiniDOT Logger, PME, U.S.A.) were used to log temperature and dissolved oxygen concentrations continuously at 20 cm below water surface and 20 cm above sediment surface. Unfiltered water samples were analysed for total phosphorus (TP) and total organic carbon (TOC) concentrations (Harpenslager *et al*., 2022). The TP analyses were carried out photometrically after digestion with 10N sulfuric acid and 30% hydrogen peroxide. The TOC concentrations were determined using a TOC analyser (Shimadzu TOC-LCPN) with an TNM-L (Total Nitrogen Measuring unit). Samples filtered through 0.45 µm filters were analysed colourimetrically for nitrate (NO_3^-) and ammonium (NH_4^+) using a continuous flow analyser (SEAL Analytical AutoAnalyzer AA3 with AACE Software 7.10.) (Harpenslager *et al*., 2022).

4.2.2.8 Sedimentation analysis

Sedimentation traps were set up on the same days as the carbon fluxes to ensure minimum disturbance and left in place for 24 hrs. Sediment cores were taken 5 cm below the sediment. Four samples were taken at each of the sites. After sampling, a known volume of sediment was dried at 60 °C for 48 hrs, weighed, homogenised and a subsample placed in 2 ml Eppendorfs and sent to IGB of C/N/P analyses. The remainder of the sediment (known DW) was ashed at 550°C for 4 hrs and weighed for ash weight (AW) to determine organic matter.

4.2.2.9 Carbon fluxes analysis

Opaque floating chambers were placed on the control and impact sites one week before, immediately after, and one and six weeks after removal of water hyacinth (Harpenslager *et al*., 2022). Headspace concentration of CH_4 was determined repeatedly approximately 3–4 times over 24 hrs. Total daily fluxes of CH_4 (including diffusion, ebullition and plant-mediated CH_4

transport) were determined *in situ*. Chambers were placed with valves open for 30 mins to equilibrate before a background sample was collected (Harpenslager *et al*., 2022). Valves were then closed, and samples were collected at different time intervals (0, 2, 8 and 24 hrs after closing the valve) over a 24-hr period. Before sampling, a 30 ml syringe was used to flush the headspace several times to ensure mixing before the actual sample was collected. The headspace samples were then transferred into 3 ml gastight vials with a septum lid (Labco, High Wycombe, UK), by displacing a known amount of demineralised water from the vial (Harpenslager et al., 2022). Samples were stored upside down to prevent leaking and analysed by injection into the portable greenhouse gas analyser. For this, a closed loop was created by connecting the inlet and outlet of the analyser by gastight tubing, with a glass injection port in between (Harpenslager et al., 2022). Samples were collected with a glass gastight syringe (Hamilton 250 µL RN syringe with 26G removable needle) and injected into the custom-built injection port through a 12.7 mm septum (premium-non-stick BTO septum, Restek), which was replaced after every 50 samples (Harpenslager *et al*., 2022). Samples were analysed within one week of collection.

4.2.2.10 Statistical analysis

Statistical analyses were conducted using RStudio statistical software v 4.2.1 (R Core Team, 2022) using Tidyverse, Plyr and Vegan. Two-way ANOVAs, ANCOVAs and Generalized Linear Models were carried out with time (Before, After) and site (Control, Impact) as fixed effects. For periphyton data analysis, the positions ‘Up’ and ‘Down’ became an additional fixed effect. For the water chemistry parameters such as pH, DO, conductivity and temperature, an extra time point was added for ‘During’ the removal together with an additional site of ‘Open water’.

4.3 Results

The study set out to understand the consequences of the removal of macrophytes on the ecosystem structure, function and services by performing *in situ* experiments using a BACI (before-after-control-impact) approach. It scrutinized the effect the removal of water hyacinth has on biodiversity, biogeochemistry, hydrology and greenhouse gas emissions (Schneider *et al*., 2024).

4.3.1 Macrophytes

Ten macrophyte species were identified in the Control and the Impact sites at varying coverage levels during the manual removal. *Pontederia crassipes* was the dominant macrophyte in the control site until a year after the manual removal on the impact site. There was a 10% water hyacinth coverage difference between the impact and the control sites. A week after removal, there was still no water hyacinth coverage on the impact site while the coverage increased to 90% in the control site. However, a year after the manual removal, the water hyacinth coverage on the impact site (60%) was three times higher than the control site (20%) (Figurec4.3). Anative species, *Persicaria senegalensis*, became dominant in the control site at 40% coverage, while *P. crassipes* accounted for 20% of macrophyte cover. However, in the impact site water hyacinth became the dominant macrophyte a year after manual removal. A new alien species, *Myriophyllum aquaticum,* was present in the impact site, while the native, *Spirodela polyrhiza,* disappeared from the control site. The native *Commelina* sp. increased its coverage from less than 1% to 10% in just a year in the control site, bringing coverage at the control site to 50% by native species while invasive *P. crassipes* and *Salvinia minima* each accounted for 20% coverage in the control site (Appendix Table S1).

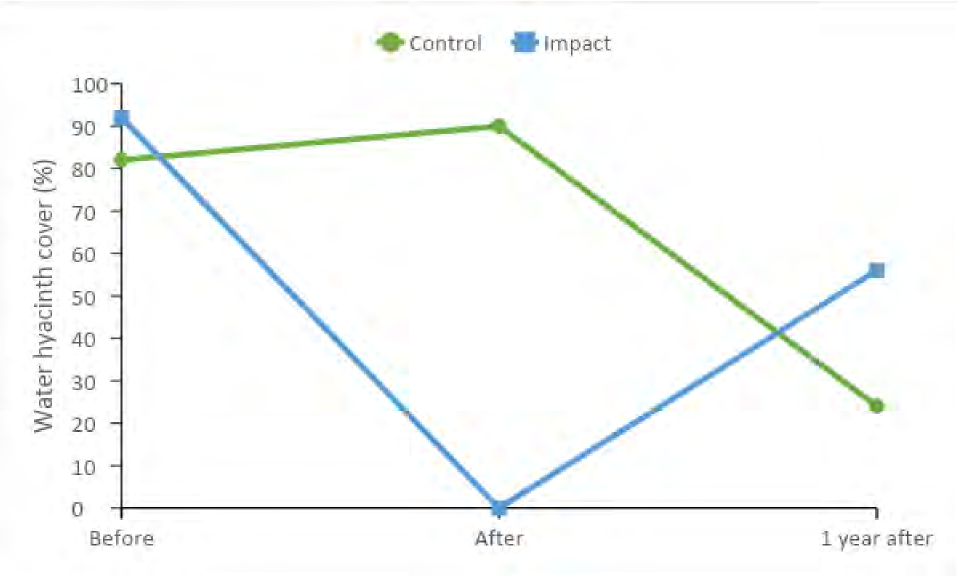

Figure 4.3. Water hyacinth percentage cover at the control and the impact site over three sampling times.

Over three tons of fresh weight of water hyacinth were removed from the 625 m^2 area on the impact site (Figure 4.4). Within a year, the fresh weight of water hyacinth that had recolonized the impact site was over two tons, while the fresh weight of water hyacinth on the control site was under a ton (Figure 4.4).

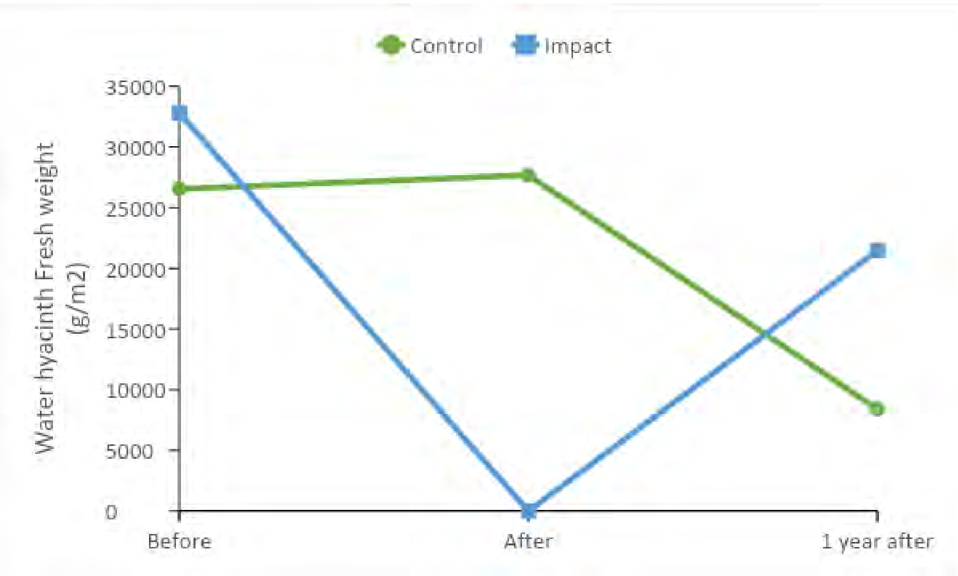

Figure 4.4. Fresh weight of water hyacinth over the three sampling times (a week before removal, a week after removal and a year after removal).

The volume of space that is occupied by the macrophytes in an aquatic system is measured as PVI. The PVI represented in Figure 4.5 is for the dominant species; in the case of Hartbeespoort Dam, that is *P. crassipes*. The volume occupied by water hyacinth in the 'control site' is lower after a year than it was initially, whereas in the impact site where manual removal was done, water hyacinth accounts for double the original infestation. This finding further supports the diversity in species in the control site and is evidence that biological control is a better control measure where biodiversity is important as it allows for native species recovery.

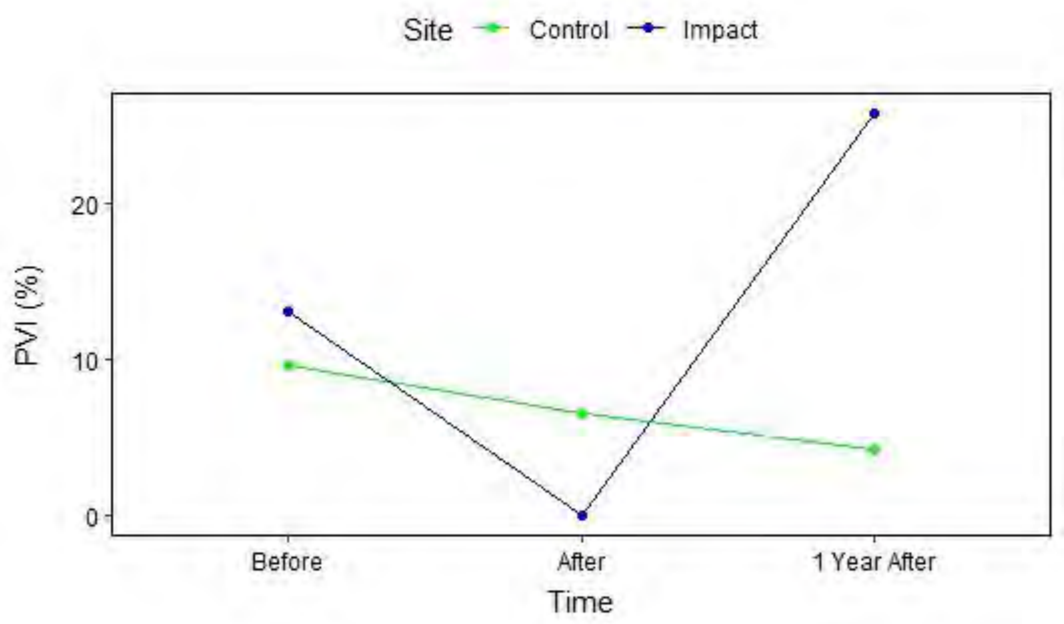

Figure 4.5. Volume occupied by water hyacinth represented as percentage PVI over time. The control site is managed by biological control while the impact site is managed through physical removal.

4.3.2 Electrofishing

Eight fish species were sampled at the control site and three fish species were sampled within the impact site before macrophyte removal. After clearing of the impact site, five species were sampled within the site with the exotic *Gambusia affinis* dominating the catch (Appendix Table S2).

There was high fish species diversity (2.00) under the water hyacinth mats with an evenness (0.93). However, the dominant species within the infested areas were benthopelagic species, which prefer swampy areas with a soft, muddy substrate, and tolerant of poorly oxygenated waters (Yongo *et al.*, 2017). Supporting the findings by Yongo *et al.* (2017) that water bodies dominated by floating macrophytes usually have higher percentage of planktivorous and benthivorous fish due to the turbidity of the water. The results were then compared to three previous studies of the fish populations in Hartbeespoort Dam by Kleynhans *et al*. (1980), Cochrane (1985) and Koekemoer and Steyn (2005).

Table 4.1. Comparison of the electrofishing catchment with the expected fish species of Hartbeespoort Dam (adapted from Froese and Pauly, 2019; Koekemoer and Steyn, 2005; Skelton, 2001).

Family	**Species**	**Common Name and Description**	**Kleynhans 1980**	**Cochrane 1985**	**Koekemoer and Steyn 2004**	**Aken 2020**
Centrarchidae	*Micropterus salmoides*	Largemouth Bass: large species (600 mm TL, 5–10 kg), prefers clear, standing, or slow-flowing water with submerged and floating vegetation. Does well in dams. Tolerant of low and high temperatures. Major freshwater game fish species.		X	X	X
Cichlidae	*Chetia flaviventris*	Canary Kurper: small to medium species (200 mm TL), favours standing or slow-flowing pools, and thrives in impounded waters.	X	X	X	X
	Oreochromis mossambicus	Mozambique Tilapia: medium to large species (400 mm SL, 3–4 kg), occurs in all but fast-flowing waters, hardy and tolerant, prefers slow-flowing or standing water in which it	X	X	X	X

		thrives. Aquaculture, fisheries and angling species. Has potential for exploitation.				
	Pseudocrenila-rus philander	Southern Mouthbrooder: small species (130 mm TL), has a wide distribution and wide habitat preference, usually favours vegetated areas.	X	X	X	X
	Tilapia sparrmanii	Banded Tilapia: small to medium species (230 mm SL, 0.5 kg), tolerant of a wide range of habitats, but prefers quiet vegetated areas. Utilised by subsistence fisheries.		X	X	X
Clariidae	*Clarias gariepinus*	Sharptooth Catfish: large species (1.4–1.7 m SL, 59 kg), hardy, has a wide habitat preference and distribution. Utilised by subsistence fisheries. An important angling and commercial food species. A good candidate for exploitation.		X	X	X
Cyprinidae	*Barbus mattozi*	Papermouth: medium to large species (400 mm SL), prefers quiet water, deep pools, and thrives in man-made impoundments. An angling species.		X	X	

	Enteromius paludinosus	Straightfin Barb: small species (150 mm SL), hardy, preferring quiet well-vegetated water. Utilised by subsistence fisheries in Malawi.			X	
	Enteromius trimaculatus	Threespot Barb: small species (110–150 mm SL), hardy and common, found in variety of habitats, prefers shallow vegetated areas.			X	
	Enteromius unitaeniatus	Longbeard Barb: small species (140 mm SL), wide habitat preference, flowing and standing waters, thrives in dams.	X	X	X	
	Cyprinus carpio	Carp: a large species (35 kg), hardy and tolerant, favours large water bodies. Thrives in dams. An aquaculture and angling species. A good candidate for exploitation.		X	X	X
	Labeobarbus marequensis	Largescale Yellowfish: a medium to large species (470 mm TL, 6 kg), favours flowing waters, uncommon in dams. An angling species.	X	X	X	
	Labeobarbus polylepis	Smallscale Yellowfish: medium to large species (460 mm TL), a cool water species, occurs in deep pools, flowing waters of permanent rivers,		X	X	

		and in dams. A popular angling species.				
	Engraulicypris brevianalis	River Sardine: small species (75mm SL), shoals and prefers well aerated open water. Used as forage fish in dams in Zimbabwe.	X	X		
Poeciliidae	*Gambusia affinis*	Mosquitofish: small species (39 mm TL), pelagic species, adults inhabit standing to slow-flowing water; most common in vegetated ponds and lakes, backwaters and quiet pools of streams.				X

4.3.3 Macroinvertebrates

Macroinvertebrates species richness decreased in the sweep sample, representing macroinvertebrates that are associated with water hyacinth roots, one week after removal of water hyacinth but increased to numbers close to the time before removal 6 weeks after the removal (Figure 4.6). Grab samples which represented macroinvertebrates in or on the sediment indicated no changes in macroinveterbrate species richness even after the removal of water hyacinth. The macroinvertebrate species richness decreased drastically after 6 weeks in the control site due to biological control reducing water hyacinth coverage (Figure 4.6).

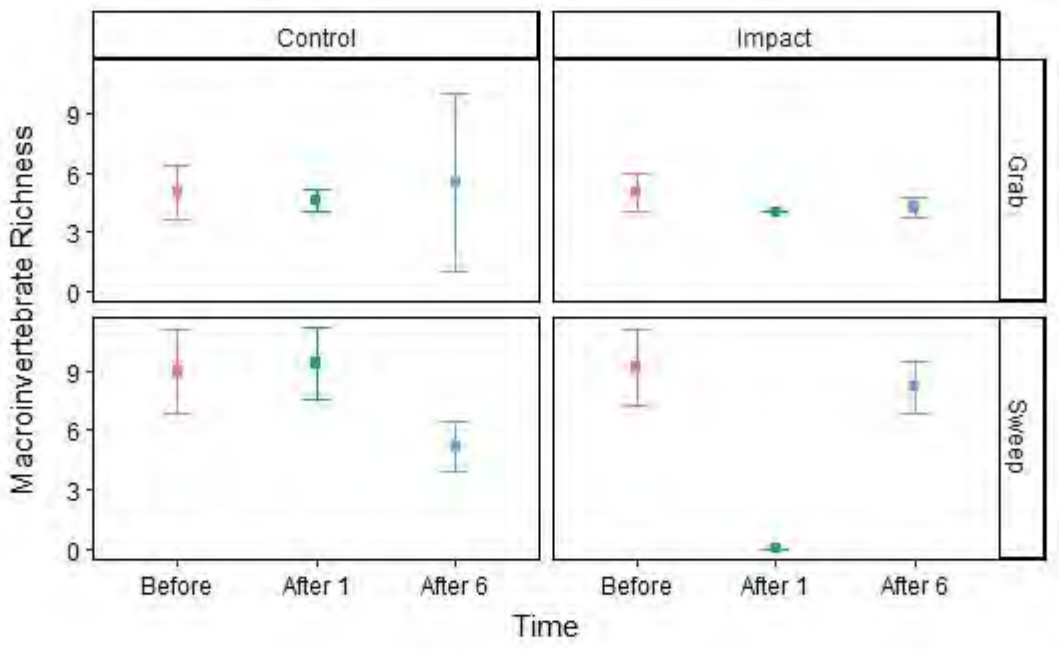

Figure 4.6. Comparison of macroinvertebrate species richness over time for macroinvertebrates associated with water hyacinth (Sweep sample) and macroinvertebrates in or on the sediment (Grab sample).

The GLM analysis for species richness is based on time (Before or After), site (Control or Impact) and the type of sample (Sweep or Grab) (Table 4.2). The intercept represents time before the weed removal and the control site.

Table 4.2. GLM results for macroinvertebrate species richness influenced by site, time and the sample type). Impact represents the mechanical/physical control site and after 1 is one week after water hyacinth removal and after 6 is six weeks after removal. Values in bold indicate significant differences.

Effect	Estimate	Std. Error	Z	*P*
Intercept	1.609e+00	2.000e-01	8.047	**8.47e-16**
Impact	5.875e-17	2.828e-01	0.000	1.0000

After 1	-8.338e-02	2.889e-01	-0.289	0.7729
After 6	9.531e-02	2.923e-01	0.326	0.7444
Sweep Sample	5.878e-01	2.494e-01	2.356	**0.0185**
Impact:Time1	-1.398e-01	4.548e-01	-0.307	0.7586
Impact:After6	-2.578e-01	4.293e-01	-0.601	0.5481
Impact:Sweep	2.198e-02	3.521e-01	0.062	0.9502
After1:Sweep	1.269e-01	3.563e-01	0.356	0.7218
After6:Sweep	1.269e-01	3.823e-01	-1.684	0.0921
Impact:After1:Sweep	-2.043e+01	2.859e+03	-0.007	0.9943
Impact:After6:Sweep	6.913e-01	5.395e-01	1.281	0.2001

The sample type 'sweep' has a significant effect on macroinvertebrate species richness ($P<0.05$), this demonstrates that sweep samples have a higher species richness than the grab sample (Table4.2). Site and time alone do not have a significant impact on macroinvertebrate species richness. The combined effect of site, time and sample type does not have a significant impact on species richness.

The sample type meaning the location, water hyacinth roots or sediment, of the macroinvertebrates has a significant impact on species richness (Table 4.3). The three-way interaction of site, time and sample type has a highly significant (P=3.13E-07) effect on macroinvertebrate species richness. Time and site on their own did not have a significant effect on macroinveterbrate species richness (Table 4.3).

Table 4.3. ANCOVA results illustrating the impact of time, site and sample type on macroinvertebrate species richness. Values in bold indicate significant effects.

Effect	**LR Chisq**	**df**	***P***
Site	0	1	1
Time	0.3581	2	0.83607
Sample Type	5.7947	1	**0.01607**
Site:Time	0.3661	2	0.83273
Site:Sample Type	0.0039	1	0.95022
Time:Sample Type	4.3881	2	0.11147
Site:Time:Sample Type	29.9544	2	**3.13E-07**

Macroinvertebrates species evenness decreased drastically from the control site for macroinvertebrates associated with water hyacinth roots, as time progressed due to the deterioration of the site as biological control caused a reduction in water hyacinth coverage (Figure 4.7). Whereas for the impact site the macroinvertebrate evenness decreased one week following water hyacinth removal but recovered to pre-removal levels after 6 weeks. For the macroinvertebrates associated the sediment, there was a slight increase in evenness in the control site 1 week after removal followed by a reduction to pre-removal evenness at 6 weeks after removal. For the impact site, the macroinvertebrate species evenness remained constant withtime (Figure 4.7).

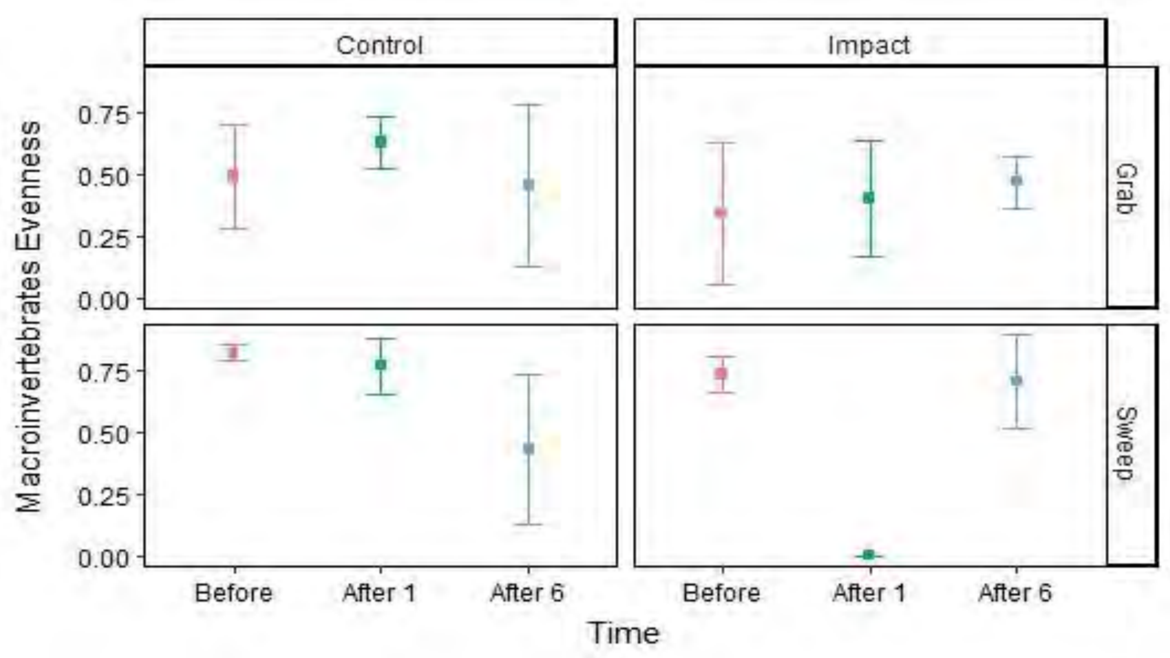

Figure 4.7. Comparative representation of macroinvertebrate species evenness over time for macroinvertebrates associated with water hyacinth (Sweep sample) and macroinvertebrates in or on the sediment (Grab sample).

Table 4.4. GLM results of macroinvertebrate species evenness impacted by the site, time and sample type. Impact represents the mechanical/physical control site and after 1 is one week after water hyacinth removal and after 6 is six weeks after removal. Bold figure represents significant impacts.

Effect	Estimate	Std. Error	t-value	*P*
Intercept	0.49107	0.08622	5.696	**1.01e-06**
Impact	-0.14986	0.12193	-1.229	0.22573
After 1	0.13872	0.12193	1.138	0.26154
After 6	-0.03365	0.12933	-0.260	0.79596
Sweep Sample	0.32937	0.12193	2.701	**0.00984**

Impact:Time1	-0.07681	0.18625	-0.412	0.68209
Impact:After6	0.16127	0.18290	0.882	0.38282
Impact:Sweep	0.06204	0.17244	0.360	0.72077
After1:Sweep	-0.19115	0.17244	-1.109	0.27380
After6:Sweep	-0.35866	0.17774	-2.018	**0.04987**
Impact:After1:Sweep	-0.60337	0.25745	-2.344	**0.02379**
Impact:After6:Sweep	0.20263	0.25137	0.806	0.42462

When comparing the two macroinveterbrate sites, the macroinverterbrates associated with the water hyacinth roots (sweep sample) had a higher species evenness than the macroinvertebrates associated with the sediment (Table 4.4). The combined effect of time 6 weeks after removal and the sample type had a significant effect on macroinvertebrate species evenness (P=0.05) (Table 4.4). The species evenness decreased for this interaction and the three-way interaction among, site, time and sample type (Table 4.4). The highly significant three-way interaction of site, time and sample type is also confirmed through the ANCOVA results (Table 4.5).

Table 4.5. ANCOVA results illustrating the impact of time, site and sample type on macroinvertebrate species evenness. Values in bold indicate significant effects.

Effect	**LR Chisq**	**Df**	***P***
Site	1.5106	1	0.219041
Time	2.1101	2	0.348178
Sample Type	7.2967	1	**0.006908**
Site:Time	1.5626	2	0.457814
Site:Sample Type	0.1294	1	0.719009
Time:Sample Type	4.0938	2	0.129134
Site:Time:Sample Type	9.9866	2	**0.006783**

Sample type is the only factor that has a significant impact on species richness as a sole factor (Table4.5).

The Shannon diversity index declined drastically in the control site 6 weeks after the removal of water hyacinth, this as the weed cover decreases due to herbivory by the biological control agents (Figurec4.8). By 6 weeks after the removal the macroinvertebrate Shannon diversity index recovered in the Impact site for the sweep sample while the diversity in the sediment (grab) remains the same over the different time points (Figure 4.8).

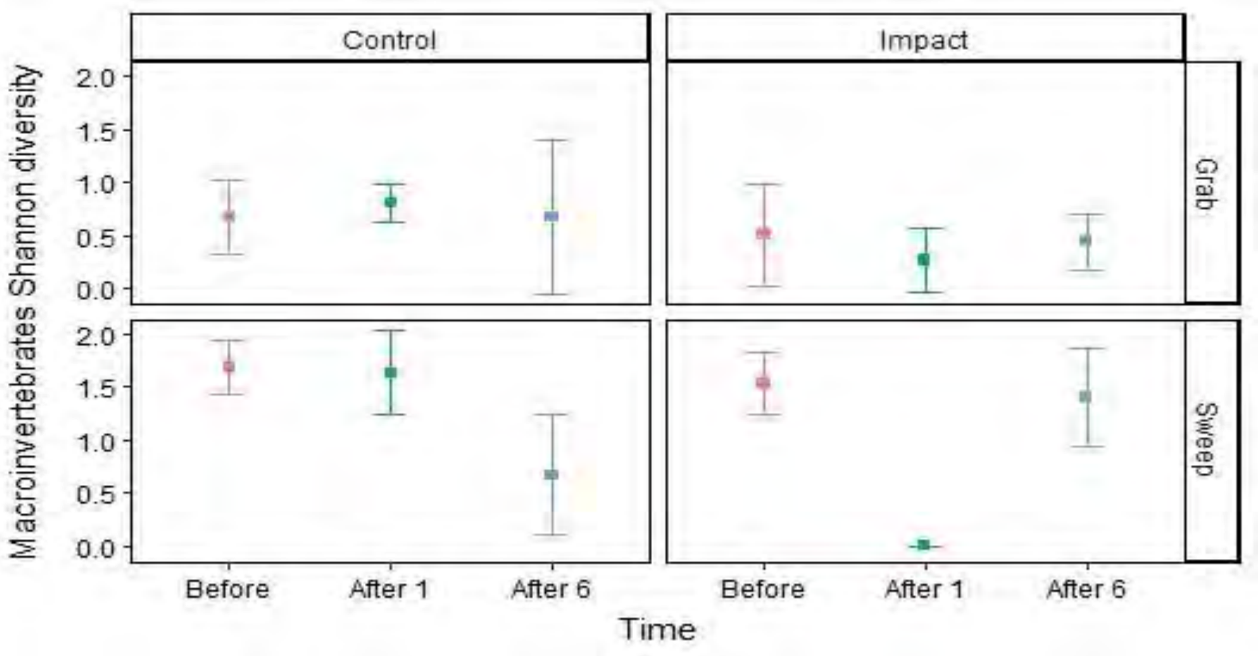

Figure 4.8. Comparative illustration of macroinvertebrate Shannon Diversity Index over time for macroinvetebrates associated with water hyacinth (Sweep sample) and macroinvertebrates in or on the sediment (Grab sample).

Table 4.6. GLM results of macroinvertebrate Shannon Diversity Index influence by the site, time and sample type. Impact represents the mechanical/physical control site and after 1 is one week after water hyacinth removal and after 6 is six weeks after removal. Bold figure represents significant impacts.

Effect	Estimate	Std. Error	t-value	*P*
Intercept	0.6713285	0.1794862	3.740	**0.000490**
Impact	-0.1678787	0.2538318	-0.661	0.511533
After 1	0.1296872	0.2538318	0.511	0.611751
After 6	-0.0003044	0.2538318	-0.001	0.999048
Sweep Sample	1.01530	0.2538318	4.000	**0.000218**
Impact:Time1	-0.3674139	0.3589724	-1.024	0.311195
Impact:After6	-0.0650459	0.3589724	-0.181	0.856973
Impact:Sweep	0.0153383	0.3589724	0.043	0.966095
After1:Sweep	-0.1785011	0.3589724	-0.497	0.621279

After6:Sweep	-1.0147474	0.3589724	-2.827	**0.006835**
Impact:After1:Sweep	-1.1178623	0.5076636	-2.202	**0.032505**
Impact:After6:Sweep	0.9493361	0.5076636	1.870	0.067588

The sweep sample has a significantly higher Shannon diversity index than the grab sample (Table 4.6). In the impact site Shannon diversity in the sweep sample decreased drastically one week after removal (Table 4.6). The Sweep sample in the control site 6 weeks after removal had a drastic decrease in Shannon diversity as illustrated by the interaction between the time after 6 weeks and the sweep sample (Table 4.6)

Table 4.7. ANCOVA results illustrating the impact of time, site and sample type on macroinvertebrate diversity. Values in bold indicate significant effects.

Effect	**LR Chisq**	**df**	***P***
Site	0.4374	1	0.5083702
Time	0.3489	2	0.8399321
Sample Type	15.9992	1	**6.34E-05**
Site:Time	1.1933	2	0.55066
Site:Sample Type	0.0018	1	0.9659182
Time:Sample Type	9.11	2	**0.010515**
Site:Time:Sample Type	16.6178	2	**0.000246**

The sample type has a highly significant impact ($P<0.001$) on macroinvertebrate Shannon Diversity (Table 4.7). The interaction between time and the sample type had a marginal significant effect ($P=0.01$) on the Shannon diversity index. While the three-way interaction among, site, time and sample type has a highly significant impact on Shannon diversity (Table4.7).

4.3.4 Periphyton

An artificial substrate was used as an adherence surface for colonization by periphyton. The artificial substrate strips placed 20 cm below the surface of the water were labelled as ‘Up’, and the artificial substrate strips 20 cm above the sediment, labelled as ‘Down’. The weight of the periphyton in the ‘Up’ position in the control site before macrophyte removal was 42.39±28.62 mg/m^2 and after the weed removal was 33.85±21.53 mg/m^2 (Figure 4.9). For the ‘Down’ position in the control site the weight before removal was 32.89±17.18 mg/$m^2$and after removal was 29.47±10.26 mg/m^2. In the 'Impact' site where the manual removal of the weed took place, the weight of the periphyton in the 'Up' position before removal was 39.03±16.47 mg/m^2 and after removal was 232.21±10.67 mg/m^2. For the 'Down' position before removal the weight was 35.14±23.24 mg/m^{2}and after removal was 38.80±15.93 mg/m^2 (Figure 4.9). The removal of water hyacinth from the impact site significantly increased the periphyton formation (F= 8.55, df=1, P<0.01) in the Up position (F=9.52, df=1, P<0.01).

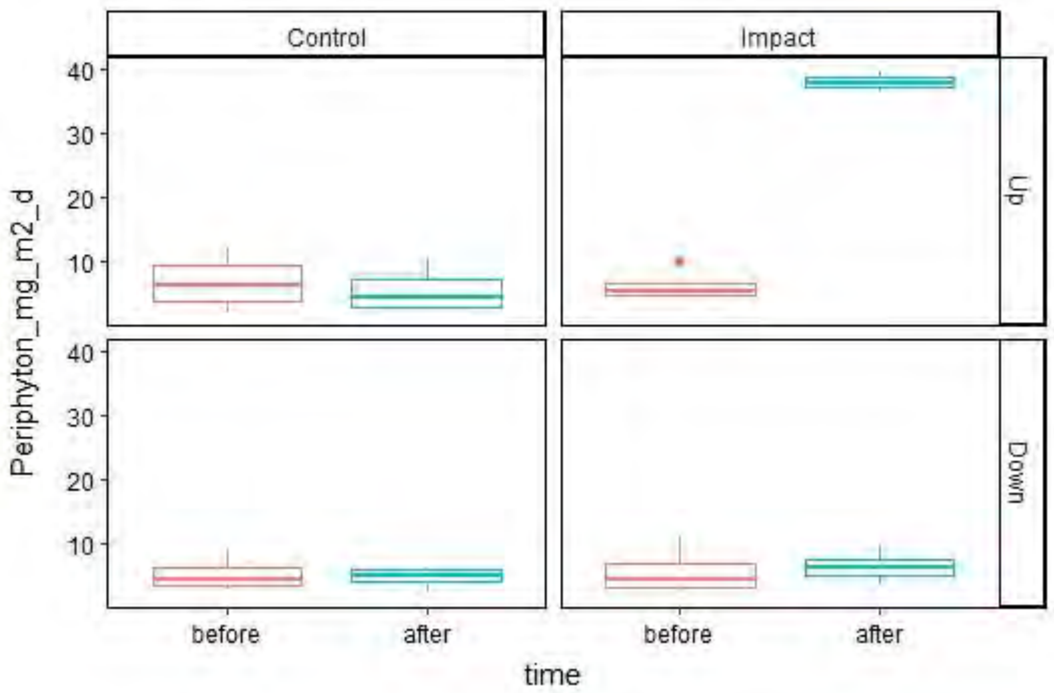

Figure 4.9. Periphyton formation in the control and impact sites before and after the removal of water hyacinth. The "Up" position was 20cm below the water surface and "Down" being 20cm above the sediment.

The site, whether impact or control, the time and location of the periphyton strip had a highly significant impact on the weight of the periphyton (Table 4.8).

Table 4.8. ANCOVA results illustrating the effects of various parameters on periphyton mass with Up_Down representing the position of the periphyton strip. The 'Up' position represents periphyton associated with the water hyacinth roots and the 'Down'position representing periphyton on or above the sediment. Bold figures indicate a significant effect.

Effect	df	Sum Sq	Mean Sq	F	*P*
Site	1	364.9	364.9	222589	< **2e-16**
time	1	305.4	305.4	186324	< **2e-16**
Up_Down	1	433.9	433.9	264691	< **2e-16**
Filtered_ml	1	63.7	63.7	38872	< **2e-16**
Time_incubated_h	1	516.5	516.5	315116	< **2e-16**
Sample_mg_m2	1	1351.5	1351.5	824482	< **2e-16**
Residuals	24	0.0	0.0		

The periphyton parameters remained the same for the 'Down' position, even after the removal of water hyacinth for the impact site. The mean weight of periphyton produced daily increased significantly in the 'Up' position following the removal of water hyacinth. The nutrient availability of the periphyton indicated the nutrient status of the waterbody in which they were found. The phosphorus content in the periphyton in the 'Up' position in the control site was 26.14±28.40 mg/m^2/d before macrophyte removal, and 10.36±10.12 mg/m^2/d after macrophyte removal (Figure 4.10). For the 'Down' position in the control site, phosphorus concentration was 21.60±15.70 mg/m^2/d before macrophyte removal, and 8.56±5.98 mg/m^2/d after macrophyte removal. In the 'Impact' site in the 'Up' position, the phosphorus content measured 10.65±7.27 mg/m^2/d before macrophyte removals, and 207.84±5. mg/m^2/d after macrophyte removal (Figure 4.10). In the 'Down' position of the impact site, phosphorus content was 2.59±1.05 mg/m^2/d before macrophyte removal and 2.80±1.36mg/m^2/d after macrophyte removal.

Nitrogen concentration in the control site in the 'Up' position before macrophyte removal was 0.44±0.32 $mg/m^2/d$, and 0.47±0.26 $mg/m^2/d$ after macrophyte removal (Figure 4.10). For the 'Down' position, nitrogen concentration was 0.32±0.18 $mg/m^2/d$ before macrophyte removal, and 2.51±0.19 $mg/m^2/d$ after the removal of the macrophyte. For the Impact site in the 'Up' position, which was 20cm below the water surface, nitrogen content was 0.37±0.13 $mg/m^2/d$ before macrophyte removal, and 2.51±0.19$mg/m^2/d$ after macrophyte removal (Figure 4.10). For the 'Down' position on the 'Impact' site, the nitrogen content was 0.43±0.19 $mg/m^2/d$ before macrophyte removal, and 0.45±0.19 $mg/m^2/d$. after macrophyte removal.

Carbon concentration in the control site in the 'Up' position before macrophyte removal was 2.62±1.88 $mg/m^2/d$, and 3.86±1.19 $mg/m^2/d$ after macrophyte removal (Figure 4.10). For the 'Down' position before macrophyte removal, the concentration of carbon was 1.82±0.97 $mg/m^2/d$ before macrophyte removal, and 3.23±0.24 $mg/m^2/d$ after macrophyte removal. In the 'Impact' site in the 'Up' position, carbon content was 2.21±0.80 $mg/m^2/d$ before macrophyte removal, and 15.50±1.33 $mg/m^2/d$ after macrophyte removal (Figure 4.10). In the 'Down' position, carbon content was 2.21±0.80 $mg/m^2/d$ both before and after macrophyte removal.

The amount of nutrient in the periphyton significantly increased in the 'Up' position following the removal of the weed and the significance is reflected as follows: carbon (F=786.37, df=1, P<0001), nitrogen (F= 1150.28, df=1, P<0.0001) and phosphorus (F=296.77, df=1, P<0.0001). Both time (F=6.07, df=1, P<0.05) and site (F=5.63, df=1, P<0.05) had a significant impact on the rapid increase of carbon in the periphyton; time, as represented before the removal and after the removal of the water hyacinth. In the absence of the weed, carbon concentrations in the periphyton closer to the water surface (Up position) increased, while carbon concentrations in the periphyton closer to the sediments (Down position) remained the same as for the control site.

Higher levels of carbon, nitrogen and phosphorus in periphyton formed on the strips placed 20 cm below the surface of the water where the macrophyte had been cleared (Impact site) than in the control site (Figure 4.10, Table S4). The absence of the water hyacinth mats allows for higher concentrations of dissolved nutrients in the water column.

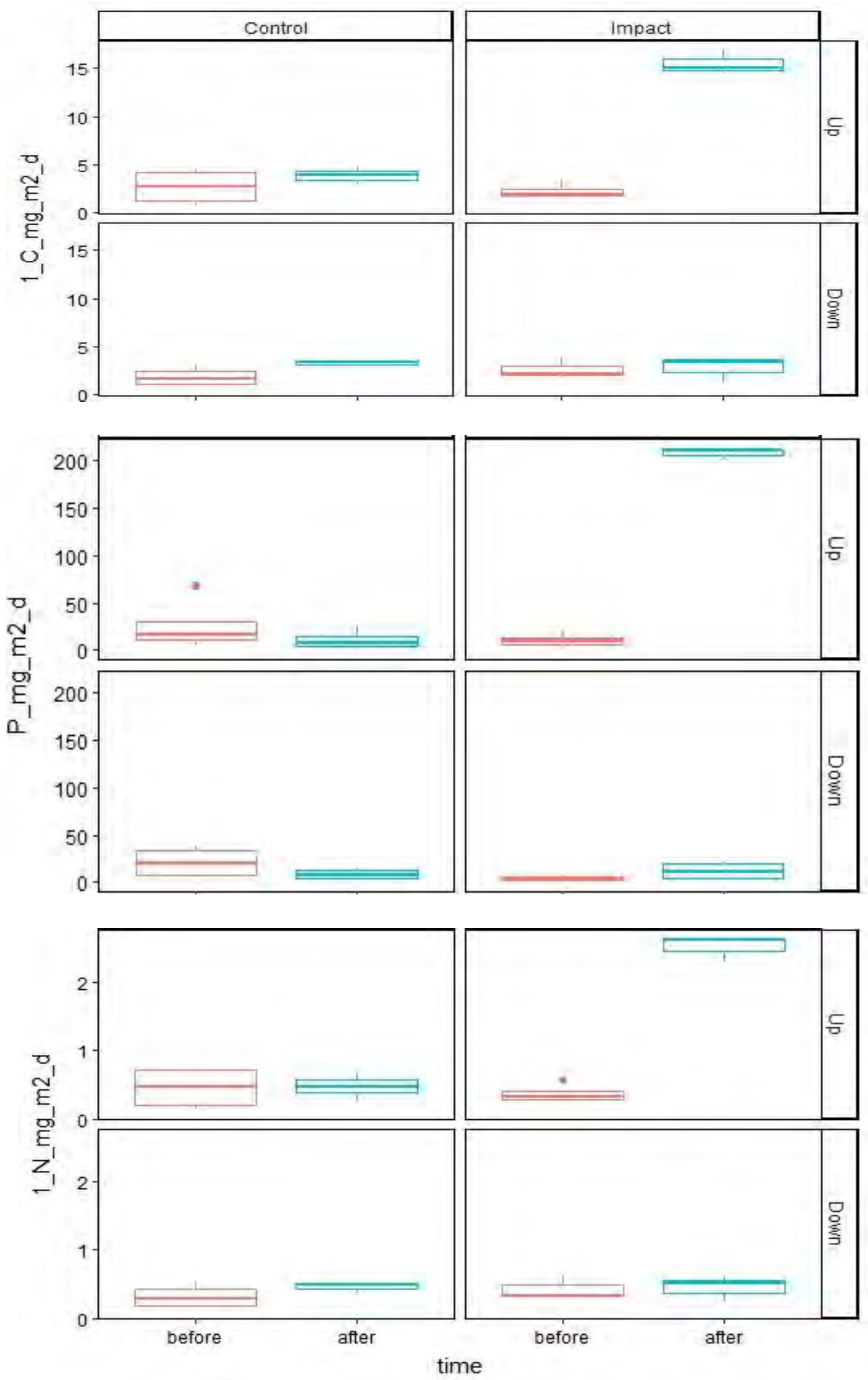

Figure 4.10. Nitrogen, phosphorus, carbon content of periphyton in the control and Impact sites, before and after the removal of water hyacinth in the impact site. The "Up" position was 20cm below the water

surface and "Down" being 20cm above the sediment. Red represents measurements before removal and green represents measurements after the removal of water hyacinth.

4.3.5 Phytoplankton

Phytoplankton richness increases drastically one week after removal in the impact site (Figure 4.11). This is due to water hyacinth and phytoplankton being in direct competition for nutrients and light. Phytoplankton richness then decreases as other macrophytes proliferate 6 weeks after removal in the temporal absence of water hyacinth (Figure 4.11).

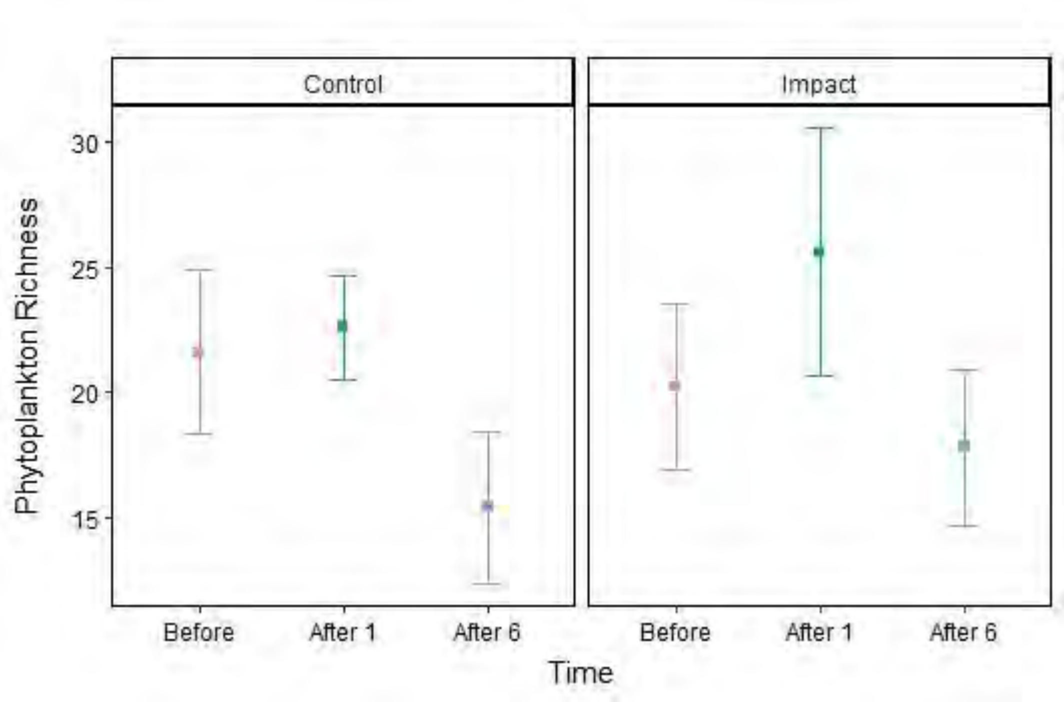

Figure 4.11. Phytoplankton species richness over time comparing biological control (Control) and manual removal (Impact) of water hyacinth.

Table 4.9. GLM results of phytoplankton species richness influenced by the site and time. Impact represents the mechanical/physical control site and after 1 is one week after water hyacinth removal and after 6 is six weeks after removal. Bold values represent significant impacts.

	Estimate	Std. Error	z value	*P*
Intercept	3.07269	0.09623	31.932	**<2e-16**
Impact	-0.06701	0.13842	-0.484	0.6283
After1	0.04526	0.13457	0.336	0.7366
After6	-0.33833	0.14915	-2.268	**0.0233**
Impact:After1	0.19165	0.18927	1.013	0.3112
Impact:After6	0.21184	0.20829	1.017	0.3091

The GLM analysis is based on the impact that water hyacinth removal (Impact site) has over time (before, after 1, after 6). Six weeks after removal has a marginally significant ($P<0.05$) effect on phytoplankton richness leading to reduction phytoplankton richness (Table 4.9).

Table 4.10. ANOVA results for phytoplankton richness as influenced by site and time. Bold values represent significant impacts.

Effect	**LR Chisq**	**df**	*P*
Site	3.4799	1	**0.0621203**
Time	8.9205	2	**0.0115595**
Site:Time	26.0427	2	**2.213e-06**

The interaction between site and time has a highly significant ($P<0.001$) on phytoplankton richness (Table 4.10). There is a marginal difference in phytoplankton richness at different time points ($P<0.05$).

Phytoplankton species evenness increased slightly one week after removal followed by a decrease six weeks after plant removal (Figure 4.12). Biological control led to a slight decrease in species evenness one week after removal followed by a slight increase at 6 weeks after removal (Figure 4.12).

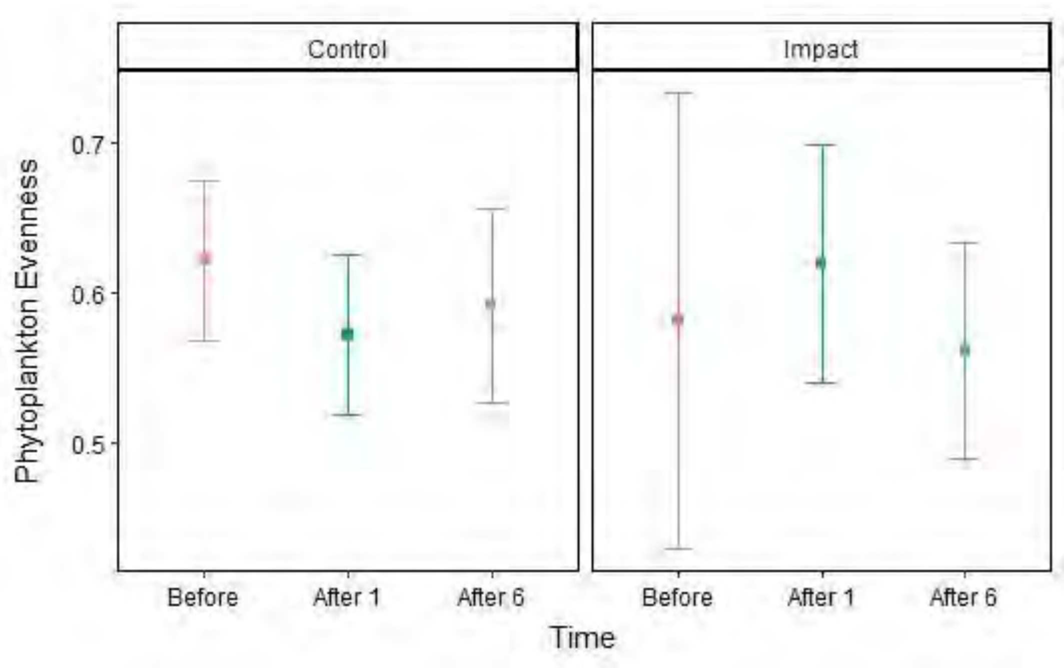

Figure 4.12. Phytoplankton species evenness over time comparing biological control (Control) and manual removal (Impact) of water hyacinth.

The GLM analysis revealed that there was no significant difference in phytoplankton species evenness between the control and impact site over time (Table 4.11)

Table 4.11. GLM results of phytoplankton species evenness influenced by the site and time. Bold values represent significant impacts.

Effect	Estimate	Std. Error	t value	*P*
Intercept	0.62197	0.03849	16.161	**2.12e-14**
Impact	-0.04044	0.05443	-0.743	0.465
After1	-0.04984	0.05443	-0.916	0.369
After6	-0.03041	0.05443	-0.559	0.581
Impact:After1	0.08758	0.07697	1.138	0.266
Impact:After6	0.01023	0.07697	0.133	0.895

Water hyacinth removal and time had no significant impact on phytoplankton species evenness (Table 4.11).

Table 4.12. ANOVA results for phytoplankton evenness as influenced by site and time. Bold values represent significant impacts.

Effect	**LR Chisq**	**df**	*P*
Site	0.06216	1	0.8031
Time	0.47117	2	0.7901
Site:Time	1.54802	2	0.4612

There was no significant differences in phytoplankton species evenness between the two sites over the different time points (Table 4.12).

Phytoplankton Shannon diversity in the control site gradually decreased with the decrease in water hyacinth coverage caused by biological control (Figure 4.13). While the Shannon diversity increased in the impact site one week after weed removal it decreased to similar levels as the control site at 6 weeks after removal (Figure 4.13).

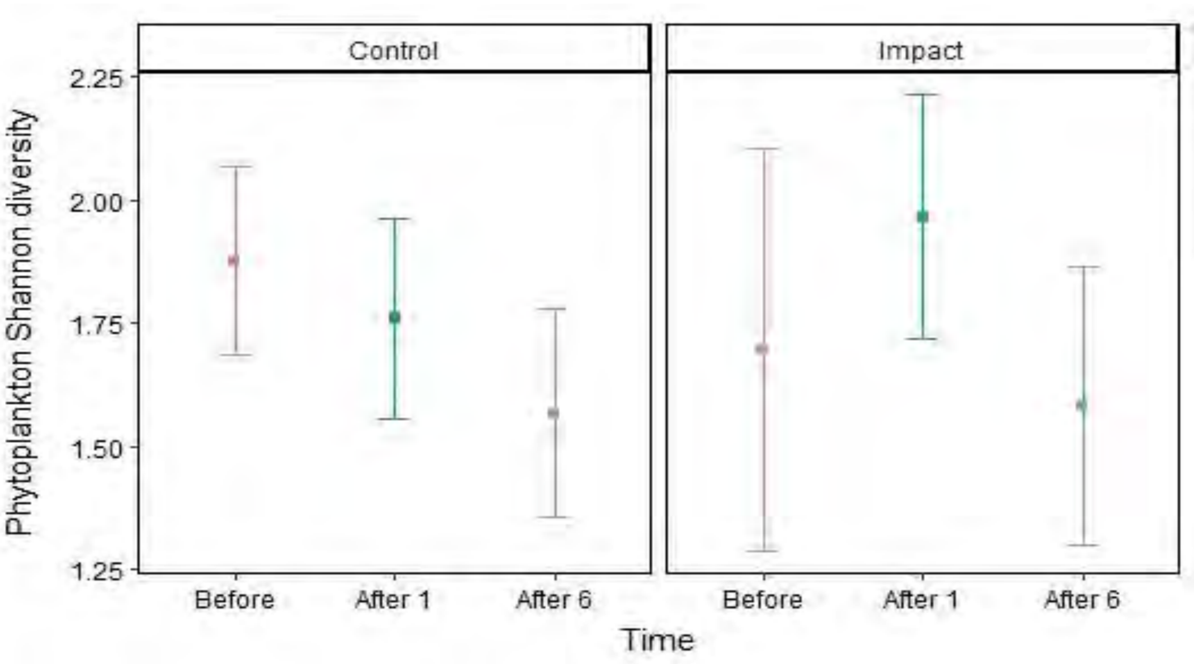

Figure 4.13. Phytoplankton Shannon Diversity Index over time comparing biological control (Control) and manual removal (Impact) of water hyacinth.

The GLM analysis for phytoplankton Shannon Diversity index is based on site and time (Table 4.13).

Table 4.13. GLM results of phytoplankton Shannon Diversity Index influenced by the site and time. Bold values represent significant impacts.

Effect	Estimate	Std. Error	t value	*P*
Intercept	1.8753	0.1199	15.639	**4.36e-14**
Impact	-0.1784	0.1696	-1.052	0.3032
After1	-0.1167	0.1696	-0.688	0.4981
After6	-0.3088	0.1696	-1.821	0.0811
Impact:After1	0.3853	0.2398	1.607	0.1212
Impact:After6	0.1947	0.2398	0.812	0.4249

There was a slight decrease in phytoplankton Shannon diversity 6 weeks after the removal of water hyacinth (Table 4.13). The plant removal on its own and the interactions between the site and time did not have a significant effect on Shannon diversity ($P>0.1$) (Table 4.13).

Table 4.14. ANOVA results for phytoplankton Shannon Diversity index influenced by site and time. Bold values represent significant impacts.

Effect	**LR Chisq**	**df**	*P*
Site	0.0232	1	0.87885
Time	6.1715	2	**0.04569**
Site:Time	2.5815	2	0.27507

There was a slight significant difference in Shannon diversity in the two sites over various time points (before, after 1, after 6) (Table 4.14).

4.3.6 Zooplankton

Zooplankton species richness is similarr in open water to the species richness in the control and impact site (Figure 4.14). Water hyacinth removal did not have an impact on zooplankton (Figure 4.14).

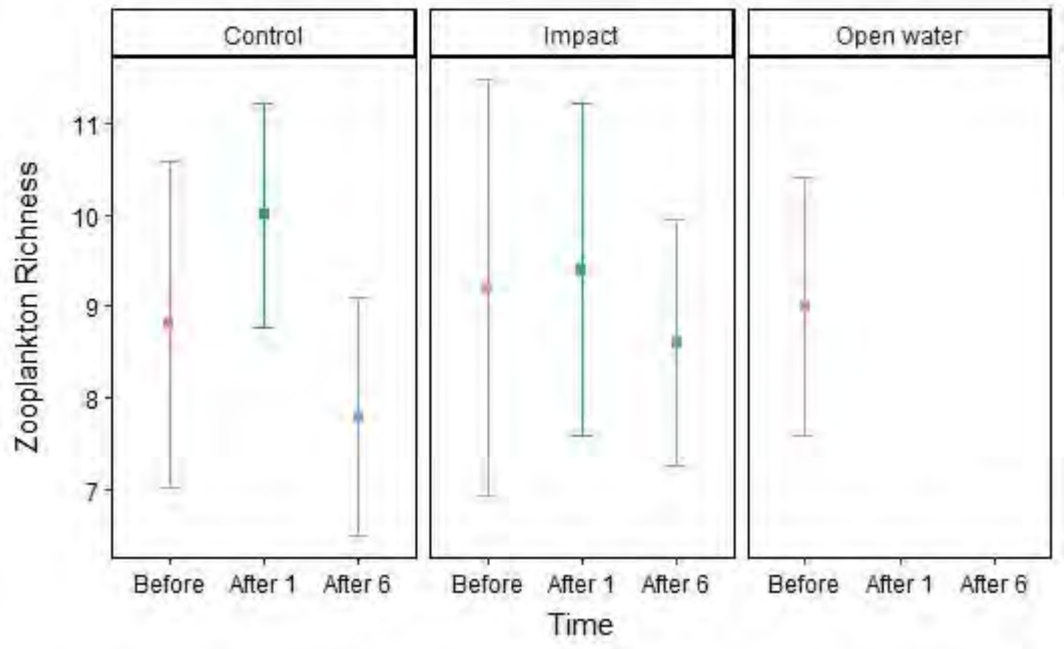

Figure 4.14. Zooplankton species richness comparing biological control (Control) and manual removal (Impact) of water hyacinth with the species richness of an Open water site.

The GLM results were based on the three sites and time (Table 4.15).

Table 4.15. GLM results of zooplankton species richness influenced by the site and time. Bold values represent significant impacts.

Effect	Estimate	Std. Error	z value	*P*
Intercept	2.17475	0.15076	14.426	**<2e-16**
Impact	0.04445	0.21087	0.211	0.833
Open Water	0.02247	0.21201	0.106	0.916
After 1	0.12783	0.20671	0.618	0.536
After 6	-0.12063	0.21993	-0.548	0.583
Impact:After1	-0.10633	0.29282	-0.363	0.717
Impact:After6	0.05319	0.30555	0.174	0.862

None of the sites and time points had significant differences or impact on zooplankton species richness (*P*>0.1) (Table 4.15).

Table 4.16. ANOVA results for zooplankton species richness. Bold values represent significant effects.

Effect	**LR Chisq**	**df**	*P*
Site	3.4799	1	**0.0621203**
Time	8.9205	2	**0.0115595**
Site: Time	26.043	2	**2.21E-06**

The interaction between time and site had a significant effect on zooplankton richness (*P*<0.001) (Table 4.16). Time had a marginally significant impact on zooplankton species richness (*P*=0.01) (Table 4.16).

Zooplankton species evenness gradually increased in both the impact and the control sites (Figure 4.15). The zooplankton species evenness was higher before water hyacinth removal at the Open water site (Figure 4.15).

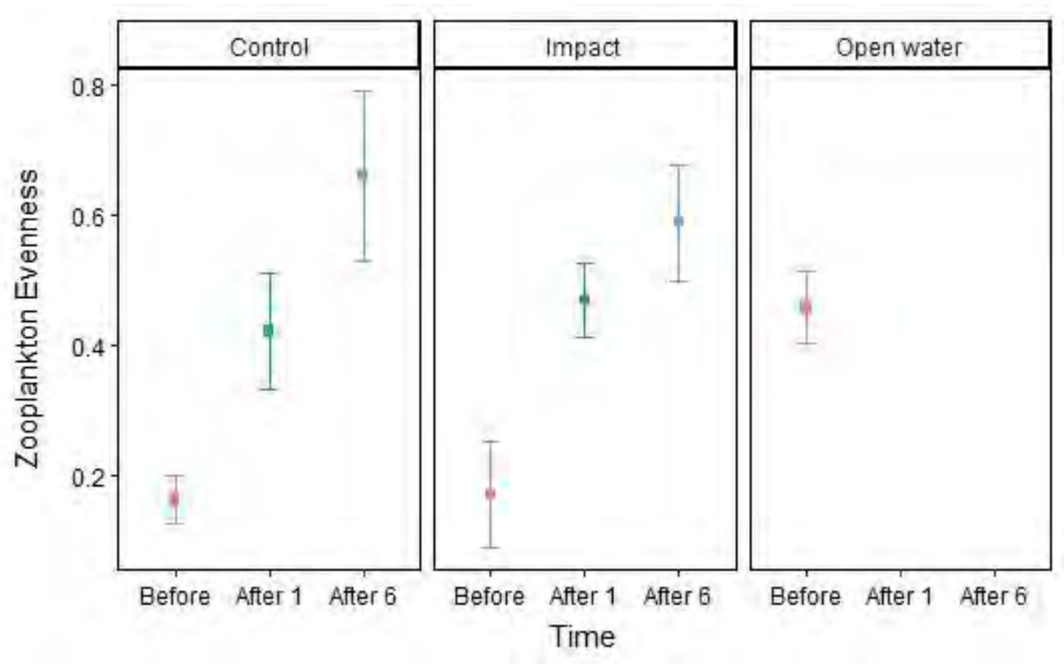

Figure 4.15. Zooplankton species evenness comparing biological control (Control) and manual removal (Impact) of water hyacinth with the species richness of an Open water site.

Table 4.17. GLM results of zooplankton species evenness influenced by the site and time. Bold values represent significant impacts.

Effect	Estimate	Std. Error	t value	*P*
Intercept	0.162316	0.036714	4.421	**0.000135**
Impact	0.008078	0.051922	0.156	0.877480
Open Water	0.295785	0.051922	5.697	**4.15e-06**
After 1	0.259046	0.051922	4.989	**2.86e-05**
After 6	0.497212	0.051922	9.576	**2.48e-10**
Impact: After1	0.038947	0.073429	0.530	0.600016
Impact: After6	-0.079640	0.073429	-1.085	0.287353

The open water has a higher species evenness than the control and the impact sites (Table 4.17). Time one week after the water hyacinth removal and time 6 weeks after removal has a highly significant (*P*<0.001) impact on zooplankton species evenness (Table 4.17).

Table 4.18. ANOVA results for zooplankton species evenness. Bold values represent significant effects.

Effect	**LR Chisq**	**df**	*P*
Site	42.13	2	**7.11E-10**
Time	157.66	2	**< 2.2e-16**
Site: Time	2.711	2	0.2579

There were highly significant differences among the sites (control, impact, open water) (*P*<0.001) over the time points (before, after 1, after6) (*P*<0.001) (Table 4.18). However, the interaction between the two effects, site and time was not significant (*P*=0.2579) (Table 4.18).

The zooplankton Shannon diversity increased gradually for both the control and impact sites (Figure 4.16). Only the before removal reading was done for the open water site (Figure 4.16).

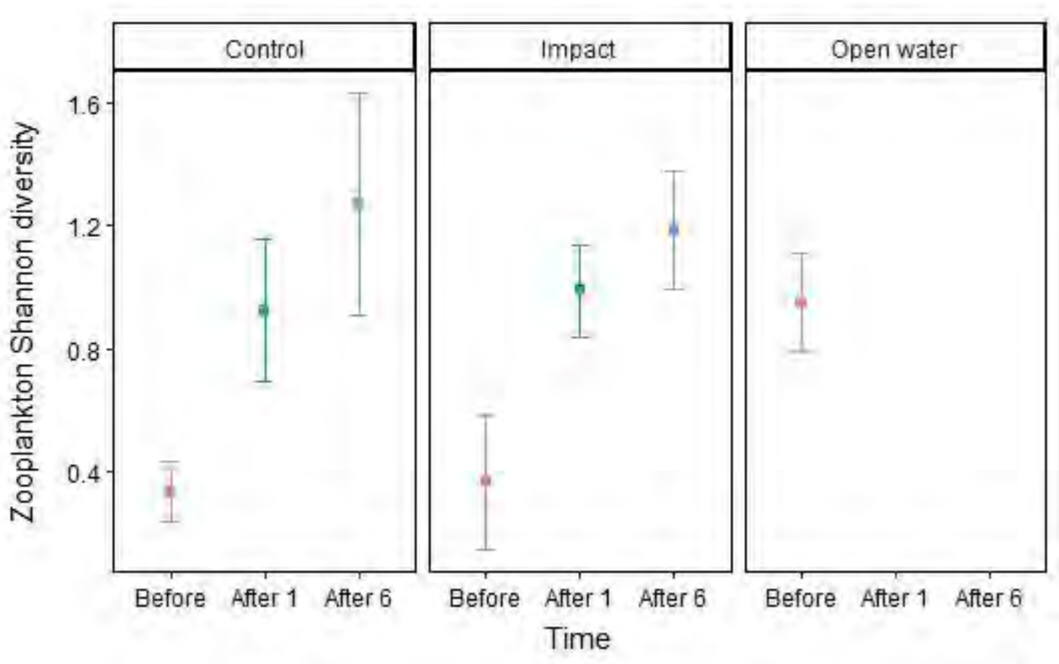

Figure 4.16. Zooplankton Shannon Diversity Index comparing biological control (Control) and manual removal (Impact) of water hyacinth with the Shannon Diversity of an Open water site.

The GLM results are based on site (Open water, control, impact) and time (before, after 1, after 6) (Table 4.19).

Table 4.19. GLM results of zooplankton Shannon Diversity Index influenced by the site and time. Bold values represent significant impacts.

Effect	Estimate	Std. Error	t value	*P*
Intercept	0.33266	0.09613	3.460	**0.001747**
Impact	0.03087	0.13595	0.227	0.822043
Open Water	0.61648	0.13595	4.535	**9.89e-05**
After 1	0.59227	0.13595	4.356	**0.000161**
After 6	0.93745	0.13595	6.895	**1.71e-07**
Impact:After1	0.03187	0.19227	0.166	0.869517
Impact:After6	-0.11521	0.19227	-0.599	0.553856

The Open water site had a significantly higher zooplankton Shannon diversity that the control and the impact sites (P<0.001). Time one week after and 6 weeks after water hyacinth removal had a highly significant effect on zooplankton Shannon diversity (*P*<0.001). However, the interactions between site and time did not have a significant effect on Shannon diversity (Table 4.19).

Table 4.20. ANOVA results for zooplankton Shannon Diversity Index. Bold values represent significant effects.

Effect	**LR Chisq**	**df**	*P*
Site	26.062	2	**2.19E-06**
Time	87.853	2	< **2.2e-16**
Site:Time	0.648	2	0.7233

There were highly significant differences between the sites (control, impact, open water) (*P*<0.001) over the time points (before, after 1, after 6) (*P*<0.001) (Table 4.20). However, the interaction between the two effects, site and time was not significant *(P*=0.7233) (Table 4.20).

4.3.7 Biogeochemistry

Dissolved oxygen levels were lower under the water hyacinth mats than in the 'Open Water' (Figure 4.17, Appendix Table S5). The control and impact sites had similar DO levels throughout the sampling period with a slight difference after the removal on water hyacinth in the impact site. The DO levels underneath the water hyacinth mat were almost half of those in "Open water" before the removal of the macrophytes (Figure 4.20, Appendix Table S5). The control and impact sites had identical DO levels during the removal process. The DO levels increased with increasing temperature after the removal of water hyacinth (F=141.99, df=1, P<0.0001). Time (F= 236.30, df=2, P<0.0001) and site (F=58.71, df=2, P<0.0001) also had a significant impact on the DO within the water column.

The mean DO levels in the Control site before weed removal were 0.73±0.54 mg/L, and 5.67±3.00 mg/L after the removal, which was in a similar range as the 'Impact' site of 0.74±0.56 mg/L before removal, and 5.97±3.36 mg/L after removal. For the open water, DO was 4.90±1.70 mg/L before removal and, 8.01±2.43 mg/L after removal (Appendix Table S5).

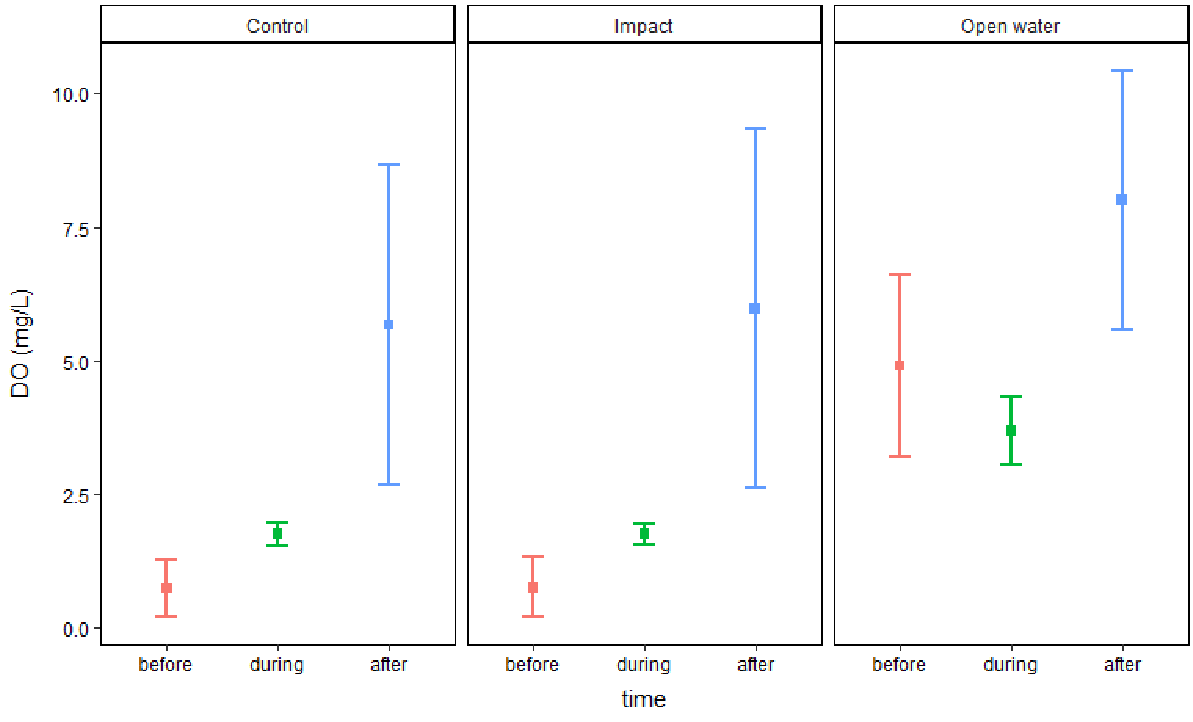

Figure 4.17. Dissolved Oxygen (DO) concentration (Mean ±SD) in the water column at the three different sites on Hartbeespoort Dam.

The average pH in the control site was alkaline when sampling was initiated (Figure 4.18, Appendix Table S5). It became neutral during the removal process in the area adjacent to it, then returned to an even higher alkaline state. The pH increased to an alkaline state after plant removal whether by physical removal, in the impact site or by insect herbivory, in the control site . The pH in the ‘Open water’ remained in the neutral range (Figure 4.18).

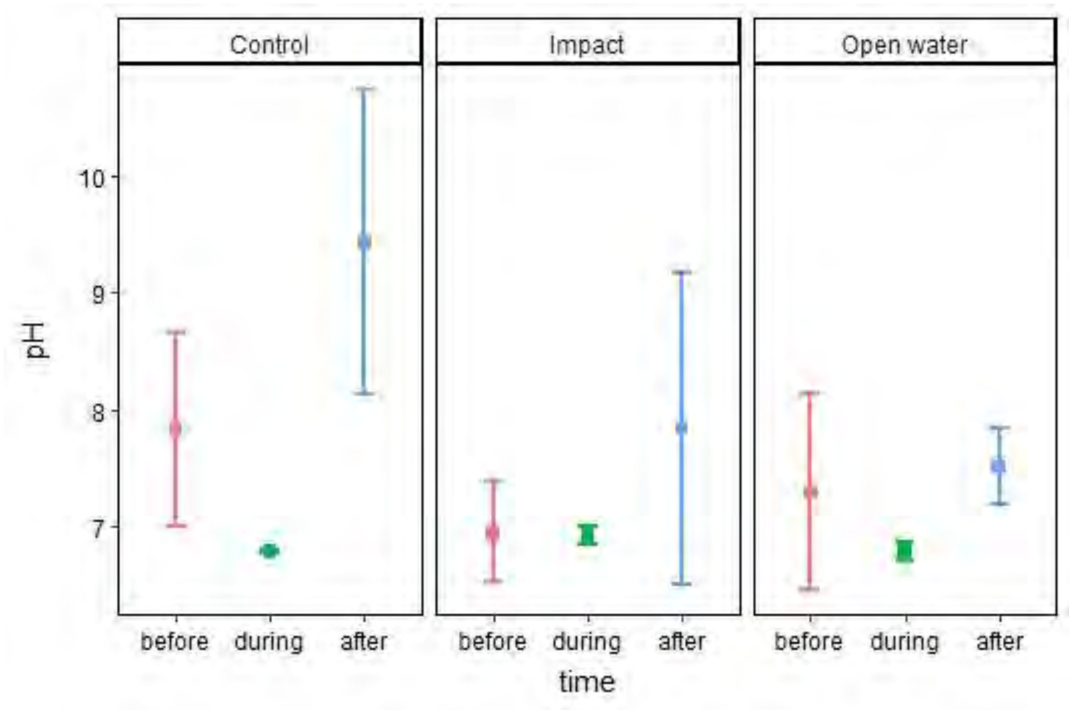

Figure 4.18. Water pH (Mean ± SD) in the different sites on the Hartbeespoort Dam.

All sites had a reduction in Conductivity following the removal (Figure 4.19, Appendix Table S5). Conductivity trends were similar across all three sites.

There was a slight difference in water temperature between all the sites, ranging from 25.5°C–26.5°C (Figure 4.20, Appendix Table S5).

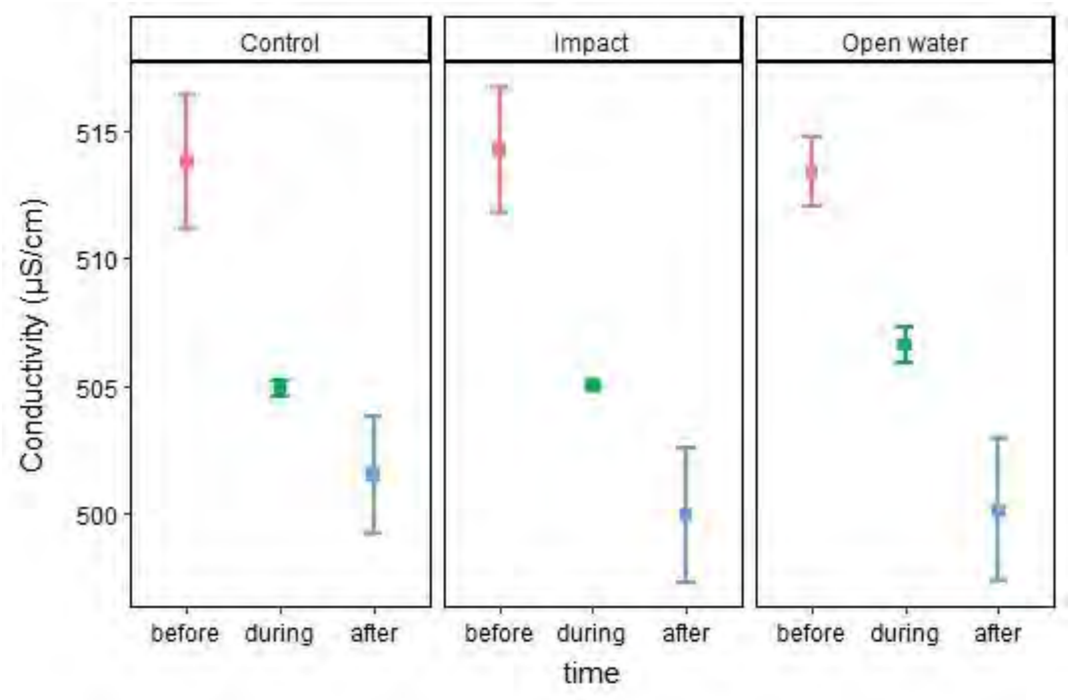

Figure 4.19. Conductivity (Mean ± SD as error bars) at the three sites on Hartbeespoort Dam.

The mean temperature levels in the Control site before weed removal were 26.40±0.56 °C, and 26.06±0.82 °C after weed removal; for the 'Impact' site 26.34±0.43 °C before macrophyte removal, and 26.27±0.91 °C after macrophyte removal. For the 'Open Water' site, temperature measured 26.55±0.40 °C and 26.01±0.85 °C after removal (Appendix Table S5).

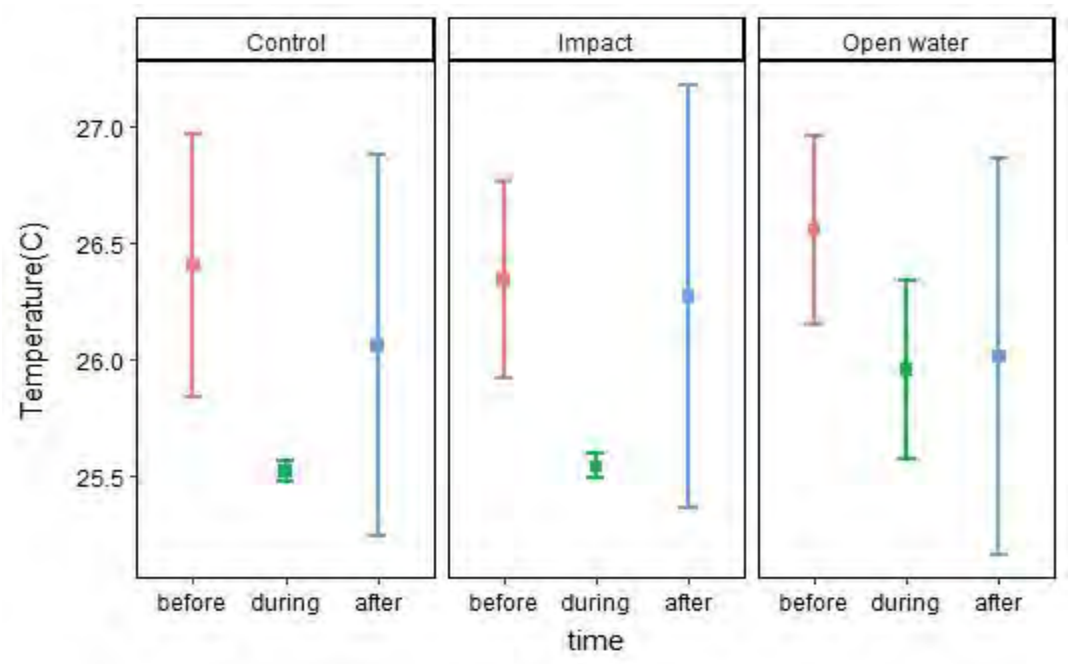

Figure 4.20. Water temperature (°C) (Mean ± SD) at the three sites on Hartbeespoort Dam.

The DO levels in the impact and control sites increased significantly after the removal of water hyacinth. Both the impact and control sites had similar temperature trends across the three sampling points (Figure 4.21). The depth of the site did not impact the DO levels within the water column.

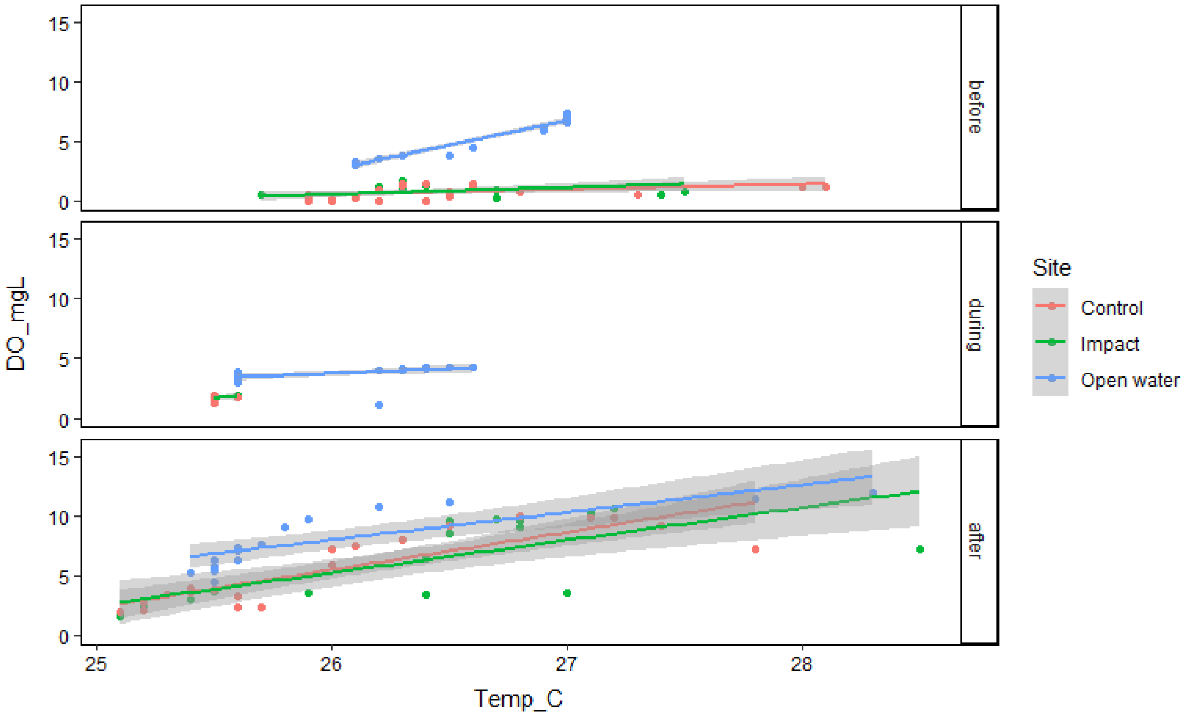

Figure 4.21. The impact of temperature on the Dissolved Oxygen (DO) in the water column.

Table 4.21. Water chemistry data (Mean ± SD) for the three different sites on Hartbeespoort Dam

Site	Time	Seston_DW_mg_L	TP_µmol L-1	NH4_µmolL	NO3_µmolL	NO2_µmolL	TOC_µmolL	SRP_µmolL
Control	Before	6.77±4.20	18.73±13.20	74.2±2.29	80.24±10.06	20.51±1.05	845±520.17	21.75±1.01
Control	During	9.84±6.46	34.87±5.78	29.53±1.23	129.09±9.13	27.04±1.44	631.67±66.51	20.19±0.53
Control	After	55.49±90.16	22.60±7.57	5.08±3.18	184.78±7.39	9.95±3.33	1343.17±1052.68	16.00±0.59
Impact	Before	70.46±90.05	27.12±11.09	72.6±1.92	67.55±8.06	18.77±2.29	1218.33±1048.67	21.74±0.62
Impact	During	5.50±0.41	33.58±5.40	51.85±4.70	140.84±6.93	31.75±1.38	593.33±13.69	18.02±0.24
Impact	After	73.82±109.72	20.18±4.84	31.05±59.26	152.48±70.73	9.44±5.26	5850±10752.40	13.77±3.64
Open Water	Before	1.70±0.47	27.12±9.02	112.65±5.08	110.62±16.48	14.27±0.68	688.33±272.63	19.79±1.16
Open Water	During	9±11.38	31.97±11.54	48.61±11.31	135.44±4.58	28.36±0.75	566.67±23.90	19.23±0.30
Open Water	After	10.42±2.23	35.52±11.42	6.48±2.94	198.97±1.77	12.95±0.49	628.33±29.81	16.84±0.14

Seston weight was lowest in the 'Open water' and increased significantly in the control site after the removal (Table 4.21). The TP was highest in the 'Open water'. Ammonia concentrations were similar in the control and impact site before the removal; following that, there was a drastic drop in the average concentration of ammonia in the control site and 'Open water' after removal. The TOC (Total Organic Carbon) was highest in the impact area after the removal of water hyacinth (Table 4.21). Time (F=1.72, df=2, *P*= 0.19; F=1.35, df=2, *P*=0. 28), site (F=1.06, df=1, *P*= 0.31; F=1.01, df=1, *P*=0.32), and depth (F=0.23, df=1, *P*= 0.63; F=1.02, df=1, *P*=0.32), did not impact the Seston weight, nor did they significantly impact the TOC in the water column**.**

4.3.5 Sedimentation

Table 4.22. Sedimentation chemistry (Mean ± SD) at the control and impact sites

Site	Time	Sedimentation_DW_g_m2_h	1_DW_g_m2_h	1_N_mg_m2_h	1_C_mg_m2_h	2_DW_g_m2_h	2_N_mg_m2_h	2_C_mg_m2_h	ml HPLC
Control	Before	2.74±1.35	2.65±1.10	0.07±0.05	0.53±0.43	2.83±1.61	0.07±0.05	0.55±0.44	9.25±3.86
Control	During	3.82±2.37	4.00±2.38	0.10±0.07	0.81±0.59	3.64±2.43	0.20±0.20	1.78±1.98	10±0
Control	After	3.75±3.37	4.27±4.13	0.14±0.08	1.30±0.80	3.23±2.63	0.12±0.09	1.01±0.86	13.5±1.73
Impact	Before	2.631±0.66	2.44±0.40	0.22±0	1.85±0	2.82±0.94	0.11±0.03	0.84±0.30	8.38±3.90
Impact	During	6.22±3.12	5.10±2.57	0.09±0.01	0.73±0.11	7.33±3.70	0.25±0.11	2.45±1.22	9.25±2.99
Impact	After	4.22±0.65	4.40±1.23	0.18±0.11	1.54±1.01	4.05±0.25	0.26±0.12	2.24±1.41	13.25±2.06

The sedimentation weight was similar for the two sites before the removal and comparable at various sampling points (Table 4.22). The control site and impact sites were comparable for the different time points for nitrogen, carbon content and dry weight.

4.3.6 Carbon Fluxes

Both time (F=6.41, df=1, *P*<0.05) and site (F=5.69, df=1, *P*<0.05) led to a significant increase of the total methane released from the system following the removal on water hyacinth (Figure 4.22). Methane released through ebullition remained at a constant 0.025g/m^2/d under the water hyacinth mat at the control and impact site; however, following the removal of water hyacinth, the amount of methane released more than doubled in the impact site (Figure 4.22).

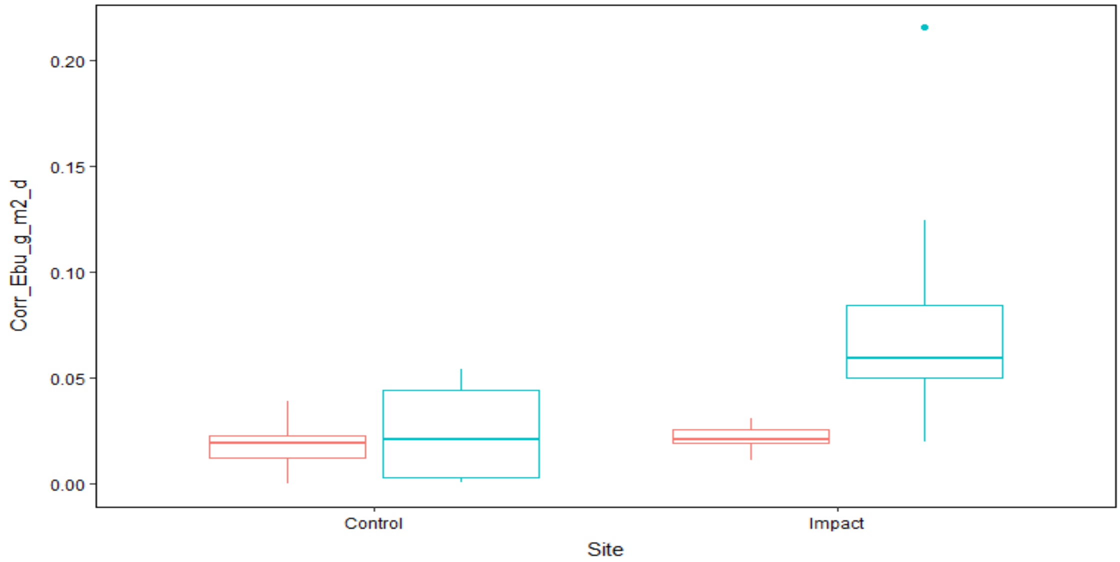

Figure 4.22. Carbon daily fluxes at the control and impact sites. Red represents readings before and the green represents those after removal of water hyacinth.

The percentage of carbon lost through diffusion has a negative relationship with an increase in daily methane released from the system (Figure 4.23).

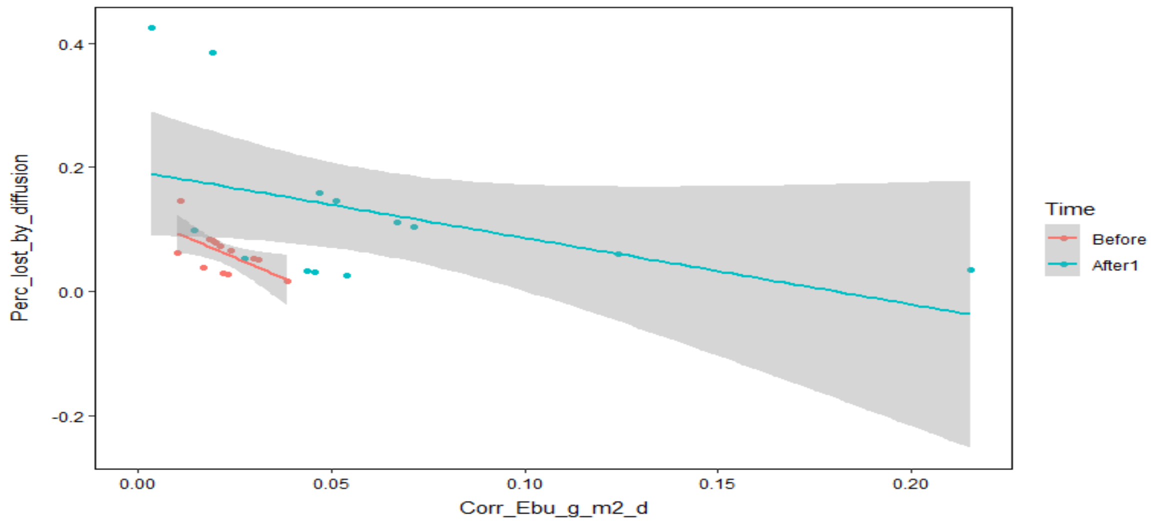

Figure 4.23. Percentage carbon lost through diffusion at the control and impact site.

4.4 Discussion

Dams, reservoirs and diversions increase water residence time, slowing river flow and creating shallow, clear permanent water system that creates the perfect conditions for plant species that evolve under such conditions such as free floating macrophytes in the Amazon (Schneider *et al*., 2024). In South Africa, impoundments have been constructed on the majority of river systems to meet its water supply needs as a water scarce country (Chikodza *et al*., 2025). Pollution has however caused most of these impoundments to be eutrophic. This state of eutrophication allows for the proliferation of invasive macrophytes in these altered aquatic ecosystems (Chikodza *et al*., 2025). The public and water users see the mass development of IAPs as a nuisance, this results in the macrophyte removal by mechanical (physical), chemical and biological methods (Schneider *et al*., 2024). These have become common practice for the management of the mass development of aquatic plants in rivers, streams, lakes and reservoirs with physical removal often being the preferred method when an initial infestation by a macrophyte occurs (Misteli *et al*., 2023; Schneider *et al*., 2024). Schneider *et al*. (2024) study partially supported the perception by water users that the mass development has a adverse impact on the biodiversity of the colonized waterbody. Water managers now have to consider the effect the plant removal has on biodiversity, as macrophytes stands also perform ecosystem services that contribute to water clarity (Misteli *et al*., 2023).

This study compared the impact manual removal of water hyacinth, *Pontederia crassipes* and its biological control on the aquatic ecosystem and its impact on biodiversity. This study found that the manual removal of water hyacinth, *P. crassipes*, on the impact site at Hartbeespoort Dam led to a proliferation of phytoplankton and algae which led to turbid water conditions in the impact site. The complete eradication of water hyacinth from a heavily colonized aquatic ecosystem has been noted to have undesirable short-term and long-term consequences, such as cyanobacteria bloom and the potential disappearance of some fish species in Kenya, Mexico and Brazil (Djihouessi *et al*., 2023).

A year after the manual removal of water hyacinth from the Impact site (2021), water hyacinth was back as the dominant species at pre-removal levels, whereas in the Control site, water hyacinth had lost its competitiveness, with the native *Persicaria senegalensis* being the dominant species. The Control site used biological control to manage and control the weed, which is widely considered an optimistic, sustainable approach to controlling water hyacinth as this method has the potential to decrease the invasive plant's competitive advantages over native plants (Ilo *et al*., 2020). Although Ilo *et al*., (2020) argued that there was a lack of evidence of this potential, the findings of this study demonstrated that recovery of native species as a consequence of using biological control as a management option is possible. Carson *et al*. (2008) held the view that successful biocontrol programmes would be those where invasive plant populations are depressed long enough to permit the re-establishment of native plant communities. The suite of water hyacinth biological control agents that were present on Hartbeespoort Dam are the *Neochetina* spp. weevils, *N. eichhorniae* and *N. bruchi,* the mite, *O. terebrantis,* the mirid, *E. catarensis,* the moth *N. albiguttalis* in combination with the recently introduced *M. scutellaris* – managed to reduce the overall water hyacinth coverage on Hartbeespoort Dam to under 7% during the summer of 2019/2020. Biological control of water hyacinth in the Control site resulted in a more diverse macrophyte coverage. Swe *et al* (2021) noted that a high diversity of macrophytes play a role in preventing a state shift towards phytoplankton dominance, which will maintain the benefit of water clarity for humans. A few months after the control of *P. crassipes* by biological control facilitated the proliferation of *Salvinia minima,* as secondary invasion of the Dam occurred. *Salvinia minima* thrives in slightly acidic, high nutrient, slow-moving freshwater. It is also resistant to periods of low temperatures, water stress and elevated pH levels (Olguin *et al*., 2002). Illustrating the findings by Shen *et al*. (2023) that subdominant invaders may respond more quickly and receive the most benefit than native species, therefore the suppression of the target plant by biological control often results in a community dominated by other invaders (Shen *et al*., 2023).

The electrofishing studies showed an increase in species diversity following the physical removal of *Pontederia crassipes* in the Impact site. The results obtained were compared to previous studies on the diversity of fish in Hartbeespoort Dam; the dominant species, *Gambusia affinis*, in the impact site was not noted as being present in the Dam in three previous studies. *Gambusia affinis*, mosquitofish, is an alien invasive species that has established across freshwater ecosystems in South Africa (Howell *et al*., 2013) and was introduced to South Africa in 1936 as a control measure for mosquitoes (Howell *et al*., 2013).

Macroinvertebrates associated with the roots drastically diminish a week after physical removal but under biological control the macroinvertebrate gradually reduced. Misteli *et al*. (2023) observed a 50% decrease in macroinvertebrate abundance and richness a week after water hyacinth removal but no impact was observed 6 weeks after the removal, indicating a system recovery. Macroinvertebrates associated with the sediment was not impacted by plant removal (Misteli *et al*., 2023).

The removal of water hyacinth in the Impact site led to an increased amount of periphyton 20cm under the water surface where the roots of the dense water hyacinth mats are found. The increased periphyton formation also contributed to an increase in the phosphorus, nitrogen and carbon content of the periphyton which is a proxy for the water nutrient status. The high nutrient status of the water column after water hyacinth removal facilitates the proliferation of phytoplankton, cyanobacteria and algae that are directly in competition with the macrophytes for nutrients and light availability. Phytoplankton was positively impacted by plant removal, with the impact evident one week after removal, continuing to 6 weeks after removal (Misteli *et al*., 2023). Misteli *et al*. (2023) found a significant increase of proportions of cyanobacteria at Hartbeespoort Dam with an increase of 45% one week after removal and 70% increase six weeks after removal. For zooplankton which usually avoids macrophyte stands there was higher Shannon diversity in the 'Open water' site than in the control and impact site. The Shannon diversity increased in the control site as the water hyacinth was cleared by biological control. Water hyacinth removal however did not have a significant effect on zooplankton as stated by Misteli *et al*. (2023).

The physiochemical attributes of the water column at the three sites – Control, Impact and 'Open water' – had similar values for temperature and conductivity across the different sampling points. The pH at the control site became more alkaline with time, whereas the impact site and 'Open water' remained in the neutral range. The removal of the plant strongly altered the water chemistry (Misteli *et al*., 2023).

The biggest benefit of the removal of macrophytes in the physiochemical profile was the increase in DO in the water column following their removal; this finding is supported by literature where the presence of dense water hyacinth mats has a negative relationship with DO, sometimes resulting in anoxic conditions under the dense stand. Grodowitz *et al.*, (2017) noted that water hyacinth coverage not only reduces light penetration to algae and submerged plants, but it also reduces the dissolved oxygen levels and the pH, ultimately leading to altered native species diversity. Lakane *et al*. (2024) noted a decrease in dissolved oxygen levels in the water column with increased water hyacinth cover. In line with several other studies, Romens et al. (2003), Mangas-Ramirez and Elias-Gutierrez (2004) and Wang et al. (2013) also showed that oxygen levels reduced as water hyacinth coverage increased (Lakane *et al*., 2024). The reduction in dissolved oxygen in turn affects biodiversity and leads to a reduction in phytoplankton production, and decreases in the abundance and diversity of zooplankton, invertebrates, and fish (Lakane *et al*., 2024).

The TOC increased significantly at the Impact site following the removal of water hyacinth. More methane was released from the system when the water hyacinth was removed, as observed in the Impact side. The presence of the macrophyte in this case would ensure a reduction in methane released from the aquatic ecosystem. The mats also prevent oxygen diffusion between the air and the water (Lakane *et al*., 2024).

Although the presence of water hyacinth is a nuisance to water managers and users, there are ecosystem services such as water clarity that is attained when there are dense mats in parts of the Dam; however, aesthetically, dense mats are undesirable. In the case of Hartbeespoort Dam, where there is a biological control programme integrated with the manual or mechanical removal, it would be beneficial for biodiversity and water quality to avoid removing the entire water hyacinth stand. From April to October 2022 water hyacinth had lost its competitiveness as the dominant macrophyte across the Dam, and *Salvinia minima,* which previously accounted for less than 1% coverage of the on the Control and Impact sites, now accounts for 80% of the macrophyte cover over the Dam in cooler months. This follows the subsequent reintroductions of the *M. scutellaris* to the system over the warmer months leading to a reduction in water hyacinth coverage.

4.5 Conclusion

Although the presence of invasive monoculture macrophytes is detrimental and alters the biodiversity of the infested site, the macrophytes still render ecosystem services, the important one being the clear water state and preventing the proliferation of algae. In managing water hyacinth, biological control proved to be more beneficial than physical removal as it allowed for the recovery of native macrophytes and a more diverse macrophyte coverage a year after study. The objectives of management programmes have shifted from direct and short-term human benefits to more comprehensive goals (Djihouessi *et al*., 2023). For instance, earlier programmes targeted improvement of aesthetics and economic status, while recent programmes target environmental and ecological status (bottom-up control) and system recovery for ecological good status of the aquatic ecosystem (Djihouessi *et al*., 2023). The eradication of water hyacinth, however, does not guarantee the restoration of ecosystem services, function and structure (Djihouessi *et al*., 2023).

Chapter 5: Socioeconomic Responses to the Infestation for Water hyacinth on Hartbeespoort Dam

5.1 Introduction

Pontederia crassipes infestations constitute a threat to biodiversity, ecosystem functionality and socio-economic growth (Ilo *et al*., 2020), and these infestations considerably reduce the aesthetic value of waterfront communities (Voukeng *et al*., 2019). The concept of water hyacinth management originates from the need for decision makers and communities to reduce the aesthetic and economic burdens caused by the plant's invasion (Djihouessi *et al*., 2023).

Since the 1970s, water hyacinth control programmes focussed on the use of herbicides, with biological control and integrated control programmes receiving less effort and investment (van Wyk & van Wilgen, 2002). Herbicidal control offers fast management programmes with control being achieved within six weeks, however, it does not offer a long-term solution (Van Wyk & van Wilgen, 2002). Ongoing applications of herbicides are essential to achieve control, and a lapse in management aspects will result in rapid reinfestations of water bodies (Van Wyk & van Wilgen, 2002).

South Africa's Department of Water Affairs and Forestry (DWAF) spent R10-15 million on aquatic weed control from 1986 to 1999, with R6 Million of that being used for herbicide applications alone (Van Wyk & van Wilgen, 2002). A further R791,67 million ($45.3 million) was spent by the Department of Forestry, Fisheries and the Environment on herbicide control of *P. crassipes* in South Africa between 2010 and 2018 (Lakane *et al*., 2024).

Hartbeespoort Dam is a nature-based tourism destination offering hiking trails and water activities. The viability of nature-based tourism is directly dependent upon the environment as a resource, therefore, in order for nature-based tourism to thrive, the natural environment needs to be pristine (Long, 2013). A water hyacinth infestation greatly hinders recreational activities, such as sunset cruises, boating and fishing, leading to a decline in revenue for water-based activity businesses and making control of water hyacinth urgent for recreational areas (Mokoena *et al*., 2017; Khatri *et al*., 2018). According to unpublished Department of Water Affairs and Forestry records, water hyacinth was first noted on Hartbeespoort Dam in 1959 (Van Wyk & van Wilgen, 2002). By 1977 approximately 60% of the water surface of the Dam was covered by the weed (Van Wyk & van Wilgen, 2002). A large-scale herbicidal control exercise was undertaken in 1977/1978, resulting in the reduction of the infestation to about 8% of the original area (Van Wyk & van Wilgen, 2002). Between

1978 and 1985, the control focussed on spot-spraying herbicide from boats and on foot (Van Wyk & van Wilgen, 2002). Hartbeespoort Dam, a large (2000 ha,186 million m^3 capacity) impound has used herbicides to control water hyacinth for 24 years (Van Wyk & van Wilgen, 2002).

The perception of aquatic vegetation being a nuisance is often activity and context-dependent; both these factors contribute to a user's willingness to pay (WTP) for the management of aquatic weeds on their waterbody of interest. (Vermaat *et al*. 2024). Beardmore (2015) found that sightseers were more concerned about shoreline property development, while different types of boaters had different concerns, and anglers were concerned about fishing quality (Vermaat *et al*. 2024). Van Wyk & van Wilgen, (2002) noted that at the time of their study, Hartbeespoort Dam was water hyacinth-free, and a single developer had invested R8 million in these property developments around the Dam with a further envisioned investment of R2.5 billion by the year 2004. Most of the property development around the D consisted of housing complexes, hotels and golf courses (Van Wyk & van Wilgen, 2002). As a tourism destination, the provision of accommodation becomes a pivotal component to ensure that tourism thrives in the area. The property market around Hartbeespoort Dam saw a boom in the years after 2000 when tourists started purchasing second homes. As a result, the area has seen an increase of second homeowners, guesthouses, and lodges (Mokoena *et al*., 2017). A study by Marajavaara (2008) into second-home development in Sweden found that waterbodies such as rivers, lakes and oceans are major attractions for second-home development; thus, Hartbeespoort Dam, with a shoreline of approximately 56 km was a great drawcard for a second home or even holiday accommodation. The rise of internet-based applications, such as AirBNB, enabled second-home owners to get more value out of the second home, with the added benefit of creating permanent jobs as the holiday homes are frequently used by holiday makers (Long, 2013).

Long's (2013) study investigated the impact associated with the degrading state of the Dam on second homes by looking at property values, recreational living characteristics valued by owners, and the attachment of owners to the property. The study also explored the potential knock-on effects, which included the undermining of the second-home tourism which directly impacts the local economy of Hartbeespoort. Mokoena *et al*. (2017) noted that with limitations to water use caused by the infestation, potential property owners were hesitant to make the investment without the guarantee that they would have use of the Dam. Halstead *et al.* (2003), in their study of the impact a *Myriophyllum heterophyllum*, milfoil infestation had on lakefront properties in New Hampshire (US), found that property values on lakes experiencing infestation may be considerably lower than similar properties on non-infested lakes, further highlighting the need to effectively manage the water hyacinth infestation on the Dam.

In South Africa, the Department of Forestry, Fisheries and Environment is responsible for the management of invasive species using funding from the fiscus, which is tax paid by workers and businesses to the South Africa Revenue Services. Encouraging riparian communities around the Dam to make further payments for the management of water hyacinth is, in essence, asking them for a double tax. However, since the moratorium on herbicide use on Hartbeespoort Dam has been in place, The Harties Foundation (NPO), consisting of residents, resorts, businesses and residential estates has made financial contributions for the manual removal of water hyacinth. A study by John *et al*. (2019) on willingness to pay for improved management of water hyacinth in Lake Victoria, Kenya found that willingness to pay was higher for fisherfolks who lived on the shoreline than those from the offshore area. This WTP is driven by a decline in fish catchability as a result of the dense water hyacinth mat formation on the fishing shoreline and docking sites (John *et al*., 2019). John *et al*. (2019) and Ogwang *et al*. (2014) also found that those who perceived water hyacinth as a very serious nuisance were more willing to pay than those who did not. Vermaat *et al*. (2024) found that perception of nuisance and the travel distance to the waterbody had a significant impact on willingness to pay for control. The survey in this section of the thesis undertook to establish the willingness to pay (WTP) for the removal of water hyacinth by different recreational users as related to their perception of the weed as a nuisance.

The aim of this chapter was to determine the perception of residents and visitors to the Hartbeespoort Dam about the presence of water hyacinth. Furthermore, the aim was to establish the willingness to pay for the management of water hyacinth to ensure sustained recreational use and maintaining the pristine state of the Dam, seeing that the main sources of revenue generated around the Dam is from tourism and residential estate development.

5.2 Materials and Methods

A survey was used to get the waterbody users' or people's perceptions on the mass development of macrophytes based on Hartbeespoort Dam (Schneider *et al*., 2024). The survey consisted of 28 questions including the types of activities people did on and around the Dam, and their levels of willingness to pay for the control of water hyacinth. The questionnaire briefly covered questions on the importance attached to the Dam and whether the plant was perceived as a nuisance. A set of socio-economic queries aimed to establish if there were underlying socio-cultural or economic factors that influenced WTP. There was a need to establish if annual income, employment, educational status and activities carried out on the Dam influenced their willingness to pay. The survey furthermore made a distinction between residents and visitors on the assumption that residents would have a higher WTP than visitors. The survey was filled anonymously (Vermaat *et al*. 2024).

The survey was distributed through a QR code in the Kormorant, a local newspaper, email, a Harties Foundation stall at the Village Mall, door-stopping shop owners and workers at The Islands Shopping Centre, and was printed for stakeholders to distribute. A total of 281 surveys were completed by 111 females and 170 males. The survey questions are in Appendix DataS1.

5.3 Results

The results include the socio-demographic characteristics of respondents as well as factors that influence their willingness to pay (WTP) for the management of water hyacinth for both residents and visitors to the area. The total number of respondents for both online and printed surveys were 299, with 204 completing the full survey. About a third (32%) of the respondents did not answer the socio-demographic questions. After the data cleaning, where surveys from respondents who did not answer the socio-demographic questions were excluded as the information would be pivotal for determining the factors that influence WTP, only 281 surveys were used for the statistical analysis.

The majority of the respondents were South African (94%) and British citizens accounted for 2% of the respondents. More males participated in the survey (60.5%) with females making up 39.5% of the respondents. Vermaat *et al*. (unpublished) found that gender had a significant impact on willingness to pay, while an economic analysis of willingness to pay by fisherfolk in Lake Victoria in Kenya found that males had a higher willingness to pay for the management of water hyacinth (John *et al*., 2019).

The ages of the respondents ranged from 19 to 86, with a median age of 48 years (Figure 5.1). Vermaat *et al*. (unpublished) found that age did not have an effect on WTP, while John *et* *al*. (2019) and Van Oijstaeijen (2020) found that age had a negative relationship with willingness to pay.

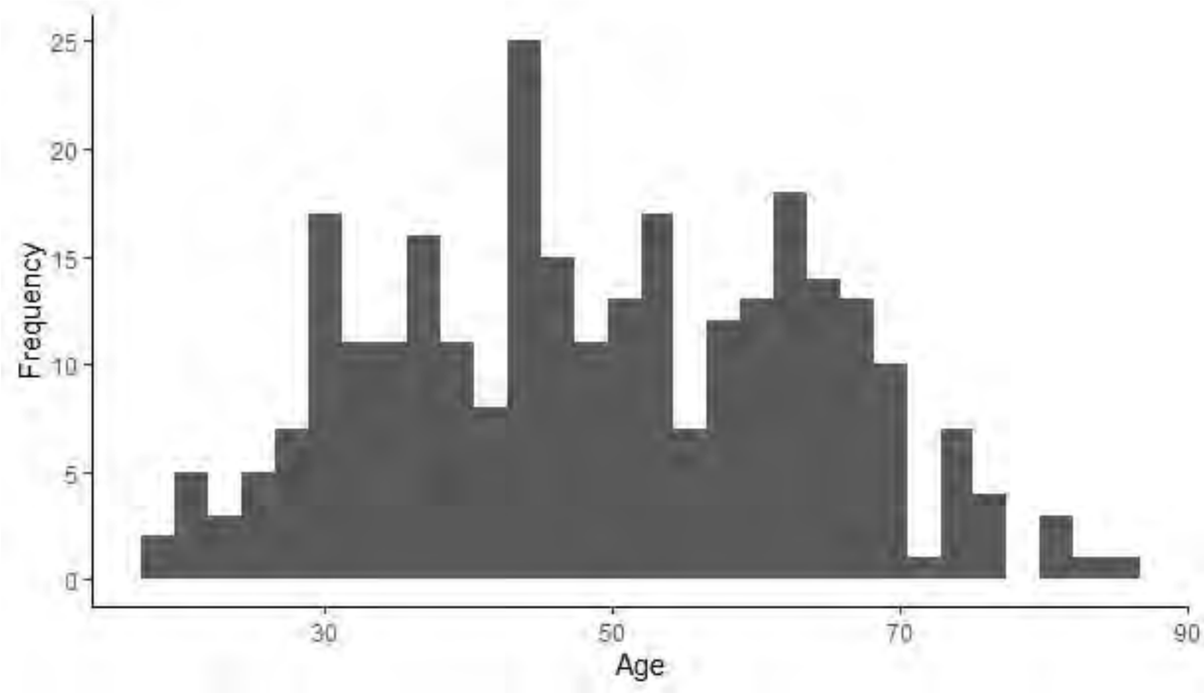

Figure 5.1. Age distribution of survey respondents.

Most residents had a monthly gross salary of between R 40 000 and R60 000, while the majority of visitors had a gross salary of less than R15 000 (Figure 5.2). John *et al*. (2019) found a positive relationship between willingness to pay and a higher income, while Vermaat *et al*. (unpublished) found that gross monthly income was a significant driver for WTP. Long and Hoogendoorn (2013) found that 46% of the property owners in the Hartbeespoort area earned more than one million rands per annum, with 26% of those home owners running their own businesses (Mokoena *et al*., 2017). This is contrary to the findings of this study conducted in 2020, where less than 20% of the residents earned more than one million rands per annum.

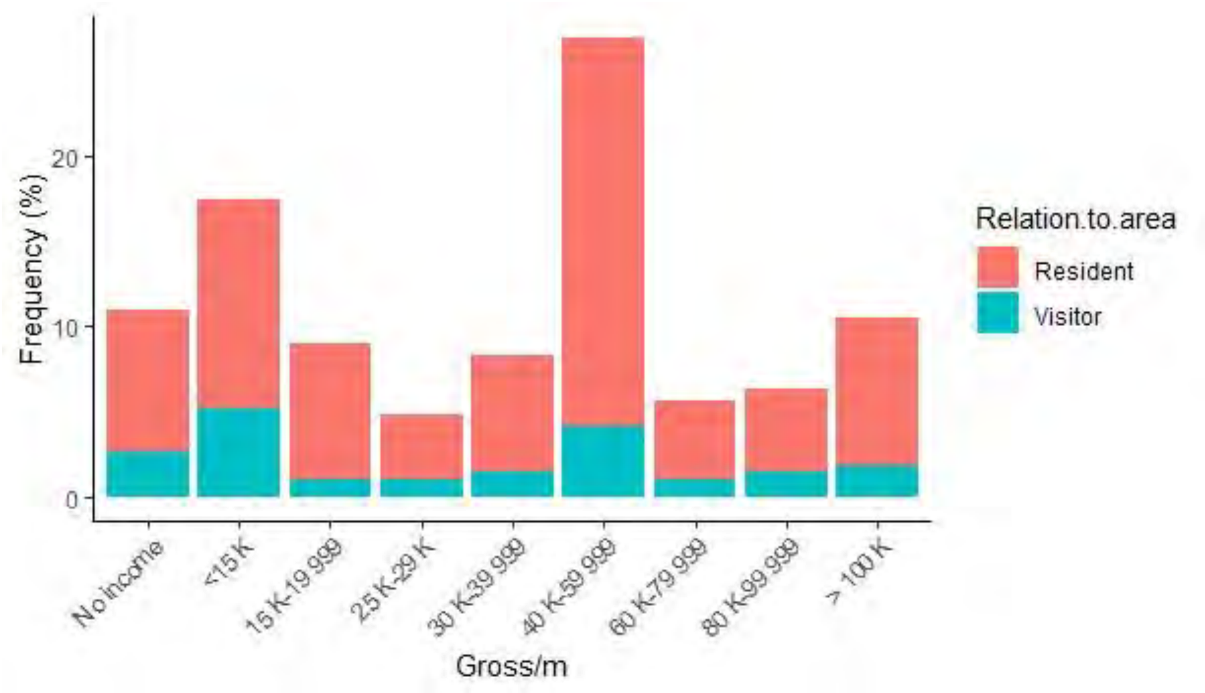

Figure 5.2. Gross income of residents and visitors in the Hartbeespoort Dam area.

Residents accounted for 79.4% of respondents while visitors accounted for 20.6%; however, over 40% of respondents said they had no property in the dam area, 18% had holiday homes in the area and over 30% owned houses and other properties around the dam, with a small percentage living in rentals.

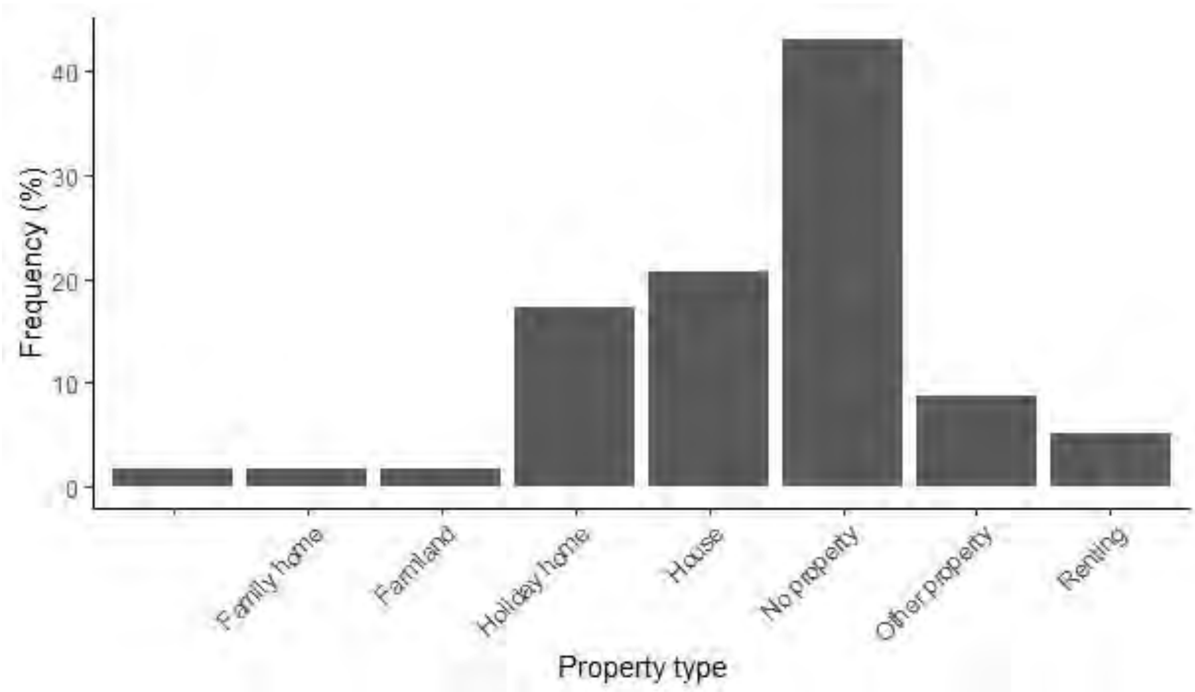

Figure 5.3. Property ownership of the residents around Hartbeespoort Dam.

Over 40% of the respondents took walks and hiked in the Hartbeespoort area (Figure 5.4). Only residents carried out art or display interests in the views around the Dam (Figure 5.4); however, most people in the Dam area spend the highest cumulative hours enjoying the landscape and views (Figure 5.4). A low number of visitors come to the Dam to fish, canoe or sail when compared to residents. While similar numbers of residents and visitors play golf in the area.

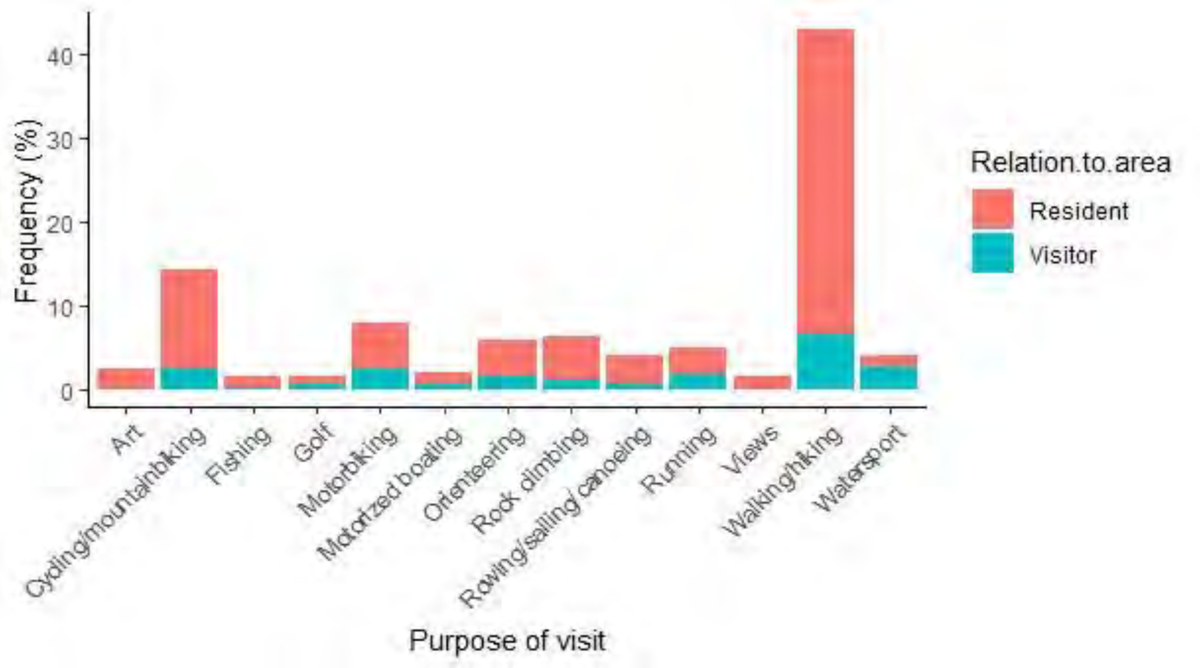

Figure 5.4. Recreational activities done by respondents in the Hartbeespoort Dam area.

Over 5000 cumulative hours are spent by residents managing their properties (Figure 5.5). Visitors are the only group who spend time hunting, while residents dominate the water activities. Water-related activities are not the prominent activities, as expected; visitors spend most of their time walking, hiking and just relaxing around the Dam. None of the groups spent time mountain climbing in the area (Figure 5.5).

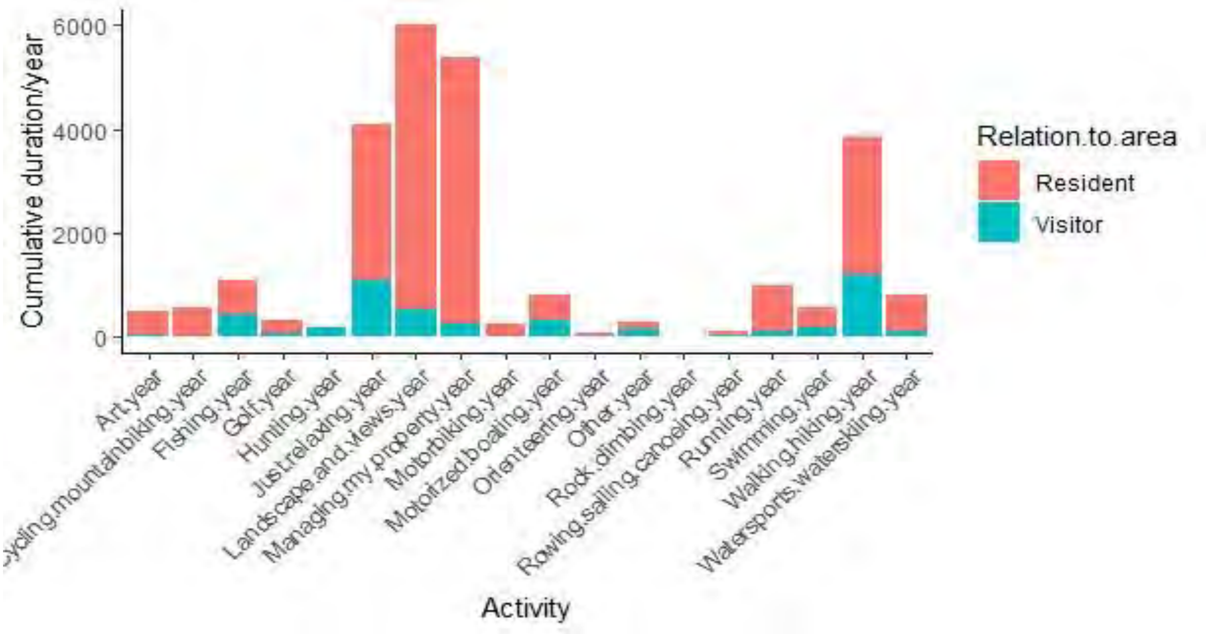

Figure 5.5. Time (cumulative hours) spent on activities around the Hartbeespoort Dam area annually.

Fifty percent of the residents had negative perceptions about water hyacinth, while only visitors were uncertain about whether the presence of the plant was negative or positive (Figure5.6). Twenty-five percent of residents had a neutral perception of water hyacinth, while 20% regarded the weed positively.

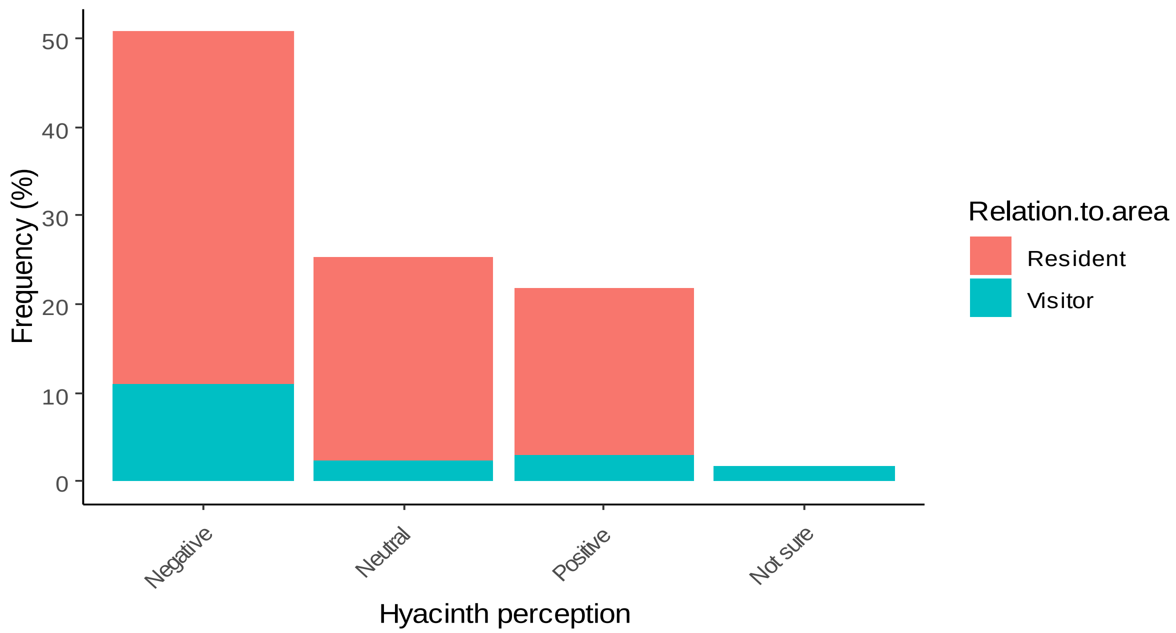

Figure 5.6. Perception of residents and visitors on water hyacinth as a plant.

Residents were concerned about the impact of the water hyacinth plants on biodiversity and the impact on the dam aesthetics (Figure5.7). Since 40% of respondents visit the area for walking and hiking, the aesthetics of the Dam is important, as observed by Vermaat *et al*. (unpublished) who found that those who use the area for running or walking regarded the aesthetic scenery of the area as more important and had a less negative perception of the water weeds than those who use boats.

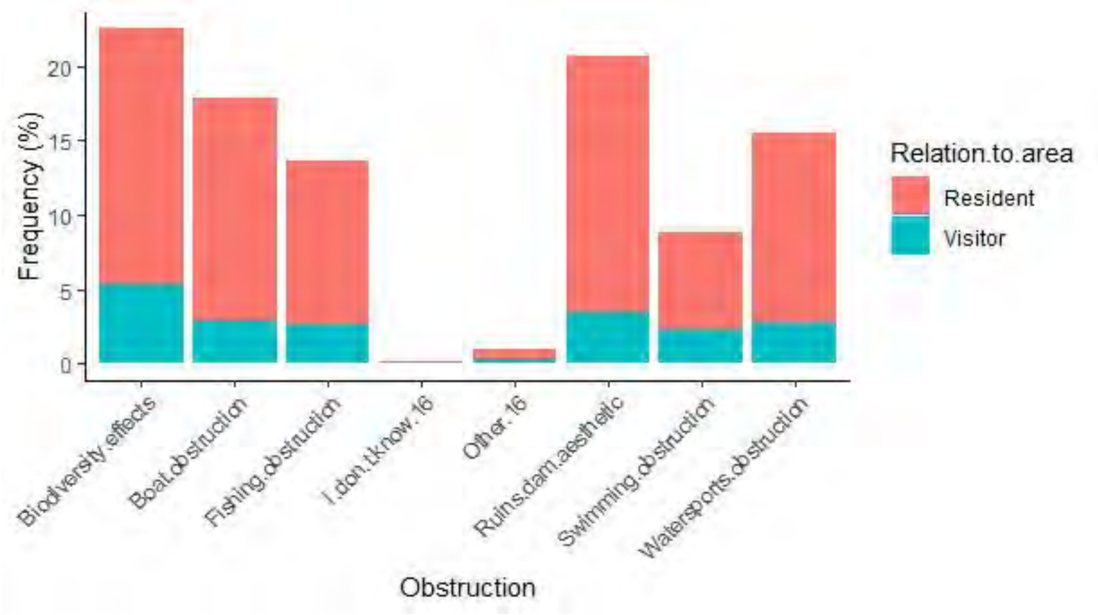

Figure 5.7. Perception of water use restrictions resulting from water hyacinth infestation.

The majority of respondents consider water hyacinth a nuisance at levels 1 to 3 (Figure 5.8 and 5.9); however, at level 5, a small percentage consider coverage along the shoreline as a nuisance (Figure 5.8). This is a positive perception where biological control is used as the control mechanism, as biological control does not eradicate the weed, but reduces it to acceptable levels that do not obstruct or restrict the recreational use of the dam.

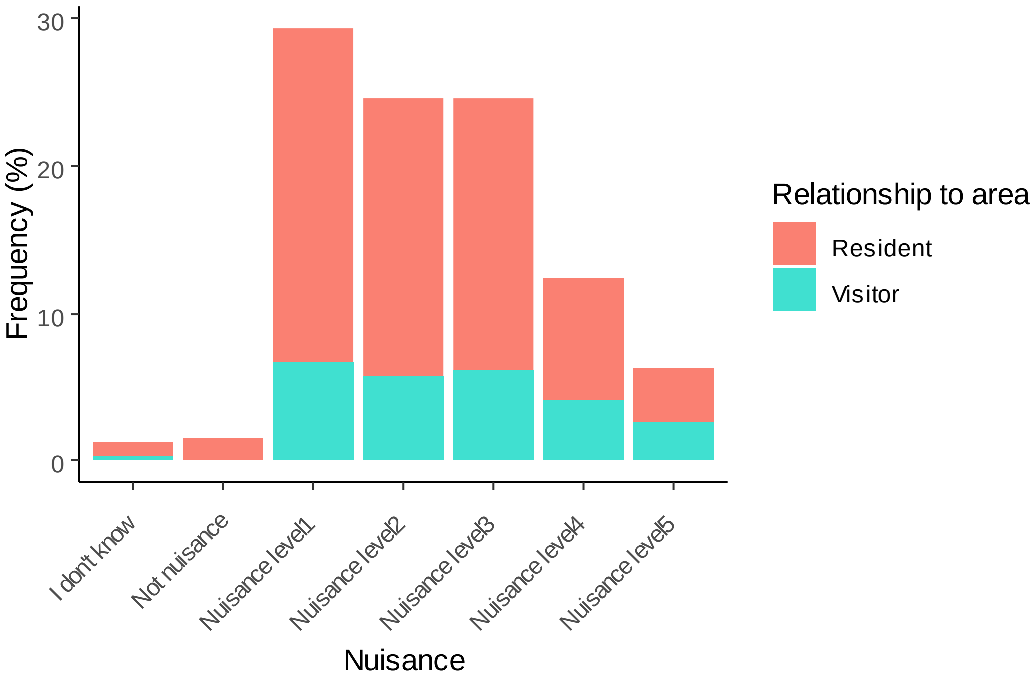

Figure 5.8. Perception of water hyacinth as a nuisance at different levels of coverage of the Hartbeespoort Dam surface**.**

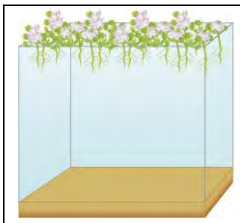	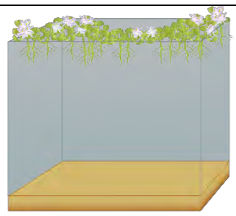	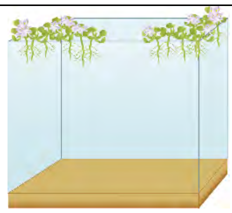		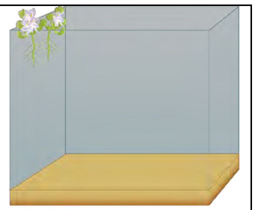
Nuisance level 1	Nuisance level 2	Nuisance level 3	Nuisance level 4	Nuisance level 5

Figure 5. 9. Illustrated nuisance levels depicted in the survey.

The overall WTP of residents (Figure 5.10 A) was lower than that of visitors with over 30% of residents (Figure 5.10A) not willing to make any payment compared to the over 20% of visitors (Figure 5.10B) who are not willing to make a contribution for the management of water hyacinth. Visitors indicated a higher willingness to pay R100 and R250 towards the management of the weed, while similar WTP levels were observed for R500 (Figure 5.10). Visitors were less certain about their willingness to pay for the management of the weed than residents were. Willingness to pay for removal on the part of residents did not increase with the level of clearance, and residents were more inclined to make contributions on behalf of a household rather than individuals (Figure 5.10A). Contrary to this trend, visitors were more inclined to make contributions as individuals (Figure 5.10B). For residents, willingness to pay more than R5000, the highest contribution level as a household levy was t only considered at the lowest level of removal (Level 1) (Figure 5.11), while visitors' willingness to pay more than R1500 was observed only at the highest level of macrophyte removal (Level 4)

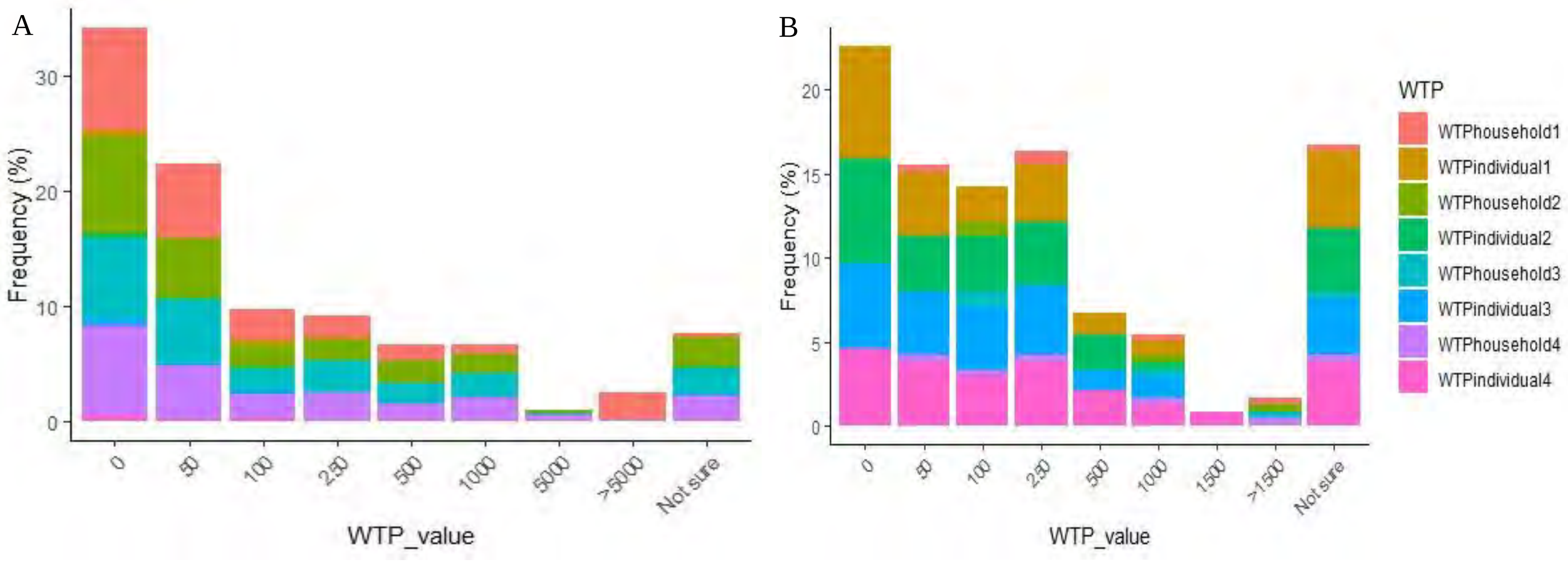

Figure 5.10. Willingness to pay (WTP) for clearing of water hyacinth at different levels for (A) residents of and (B) visitors to Hartbeespoort Dam.

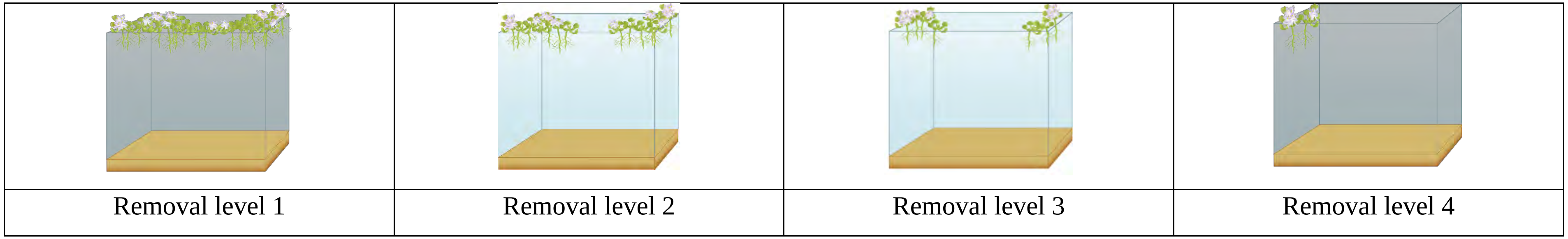

Figure 5.11. Water hyacinth removal levels corresponding to willingness to pay (WTP) by respondents with different values for residents and visitors.

Table 5.1. ANCOVA results illustrating the effects of socio-economic parameters and perception of water hyacinth by residents and visitors on their willingness to pay (WTP) for the management of the weed. The numbers 1-4 indicate the level of removal as illustrated in Figure 5.11. Values in bold indicate significant differences.

	WTP Household 1					WTP Individual 1					WTP Household 2					WTP Individual 2				
Effect	df	Sum Sq	Mean Sq	F value	*P*	df	Sum Sq	Mean Sq	F value	*P*	df	Sum Sq	Mean Sq	F value	*P*	df	Sum Sq	Mean Sq	F value	*P*
Resident	1	2302719	2302719	22,699	**4,58E-06**	1	5 261	5 261	0,16	0,6928	1	3 149 395	3 149 395	7,785	**0,00605**	1	29 242	29 242	2,584	0,122
Gross income	8	2405254	300657	2,964	**0,00423**	8	624 532	78 066	2,375	**0,0499**	8	7 850 316	981 290	2,426	**0,01772**	8	806 947	100 868	8,912	**1,71E-05**
Hyacinth perception	4	273613	68403	0,674	0,61085	4	95 066	23 766	0,723	0,585	4	748 633	187 158	0,463	0,76305	4	33 141	8 285	0,732	0,579
Resident:Gross income	5	4233018	846604	8,345	**5,95E-07**	5	76 196	15 239	0,464	0,7991	5	6 716 902	1 343 380	3,321	**0,0074**	5	75 655	15 131	1,337	0,284
Resident:Hyacinth perception	4	312209	78052	0,769	0,5468	2	1 739	870	0,026	0,9739	4	256 050	64 012	0,158	0,95896	1	314	314	0,028	0,869
Gross income:Hyacinth perception	25	1946188	77848	0,767	0,77693	9	815 652	90 628	2,758	0,0239	25	8 827 445	353 098	0,873	0,64135	8	460 318	57 540	5,084	**0,001**
Resident:Gross income:Hyacinth perception	2	178303	89152	0,879	0,41749						1	9 271	9 271	0,023	0,87991					
Residuals	144	14608077	101445			23	755 855	32 863			132	53 401 409	404 556			23	260 325	11 318		
	WTP Household 3					WTP Individual 3					WTP Household 4					WTP Individual 4				
Effect	df	Sum Sq	Mean Sq	F value	*P*	df	Sum Sq	Mean Sq	F value	*P*	df	Sum Sq	Mean Sq	F value	*P*	df	Sum Sq	Mean Sq	F value	*P*
Resident	1	3 755 869	3 755 869	8,339	**0,00455**	1	23 072	23 072	0,91	0,349612	1	4 184 187	4 184 187	5,675	**0,01865**	1	38 640	38 640	0,455	0,5068
Gross income	8	10 069 764	1 258 721	2,795	**0,0069**	8	1 142 142	142 768	5,631	**0,00045**	8	14 312 015	1 789 002	2,426	**0,01773**	8	1 630 781	203 848	2,399	**0,0481**
Hyacinth perception	4	1 017 080	254 270	0,565	0,68883	5	30 795	6 159	0,243	0,939292	4	3 675 287	918 822	1,246	0,29463	5	224 623	44 925	0,529	0,7522
Resident:Gross income	5	8 398 996	1 679 799	3,729	**0,00346**	4	106 681	26 670	1,052	0,401508	5	13 964 141	2 792 828	3,788	**0,00309**	5	531 288	106 258	1,251	0,3185
Resident:Hyacinth perception	4	191 880	47 970	0,106	0,98007	1	563	563	0,022	0,882818	4	298 933	74 733	0,101	0,98183	2	78 076	39 038	0,459	0,6373
Gross income:Hyacinth perception	25	7 966 915	318 677	0,708	0,8419	8	371 219	46 402	1,83	0,120405	25	5 880 378	235 215	0,319	0,99922	9	610 645	67 849	0,799	0,6214
Resident:Gross income:Hyacinth perception	1	39 364	39 364	0,087	0,76799						1	51 199	51 199	0,069	0,79257					
Residuals	130	58 554 937	450 423			24	608 452	25 352			131	96 588 860	737 320			23	1 954 230	84 967		

The respondents' perception of water hyacinth as a nuisance did not have a significant effect on willingness to pay for the clearance of water hyacinth at all clearance levels (Table 5.1). Furthermore, none of the categories (Neutral, Positive, Very Negative, Very Positive) had a highly significant impact on willingness to pay, only the Negative perception had a borderline significant impact on willingness to pay household levies at all clearance levels (for residents) and an individual annual levy (for visitors).

To evaluate if other socio-economic factors influence willingness to pay, the study looked at the impact of demographic characteristics.

Table 5.2. ANCOVA results illustrating the effects of age and gross income of residents and visitors on their willingness to pay (WTP) for the management of the weed. The numbers 1-4 indicate the level of removal as illustrated in Figure 5.11. Values in bold indicate significant differences

	WTP Household 1					WTP Individual 1					WTP Household 2					WTP Individual 2				
Effect	df	Sum Sq	Mean Sq	F value	*P*	df	Sum Sq	Mean Sq	F value	*P*	df	Sum Sq	Mean Sq	F value	*P*	df	Sum Sq	Mean Sq	F value	*P*
Age	1	758	758	0,01	0,9199	1	6800	6800	0,111	0,742	1	3989	3989	0,013	0,90924	1	41739	41739	1,594	0,21838
Resident	1	2599913	2599913	34,793	**2,04E-08**	1	5652	5652	0,092	0,764	1	3620148	3620148	11,835	**0,00075**	1	23586	23586	0,901	0,35164
Gross Income	8	2229890	278736	3,73	**0,00049**	8	621488	77686	1,269	0,303	8	7602088	950261	3,107	**0,00283**	8	767233	95904	3,663	**0,00593**
Age:Resident	1	71535	71535	0,957	0,32931	1	46284	46284	0,756	0,393	1	32748	32748	0,107	0,74397	1	3728	3728	0,142	0,70912
Age:Gross Income	8	1536019	192002	2,569	**0,01147**	8	86634	10829	0,177	0,992	8	5785164	723145	2,364	**0,02001**	8	126660	15833	0,605	0,76508
Resident:Gross Income	5	3481856	696371	9,319	**7,87E-08**	5	66548	13310	0,217	0,952	5	3101667	620333	2,028	0,07781	5	44570	8914	0,34	0,88344
Age:Resident:Gross Income	4	4072108	1018027	13,623	**1,30E-09**	2	6380	3190	0,052	0,949	4	14569088	3642272	11,907	**1,96E-08**					
Residuals	164	12255071	74726			25	1530121	61205			151	46189609	305891			25	654535	26181		
	WTP Household 3					WTP Individual 3					WTP Household 4					WTP Individual 4				
Effect	df	Sum Sq	Mean Sq	F value	*P*	df	Sum Sq	Mean Sq	F value	*P*	df	Sum Sq	Mean Sq	F value	*P*	df	Sum Sq	Mean Sq	F value	*P*
Age	1	414321	414321	1,172	0,28076	1	67566	67566	3,967	0,0566	1	1273970	1273970	2,097	0,14963	1	289299	289299	10,314	**0,0035**
Resident	1	4096936	4096936	11,588	**0,00085**	1	19002	19002	1,116	0,3002	1	4425470	4425470	7,286	**0,00775**	1	39648	39648	1,414	0,2452
Gross Income	8	10131086	1266386	3,582	**0,00079**	8	1087950	135994	7,985	**1,80E-05**	8	14662343	1832793	3,017	**0,0036**	8	1582520	197815	7,053	**6,08E-05**
Age:Resident	1	85299	85299	0,241	0,62401	1	2317	2317	0,136	0,71512	1	3629	3629	0,006	0,93849	1	44395	44395	1,583	0,2195
Age:Gross Income	8	6752730	844091	2,388	**0,0189**	8	616254	77032	4,523	**0,00141**	8	14604941	1825618	3,006	**0,00371**	8	1901419	237677	8,474	**1,31E-05**
Resident:Gross Income	5	4785039	957008	2,707	**0,02261**	4	25308	6327	0,371	0,82684	5	6768422	1353684	2,229	0.05432 .	5	385768	77154	2,751	**0,0401**
Age:Resident:Gross Income	4	10971671	2742918	7,758	**1,05E-05**						4	5984109	1496027	2,463	**0,04763**	2	79765	39882	1,422	0,2594
Residuals	149	52678155	353545			27	459853	17032			150	91108933	607393			26	729265	28049		

Age alone did not have a significant impact on the willingness to pay on the part of the majority of respondents (Table 5.2); however, the interaction between age, residential status and gross income has a strong combined impact on residents' willingness to pay for clearance of water hyacinth.

Table 5.3. ANCOVA results illustrating the effect of the gender of residents and visitors on their willingness to pay((WTP) for the management of the weed. The numbers 1-4 indicate the level of removal as illustrated in Figure 5.10. Values in bold indicate significant differences.

	WTP Household 1					WTP Individual 1					WTP Household 2					WTP Individual 2				
Effect	df	Sum Sq	Mean Sq	F value	*P*	df	Sum Sq	Mean Sq	F value	*P*	df	Sum Sq	Mean Sq	F value	*P*	df	Sum Sq	Mean Sq	F value	*P*
Age	1	697	697	0,006	0,9374	1	6667	6667	0,135	0,715	1	32782	32782	0,08	0,77777	1	40315	40315	1,162	0,287
Gender	1	515386	515386	4,575	**0,0337**	1	5463	5463	0,11	0,741	1	1658924	1658924	4,043	**0,04585**	1	66462	66462	1,916	0,173
Resident	1	2435929	2435929	21,625	**6,16E-06**	1	10082	10082	0,203	0,654	1	2891626	2891626	7,047	**0,00865**	1	38467	38467	1,109	0,298
Age:Gender	1	27912	27912	0,248	0,6192	1	39967	39967	0,806	0,374	1	286884	286884	0,699	0,40417	1	1	1	0	0,996
Age:Resident	1	4565	4565	0,041	0,8407	1	40051	40051	0,808	0,373	1	112960	112960	0,275	0,60045	1	48	48	0,001	0,97
Gender:Resident	1	1976175	1976175	17,544	**4,28E-05**	1	24856	24856	0,502	0,482	1	2618616	2618616	6,382	**0,0124**	1	53421	53421	1,54	0,221
Age:Gender:Resident	1	481992	481992	4,279	0,0399	1	5425	5425	0,109	0,742	1	732446	732446	1,785	0,18322	1	25475	25475	0,734	0,396
Residuals	192	21627331	112642			49	2428247	49556			179	73445868	410312			47	1630630	34694		
	WTP Household 3					WTP Individual 3					WTP Household 4					WTP Individual 4				
Effect	df	Sum Sq	Mean Sq	F value	*P*	df	Sum Sq	Mean Sq	F value	*P*	df	Sum Sq	Mean Sq	F value	*P*	df	Sum Sq	Mean Sq	F value	*P*
Age	1	577134	577134	1,268	0,26163	1	64063	64063	1,449	0,235	1	1560842	1560842	2,197	0,14008	1	257545	257545	2,859	0.0971 .
Gender	1	1602861	1602861	3,522	0,0622	1	84460	84460	1,91	0,173	1	1443577	1443577	2,032	0,15581	1	216876	216876	2,407	0,1271
Resident	1	3323781	3323781	7,304	**0,00755**	1	45639	45639	1,032	0,315	1	3700917	3700917	5,208	**0,02366**	1	75059	75059	0,833	0,3657
Age:Gender	1	157916	157916	0,347	0,55656	1	33692	33692	0,762	0,387	1	23699	23699	0,033	0,8553	1	85992	85992	0,954	0,3333
Age:Resident	1	93229	93229	0,205	0,65138	1	1185	1185	0,027	0,871	1	224721	224721	0,316	0,57457	1	11657	11657	0,129	0,7206
Gender:Resident	1	3457966	3457966	7,599	**0,00645**	1	86966	86966	1,966	0,167	1	5629731	5629731	7,923	**0,00543**	1	60500	60500	0,672	0,4164
Age:Gender:Resident	1	1042319	1042319	2,29	0,13196						1	837455	837455	1,179	0,27911	1	16915	16915	0,188	0,6667
Residuals	177	80548631	455077			49	2167107	44227			178	126480630	710565			50	4504649	90093		

Overall, the residential status of the respondents had a significant impact on their willingness to pay for the removal of the weed with the interaction between gender and residential status having a significant impact on the wiliness to pay (Table 5.3)

The respondents' perspectives on the services and benefits society derives from Hartbeespoort Dam show that they believe that the Dam is very important for the beauty of the landscape, nature, and clean water provision for nature (Figure 5.12). Respondents understand that the Dam is crucial for the provision of drinking and irrigation water but were uncertain of the importance of the Dam for swimming and recreational fishing.

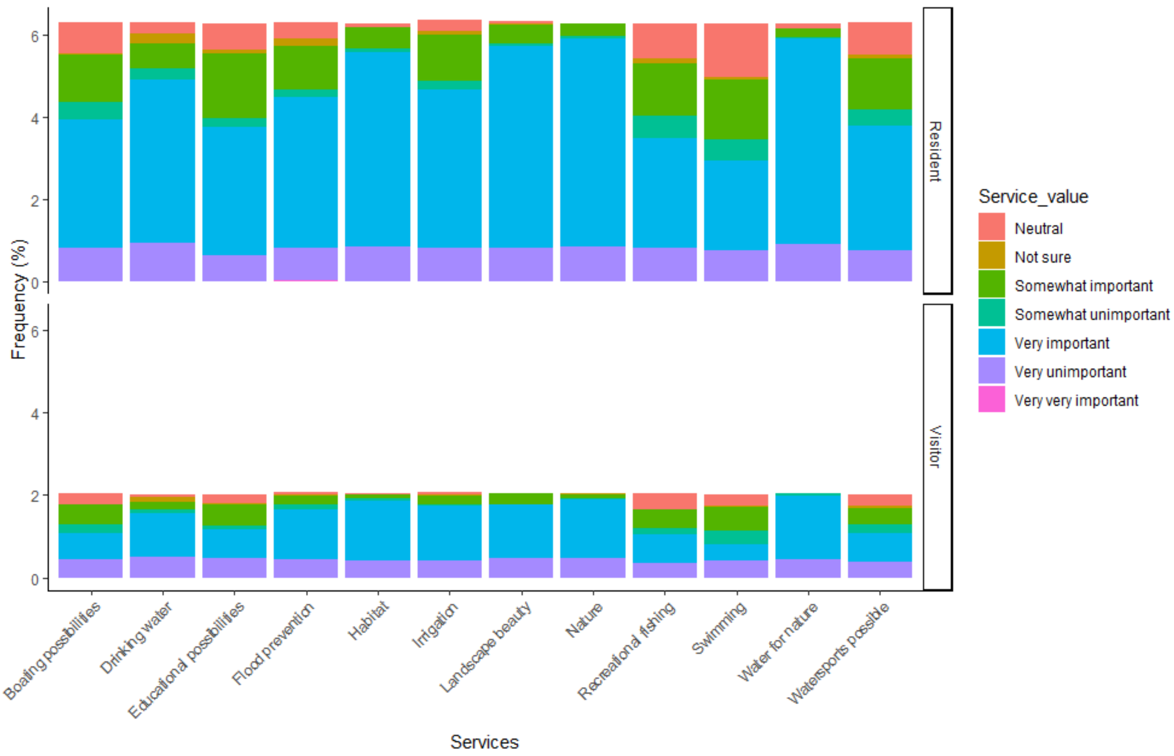

Figure 5.12. The perception of benefits of Hartbeespoort Dam for society**.**

To determine the New Ecological Paradigm (NEP) scale, the respondents were asked the standard fifteen questions to establish their environmental concerns (Anderson, 2014) as seen in Figure 5.13. The respondents had a NEP score was determine to be 3.7, which falls in the spectrum of respondents that place an average to high value on nature.

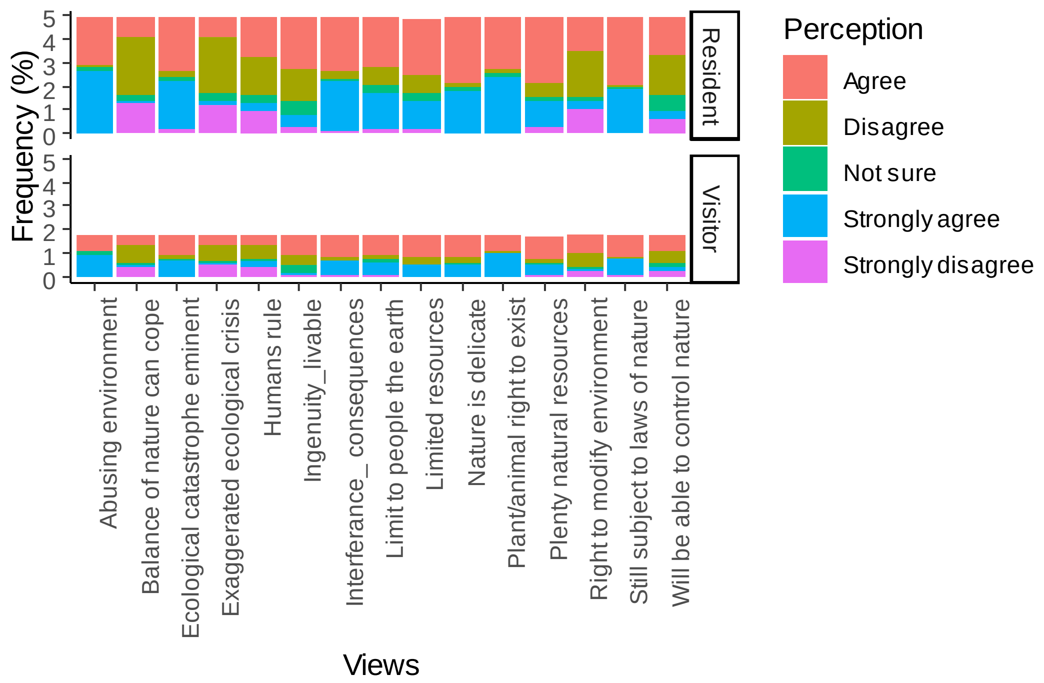

Figure 5.13. New Ecological Paradigm scale responses

5.4 Discussion

Macrophyte development can be seen as a nuisance, particularly at high biomass levels as this restricts the use of the waterbody. Schneider *et al*. (2024) found that the denser the macrophyte mass development, the more likely it was to be perceived as a nuisance. This negative perception is often driven by the aquatic weed's interference with water-based recreational activities, such as swimming, boating and angling (Schneider *et al*., 2024). For Hartbeespoort Dam, which is a tourist attraction, respondents perceived water hyacinth as a nuisance by at different coverage levels, supporting findings by van Nes *et al*. (2002) that floating macrophytes even at low densities would be perceived as a nuisance.

The perception of dense beds of aquatic macrophytes as a nuisance by users of a waterbody contributes to the need to remove the weed, and physical removal of weeds is done at a substantial cost annually across the world (Vermaat *et al*., 2024). Further, the perception by communities of the aquatic weeds as a nuisance impacts willingness to pay for their management. However, this study found that willingness to pay (WTP) was significantly influenced by the gross income of the participants for both the residents and visitors rather than the respondent's perception of the weed being a nuisance, with gross income having a positive relationship with the willingness to pay for the removal of water hyacinth. Van Oijstaeijen *et al*. (2020) however, found that in low-income households in Lake Tana in Ethiopia, willingness to pay may not fully reflect the value placed by farmers on the management of water hyacinth and subsequent protection of the Lake. The farmers were willing to contribute labour for the management of water hyacinth on Lake Tana, a willingness that was positively influenced by the community's attendance at the water hyacinth local conferences (Van Oijstaeijen *et al*. 2020), thus reflecting the importance of community education programmes for water hyacinth management projects. Abba and Sankarannair (2024) also found that, in rural areas, the eradication of water hyacinth and responsibility for managing the weed was enhanced by involving stakeholders who encouraged active engagement in sustainable practices. Similarly, Faulthauser *et al*. (2023) found that education was pivotal for the success of biological control of water hyacinth on a dam in Dique Los Sauces in Argentina. A study by Hill and Coetzee (2008) noted that engagement with communities who live around or along the shoreline of an infested waterbody is important for the success of a biocontrol programme. These findings support the involvement of shoreline communities in the management of aquatic weeds, both from the point of success and sustainability.

In addition, Vermaat *et al*. (2024), of which this study forms a part, found that willingness to pay for the removal differs with each category of user. Since the respondent's perception of the nuisance alone did not significantly influence willingness to pay (WTP), other socio-economic factors were assessed. Willingness to pay did not increase with increasing clearance levels; however, being a resident had a significant and positive impact on WTP. Schneider *et al*. (2024) found that residents are more likely to perceive mass developments of macrophytes more negatively than visitors. For residents, a combination of gross income and perception of water hyacinth had a significant impact on WTP at clearance level 3. Age did not have a significant impact on the willingness to pay. However, studies by John *et al*. (2019) and Van Oijstaeijen *et al*. (2020) found that there was a negative correlation between age and willingness to pay, with John *et al*. (2019) attributing the negative relationship to older individuals having responsibilities for the basic needs of the household, school fees and medical expenses.

5.5 Conclusion

This chapter first explores the perceptions of respondents of the water hyacinth infestation as expressed through the survey. Although a majority of respondents had a negative perception of the weed as it interferes mostly with boating, respondents expressed a low willingness to pay for the plant's management, with sentiments such as it was government's responsibility to manage the Dam as they already pay taxes towards the Dam's upkeep. Second, the survey it attempted to determine what socio-economic factors influence willingness to pay for the weed's management if negative perceptions had only a marginal significance on WTP. With a median age of 48, it was expected that middle-aged people would have a lower WTP because of the financial responsibilities they have towards their household, but there was no correlation between age and willingness to pay; instead, the respondent's gross income was the most influential variable, predominantly for high-income earners. Although John *et al*. (2019) and Van Oijstaeijen *et al*. (2020) found that there was a negative correlation between age and willingness to pay, only John *et al*. (2019) attributed this to older individuals having responsibilities for the basic needs of the household, school fees and medical expenses. Long (2013) noted that there is a high proportion of second-home ownership around Hartbeespoort Dam, which suggests that they are high income earners. For lower income earners an option of willingness to contribute labour would be beneficial for the next survey and would better gauge the commitment to the remediation and maintenance of the pristine conditions for the Dam, particularly in maintaining the satellite insect mass-rearing centres.

Chapter 6: General Discussion

6.1 Introduction

Global migration has increased the number of organisms introduced to regions where they are not native (Faulkner *et al*., 2020). In the course of its history, South Africa has experienced waves of colonization and migration which have resulted in the deliberate introduction of plants and animals (Van Wilgen *et al*., 2020). Among them, water hyacinth, which was introduced as an ornamental plant in the early 1900s (Faulkner *et al*., 2020). Since then, water hyacinth has colonized many freshwater bodies in the country, facilitated by the high nutrient load found in the country's freshwater systems as a result of agricultural, industrial and wastewater treatment plant effluents being released into rivers, the changes in hydrological flows due to the damming of rivers into impoundments, and the lack of natural enemies. Chapter 1 provided a general overview of the introduction of alien plant species into South Africa, with a special focus on water hyacinth which is the topic of the thesis. The chapter identified the gap in our understanding of how water hyacinth might be managed in a high elevation cool, highly eutrophic site with a long history of herbicide application.

6.2 Biological control efficacy of water hyacinth on a high elevation hypereutrophic impoundment

The geology of southern Africa limits the development of natural lakes and, as a result, South Africa relies on constructed impoundments for the socio-economic well-being and to meet its water supply demands in a water scarce country (Pérez *et al*., 2011. Coetzee *et al*., 2022a; Coetzee *et al*., 2014; Chikodza *et al*., 2025). As these impoundments are often found downstream of densely populated areas and have a high nutrient influx, South Africa has some of the most hypertrophic freshwater systems in the world. It is this nutrient influx and the high nutrient status of Hartbeespoort Dam that has facilitated the proliferation of water hyacinth, exacerbated by the lack of natural enemies to keep it under control. Water hyacinth, has been an issue on the Dam since the 1970s with herbicide use being the main measure of control, however in the 1980s, biological control agents were also released against the weed. Biological control involves introducing natural enemies, biocontrol agents to help reduce the harmful impact of a weed (Shea & Possingham, 2000; van Wyk & van Wilgen, 2002; Coetzee *et al*., 2017; Hinz *et al*., 2019). A suite of biological control agents has been released on the dam since the 1990s with variable success. Their ability to bring water hyacinth under control was limited by a combination of cold winter temperatures, the hypertrophic state of the dam and, most importantly, the application of herbicides which continued until 2016 (Coetzee *et al*., 2022a).

The success of biological control is seldom evaluated at a landscape level, despite being a landscape level intervention (Paterson *et al*., 2023). In this study, the landscape level impact of biological control was assessed using satellite imagery and monitoring the distribution of macrophytes on the dam over time, while correlating it with the population density of the most recently released agent, *M. scutellaris*. The success of biological control in this case was measured by the decline in water hyacinth coverage which correlated with an increase in *M. scutellaris* density, showing that *M. scutellaris* herbivory contributed to the reduction in water hyacinth coverage of Hartbeespoort Dam (Coetzee *et al*., 2022a).

The results presented in Chapter 3 confirmed that the introduction, and subsequent augmentative releases of high numbers of *M. scutellaris* early in spring onto the system, brought about effective control. This was contrary to the ideas of Hill and Olckers (2000), Hill and Coetzee (2008), Téllez *et al*. (2008) and Tipping *et al*. (2017) who suggested that an integrated approach with nutrient control and limited herbicide application would be necessary to obtain effective control of the weed at cool sites characterized by frosts and especially in eutrophic waters. The high insect densities of *M. scutellaris* were achieved by conducting inundative releases which is a break in tradition from the classical biological control approach which assumes that once released, the biological control agent would establish self-sustaining populations (Crowder, 2007; Maseko, 2021; Falthauser *et al*., 2023). Stakeholder participation in the production and release of *M. scutellaris* on the dam was key to successful control of the weed and provides a template that should be implemented on other appropriate programmes locally and globally (Coetzee et al. 2022a).

Although the other water hyacinth biological control agents no doubt contributed to the control of the plants, none built up numbers comparable to *M. scutellaris* (Coetzee *et al*., 2022a). Large counts of *M. scutellaris* were always accompanied by brown, unhealthy water hyacinth plants. However, *M. scutellaris* numbers declined significantly over winter (Coetzee *et al*., 2022a), while the weevils dominated the feeding in the early stages of the plant's growth period. Similar, to the research conducted by Goode *et al*. (2020), this study found that it was rare to see a plant on Hartbeespoort Dam without feeding damage from *Neochetina* spp. weevils.

Some of the most problematic aquatic weeds such as water hyacinth, alligator weed (*Alternanthera philoxeroides* (Mart) Griseb.; Amaranthaceae) and giant salvinia originate in the tropics but readily invade, subtropical and temperate areas (Harms *et al*., 2021), leading to climatic mismatches between the biological control and the host plant in its introduced regions. The influence of geographic variation on the outcome of biological control programmes is often related to the differential response of agents and target weeds to biotic or abiotic factors with precipitation and temperature being the most critical factors (Harms *et al*., 2021). Differences in climatic tolerance between host plants and the plant's natural enemies results in inconsistent successes of biological control programmes (Harms *et al*., 2021). However, this study has shown that by manipulating the releases of agents at the appropriate times, effective control of subtropical weeds by agents in cool temperate areas can be achieved. The second important factor that biological control agents need to overcome to successfully control the weed is eutrophication. The negative impact of eutrophication on biological control efficacy has been investigated for the *Neochetina* species (Heard & Winterton, 2000), *E. catarinensis* (Coetzee *et al*., 2007a), *N. albiguttalis* (Canavan *et al*., 2014), *O. terebrantis* (Marlin *et al*., 2013), and more recently for *M. scutellaris* (Miller *et al*., 2019; Coetzee *et al*., 2022). Marlin *et al*. (2013a) and Canavan *et al*. (2014) showed that macrophytes growing in eutrophic aquatic systems compensate for herbivory by increasing their leaf turnover. Previous studies by Coetzee *et al*. (2007), Marlin *et al*. (2013a), Canavan *et al*. (2014) and Miller *et al*. (2019) all concluded that biocontrol is effective in mesotrophic freshwater systems, and that nutrient pollution limits the success of biological control programmes, particularly in the early stages of plant growth where biocontrol agent numbers are extremely low (Coetzee *et al*., 2022a). Chapter 3 supports the hypothesis of Hill *et al*. (2021) that adopting an augmentative approach to water hyacinth biological control, can effect control, even where the plant is growing under highly eutrophic conditions.

The mass-rearing of water hyacinth biological control agents is, however, not unique to South Africa. In the 1990s, *Neochetina* spp. were mass-released on Lake Victoria (Wilson *et al*., 2007), in Papua New Guinea (Julien & Orapa, 1999) and in Benin (Ajuonu *et al*., 2003) leading to a decline in water hyacinth coverage. However, these sites were all in tropical parts of the world where the winters are milder than they are at Hartbeespoort Dam, thus allowing the control agent populations to increase year-round. In the Hartbeespoort Dan situation, timing of the mass releases in early spring was important to prevent the summer build up of the weed.

The role of community-based application of biological control is a fairly new idea, although it was used to great success for the biological control of water hyacinth on Lake

Victoria (Hill & Julien, 2004), and the Shire River in Malawi (Hill *et al*., 1998). However, it is important to engage with the community right from the start as biological control is still regarded with scepticism by the broader community. In South Africa great strides have been made to engage with interested and affected parties for these communities to take responsibility for the biological control of "their" weeds (Weaver *et al*., 2021). Much of the success of these initiatives relies on public perception of the impact of the weed, and who should be responsible for controlling it, as explored in Chapter 5. With buy-in from affected communities, initiatives to manage invasive species may become less difficult to coordinate (Moffat *et al*., 2024). Hill and Julien (2004) noted that a factor in the success of biological control programmes is the involvement of dedicated individuals who understood the potential of biocontrol and who ensure that the projects progress. Weaver *et al*. (2021) argued that this capacity building was vital for the mass-rearing of healthy insects and, subsequent releasing of the biological control agents. The Centre for Biological Control at Rhodes University, educates the public in the mass-rearing of biological control from primary school level, all the way to communities where the invasive plants occur (Weaver *et al*., 2021). In the Hartbeespoort area, Pecanwood College and Mountain Cambridge School were first sites where local mass-rearing occurred.

Due to this need for community involvement for the success of biological control programmes, Weaver *et al*. (2021) stressed that biological control has evolved from an applied science to a community engagement-based activity. Hill and Julien (2004) concluded that key to any biological control programme in Africa was that the technology that was transferred, in the form of simple mass-rearing techniques, must be appropriated to the situation and that all programmes must be flexible. This ensures the release of high numbers of healthy insects which are essential for biological control success.

Furthermore, Hill and Julien (2004) concluded that no biological control programme will succeed without political support. This support is garnered through the publishing of successes, where the impact of biological control of weeds can be observed at landscape level and has easily identifiable benefits for the affected communities. To this end Weaver *et al*. (2021) acknowledged that with support by the national government in South Africa, over the last decade, the number of functional mass-rearing facilities that provide insects for use in weed biocontrol across the country has increased (Weaver *et al*., 2021).

6.3 Impact of control

Post-release evaluations of biological control programmes are seldom conducted and even less so at the landscape level (Schaffner *et al*., 2020). Furthermore, when post-release evaluations are conducted, they concentrate on measuring the decline in the population density of the target weed and not the recovery of the ecosystem (Motitsoe *et al*., 2022). The MadMacs project (Chapter 4) investigated the impact on the Hartbeespoort Dam aquatic ecosystem of a rapid removal of a large mat of water hyacinth. This study showed that in the absence of the weed, much of the water chemistry changed, there was a significant change in the abundance and diversity of aquatic invertebrates, and indigenous macrophyte species, such as *Persicaria senegalensis* (Meisn.) Soják and *Commelina* sp. returned. This study supports the view by Carson *et al*. (2008) that successful biological control programmes would be those where invasive plant populations are depressed long enough to permit the re-establishment of native plant communities. However, the manual removal of water hyacinth also resulted in the proliferation of phytoplankton (cyanobacteria) which affects water clarity which is one of the ecosystem services provided by the water hyacinth mats. Hussner *et al*. (2017) argued that the weeds could potentially provide habitats that support biodiversity, and can perform key ecosystem services such as nutrient retention, enhanced water clarity and inhibit algal blooms within an aquatic system (Dhote, 2007; Gupta *et al.*, 2012). Following the mat removal there was a marked decrease in macroinvertebrate richness. However, it must be noted that this study was only conducted over the short term of six weeks and it is likely that the invertebrate community would recover.

Jones *et al*. (2017) showed that the removal of water hyacinth through biological control on a subtropical Nseleni River in South Africa resulted in a secondary invasion by an invasive snail, *Tarebia granifera* (Lamarck, 1822). Secondary invasions in aquatic ecosystems are not uncommon, and Motitsoe (2020) found that following the mechanical removal of *Salvinia molesta* from Westlake River in the Western Cape Province of South Africa resulted in an ecological succession from the free-floating *S. molesta* dominated state, followed by a clear-water state, which was followed by submerged- *Ceratophyllum dermersum*- dominant state and ultimately replaced by a floating-leaved, emergent *Nymphaea mexicana*- dominated state. This illustrates a new era of invasive alien plant invasions where following the control of a target weed there can be a secondary invasion because the primary driver of the invasion, in this case eutrophication, is not addressed or reversed (Motitsoe, 2020). Similarly, Schaffner *et al*. (2020), Shen *et al*. (2023) and Chikodza *et al*. (2025) highlighted an emerging concern in weed management, where secondary invasion occurs on as system where the suppression of a targeted invasive species may promote non-target exotics. On Hartbeespoort Dam, the control of water hyacinth resulted in the explosion of *Salvinia minima* that was first recorded on the Dam in 2012, but had been supressed by the vast mats of water hyacinth (Coetzee *et al*., 2022b). Schaffner *et al*. (2020) decried the lack of studies that investigate how the dominant weed may have altered ecosystems conditions in such a way that it favours the proliferation of other non-native invasive species rather than native species. Chapter 4 investigate the changes in ecosystem conditions, albeit for a short term. It would be beneficial for the water chemistry and nutrient analysis to continue for several months, as *S. minima* rapidly increases in late autumn on the Dam.

6.4 Funding environmental management programmes

Public engagement and communication have become increasingly important in the sustainable implementation and monitoring of biological control programmes (Moffat *et al*., 2024). The sustainable control of water hyacinth hinges on active engagement from pertinent stakeholders, particularly in the local communities where the water hyacinth infestation has occurred (Weaver et al., 2021; Abba & Sankarannair, 2024). Diop and Hill (2009) attributed the success of a multi-site biological control programme in Senegal to several biotic and abiotic factors, but also highlighted that an awareness campaign was conducted which resulted in riparian communities accepting and participating in the release of *Neohydronomous affinis* to manage water lettuce.

Khatri *et al*. (2018) noted that water hyacinth in lakes can lead to plummeting tourism revenues from boating and other water-based activities. Hartbeespoort Dam is a tourist attraction and the water hyacinth infestation has had a negative impact on tourism as most of the respondents mentioned boating, aesthetic-dependent activities such as hiking, walking and just relaxing as what brings them to the Dam (Chapter 5). The negative perception of water hyacinth is driven by the inability to participate in activities that respondents do on the waterbody (Thiemer *et al*., 2023; Vermaat *et al*., 2024; Schneider *et al*., 2024). The results from Chapter 5 indicate that the perception of the respondents of water hyacinth being a nuisance did not encourage their willingness to pay for its management. Interestingly, residential status of the respondent influenced their willingness to pay (WTP), with residents being willing to pay more than visitors for the management of the macrophyte (Vermaat *et al*., 2024). However, that response was also strongly influenced by their personal gross income.

Similarly, John *et al*. (2019) found that the willingness to pay of fisherfolk who were dependent on Lake Victoria for income, was positively influenced by the income they made. Khatri *et al*. (2018) found that expenditure, which the study used as a proxy for income, significantly impacted willingness to pay, while Vermaat *et al*. (2024) found that gross income and whether the respondent did recreational boating and angling were the main contributors to willingness to pay.

The willingness to pay as noted by John *et al*. (2019) is not a true reflection of the population's interest in preserving the pristine state of the Dam, as the willingness to contribute labour, or some other currency, should be an option, particularly for low-income households. However, for this study, willingness to contribute labour was not offered as an option but would be useful as there is a need to sustain the satellite insect-rearing centres around the Dam.

To determine the level of environmental consciousness, the survey asked fifteen questions that establish the respondent's New Ecological Paradigm (NEP) score. The respondents had a NEP score of 3.7 supports the findings by a meta-analysis conducted by Hawcroft and Milfont (2010) which shows that the expected NEP scores fall within an expected range of 3.8±0.35 which proves that respondents place an average to high value on nature. This score also reflects that respondents show concern for nature (Chapter 5) (Thiemer *et al*., 2023).

The majority of residents in the survey indicated that they were not willing to pay more (Chapter 5, Appendix Data 1), citing that they are already paying taxes to the state and believe the state should be responsible for the management of the weed. This responsibility currently lies with the Department of Forestry, Fisheries and Environment (DFFE). However, since the main tributaries contributing to the nutrient load flowing into the Dam are within the parameter of the Gauteng Province in South Africa, the recommendation is that additional funding should be contributed by the Gauteng Department of Agriculture and Rural Development in order to comply with the polluter pays principle as in this case the user is expected to contribute to manage weed proliferation as a result of upstream pollution.

6.5 Recommendations for future research

Future research should focus on a post-release evaluation on another water hyacinth-infested site in an urban space where no other agents are present or released in order to observe the efficacy of *M. scutellaris* as a sole biological control agent on a cool temperate hypertrophic system in the highveld to also establish if it had an additive impact. For Hartbeespoort Dam, a seed bank analysis should be carried out as information on seed banks could influence future management strategies. The limitation of this study was that no nutrient level assays were carried out when the monthly assessments were done. The primary driver of infestation is the nutrient load and secondary infestation demonstrates that there will be subsequent infestations from other invaders once both water hyacinth and *S. minima* are under control. A study by Atta *et al*. (2020) proposed a chemical phosphate removal programme for the Dam with the aim to lowered from the current phosphate level of 0.2 mg/L to less than 0.05 mg/L in an attempt to control eutrophication and prevent algal blooms and the proliferation of invasive macrophytes. Atta *et al*. (2020) included the proposed monitoring of water hyacinth growth over 12 months to assess the seasonal impact on the plant's growth. A multi-disciplinary study on the Dam to find ways to reduce nutrient inflow by both chemical and biological means should be conducted, while monitoring macrophyte growth.

6.6 Conclusion

Megamelus scutellaris is essential for the management of water hyacinth on the Dam and, because its numbers plummet during the colder moths, stock-releasing in large numbers is required post winter. For *M. scutellaris* numbers to remain high throughout winter, community-based insect rearing centres maintained by communities are essential, even though the infrastructure set up should be provided by the Department of Forestry, Fisheries and Environment (DFFE). The department should provide the temporary infrastructure (insect tubs and tunnels) needed for the satellite mass-rearing sites as they are the custodians of biodiversity. Furthermore, in South Africa, the DFFE is mandated to evaluate the successes of the management programmes they fund in order to manage IAPs (Paterson *et al*., 2023).

The success of the biocontrol programme relies on the high number of insects released onto the Dam during the growth season of the plant (mid-spring). Therefore, the buy-in of the community in the area, as well as key stakeholders at the Department of Water and Sanitation (DWS), who are the owners of the Dam, and the Department of Forestry, Fisheries and the Environment is pivotal. Over a six-year period, 2018 to 2023, the number of volunteer partners around the Dam that were involved in the mass rearing of *M. scutellaris* increased from four to 19 (Moffat *et al*., 2024). This partner programme was successful in creating awareness and educating the Hartbeespoort Dam community in the science and practice of biological control (Moffat *et al*., 2024). The DWS must minimize nutrient influx by constructing activated wetlands that would filter the water before it reaches the Dam. The DWS should further work with water forums upstream of the Dam to educate and attempt to mitigate excessive nutrient influx from the feeder rivers.

A secondary biological control programme should be carried out from the onset of autumn to deal with *S. minima* infestation. Should the moratorium on herbicide use be lifted, then sub-lethal sprays should be carried out, similar to what was done on the Roodeplaat Dam in Gauteng Province, in order to stress the plants before the inundative releases of *M. scutellaris* are made.

Lastly, without managing the biggest problem for the Hartbeespoort Dam – the high nutrient inflow – the Dam will continue to be at risk of invasion by newly introduced invasive alien plants.

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Appendix

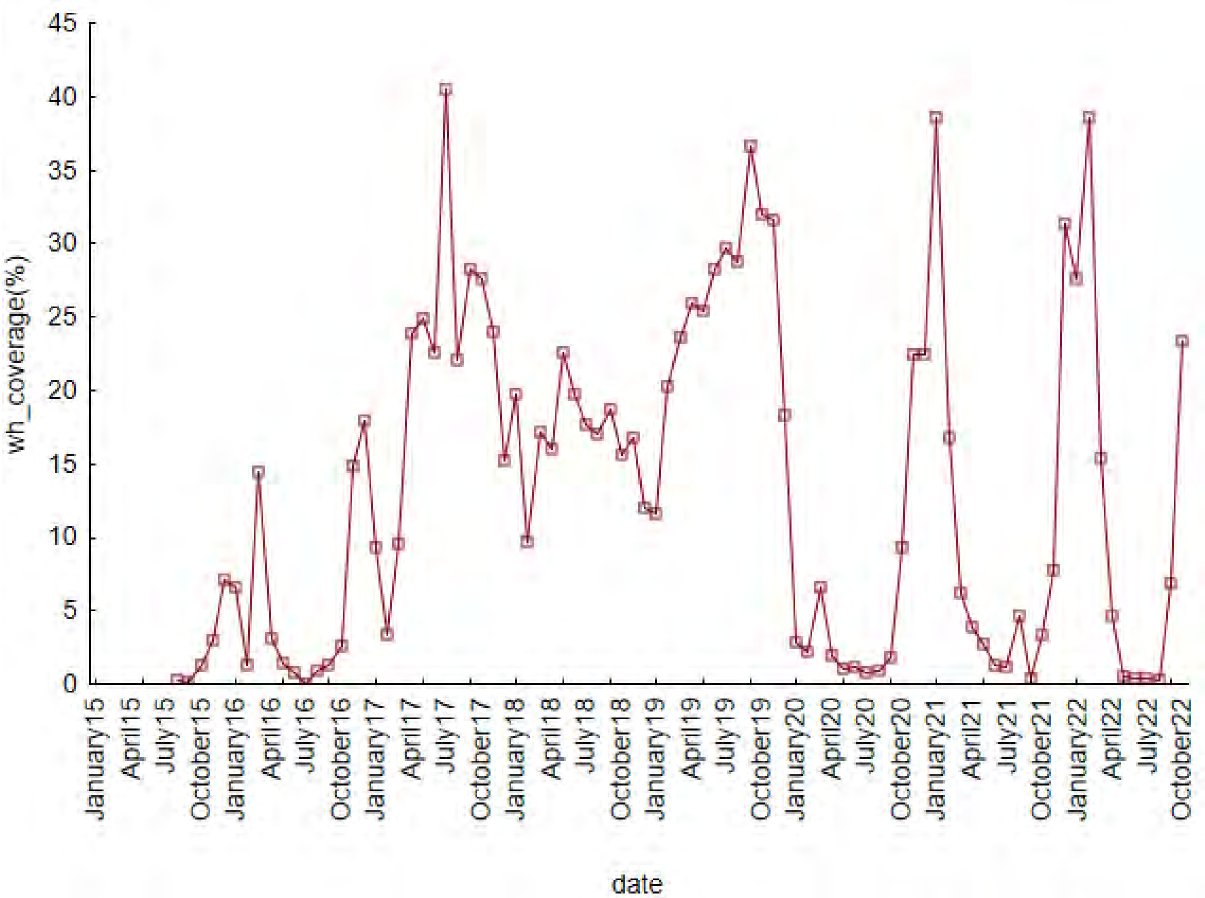


Figure S2: Water hyacinth coverage on the Hartbeespoort Dam from July 2015 to October 2022

Table S1. Macrophyte diversity at the control and impact site before and after removal

Species type	Before	After	After 1 year

(Native/Alien)		Species	Cover	Species	Cover	Species	Cover
Control	Alien	*Pontederia crassipes*	80	*Pontederia crassipes*	90	*Pontederia crassipes*	20
	Native	*Persicaria senegalensis*	10	*Persicaria senegalensis*	5	*Persicaria senegalensis*	40
	Native	*Cyperus papyrus*	8	*Cyperus papyrus*	4	*Cyperus papyrus*	<1
	Native	*Persicaria decipiens*	<1	*Persicaria decipiens*	<1	*Persicaria decipiens*	<1
	Native	*Commelina sp. (maybe diffusa scadens)*	<1	*Commelina sp. (maybe diffusa scadens)*	<1	*Commelina sp. (maybe diffusa scadens)*	10
	Native	*Spirodela polyrhiza*	<1	*Spirodela polyrhiza*	<1	*Spirodela polyrhiza*	-
	Alien	*Salvinia minima*	<1	*Salvinia minima*	<1	*Salvinia minima*	20
	Native	*Cyperus sexangularis*	<1	*Cyperus sexangularis*	<1	*Cyperus sexangularis*	<1
	Alien	*Alternanthera sessilis*	<1	*Alternanthera sessilis*	<1	*Alternanthera sessilis*	<1
	Native	*Typha capensis*	<1	*Typha capensis*	<1	*Typha capensis*	<1
Impact	Alien	*Pontederia crassipes*	60	-	-	*Pontederia crassipes*	60
	Native	*Persicaria senegalensis*	20	-	-	*Persicaria senegalensis*	20
	Native	*Commelina sp. (maybe diffusa scadens)*	10	-	-	*Commelina sp. (maybe diffusa scadens)*	5
	Alien	*Alternanthera sessilis*	<1	-	-	*Alternanthera sessilis*	5
	Native	*Cyperus papyrus*	<1	-	-	*Cyperus papyrus*	<1
	Native	*Cyperus sexangularis*	<1	-	-	*Cyperus sexangularis*	<1
	Alien	*Salvinia minima*	<1	-	-	*Salvinia minima*	-
	Native	*Spirodela polyrhiza*	<1	-	-	*Spirodela polyrhiza*	-
	Native	*Persicaria decipiens*	<1	-	-	*Persicaria decipiens*	<1
	Native	*Typha capensis*	<1	-	-	*Typha capensis*	<1
	Alien	*Myriophyllum aquaticum*	-	-	-	*Myriophyllum aquaticum*	<1

Table S2. Percentage volume infested by water hyacinth in the control and impact site.

Site	**Time**	**PVI (%)**
Control	Before	9.62±4.79
	After	6.59±2.45

	1 year after	4.26±4.07
Impact	Before	13.08±9.20
	After	0±0
	1 year after	25.69±37.47

Table S3. Observed fish species in Hartbeespoort Dam

Species	Control Site Before Removal 14 January 2020	Impact Site Before Removal 14 January 2020	Impact Site After Removal 28 January 2020
Chetia flaviventris	10		
Clarias gariepinus	2	OBS	3
Cyprinus carpio	1		2
Gambusia affinis	25	16	>100
Micropterus salmoides	OBS		
Oreochromis mossambicus	OBS		OBS
Pseudocrenilabrus philander	14	4	9
Tilapia sparrmanii	1		

Diversity	**8**	**3**	**5**

Table S4. The mean±SD of periphyton parameters

Site	Time	Up_Down	1_N_mg_m2_d	1_C_mg_m2_d	P_mg_m2_d	Filtered_HPLC_ml	Time_incubated_h	Sample_mg_m2
Control	Before	Up	0.44±0.32	2.62±1.88	26.14±28.40	25.25±10.53	149.67±0	42.39±28.62
Control	Before	Down	0.32±0.18	1.82±0.97	21.60±15.70	27±10.86	149.67±0	32.89±17.18
Control	After	Up	0.47±0.26	3.86±1.19	10.36±10.12	15.25±2.36	147.03±0	33.85±21.53
Control	After	Down	0.45±0.08	3.23±0.24	8.56±5.98	15±4.55	147.03±0	29.47±10.26
Impact	Before	Up	0.37±0.13	2.21±0.80	10.65±7.27	26.75±5.12	149.42±0	39.03±16.47
Impact	Before	Down	0.43±0.19	2.59±1.05	4.19±3.05	35±13.52	149.42±0	35.14±23.24
Impact	After	Up	2.51±0.19	15.50±1.33	207.84±5.97	12.5±2.89	146.75±0	232.21±10.67
Impact	After	Down	0.45±0.19	2.80±1.36	11.60±9.34	15±2.94	146.75±0	38.80±15.93

Table S5. Physiochemical profiles (Mean ± SD) of the water at the three sites on Hartbeespoort Dam

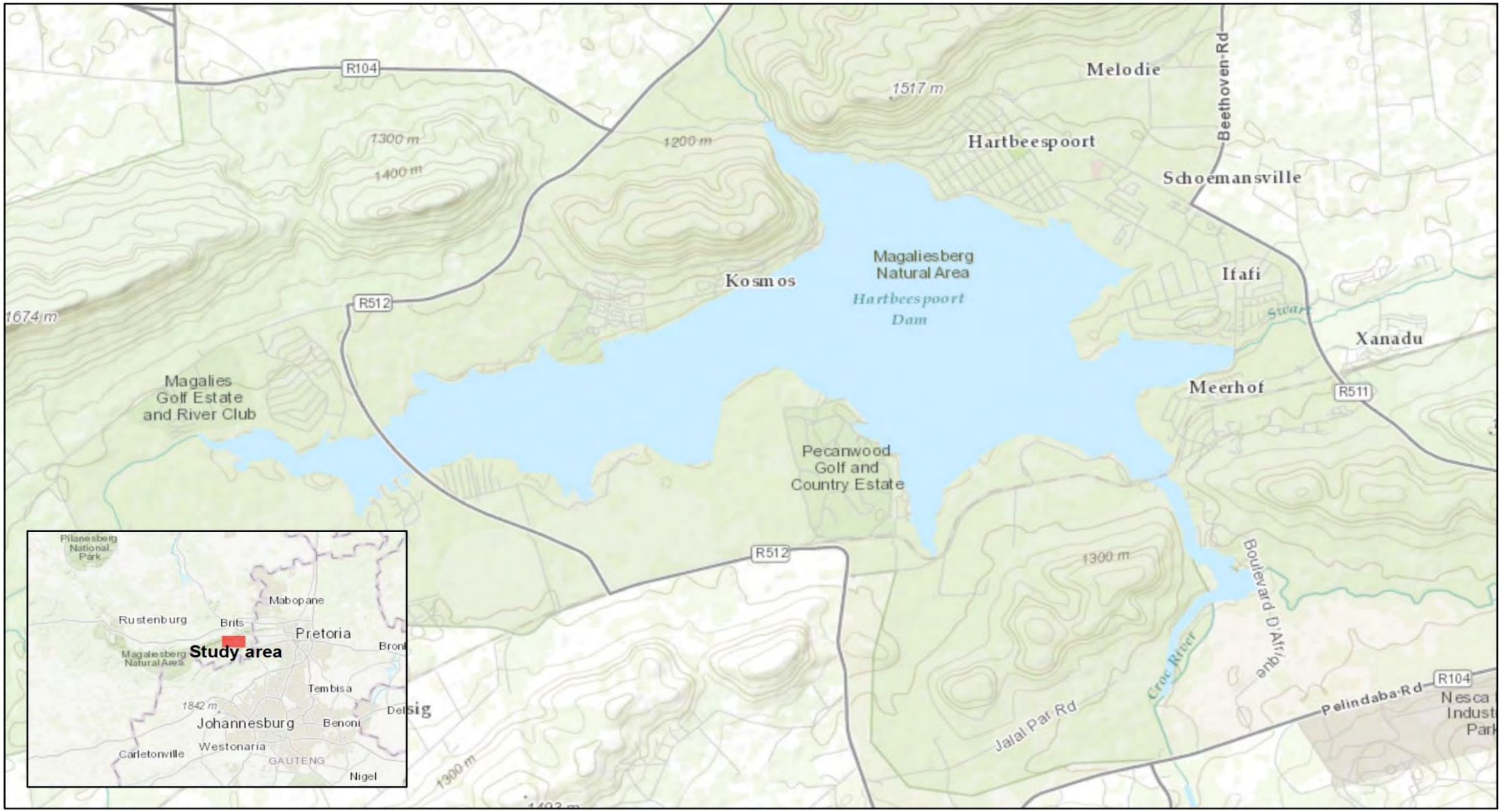
Site	Time	Mean DO (mg/L)	Mean Temp_C	Mean pH	Mean Conductivity_µS_cm	Mean Depth_m
Control	Before	0.73±0.54	26.40±0.56	7.83±0.84	513.79±2.64	0.88±0.55
Control	During	1.74±0.23	25.52±0.04	6.78±0.01	504.9±0.32	0.91±0.59
Control	After	5.67±3.00	26.06±0.82	9.44±1.31	501.5±2.31	0.91±0.57
Impact	Before	0.74±0.56	26.34±0.43	6.94±0.43	514.28±2.43	0.91±0.57
Impact	During	1.75±0.18	25.54±0.052	6.92±0.07	505±0	0.91±0.59
Impact	After	5.97±3.36	26.27±0.91	7.84±1.34	499.95±2.65	0.91±0.57
Open water	Before	4.90±1.70	26.55±0.40	7.29±0.84	513.38±1.36	1.51±0.94
Open water	During	3.67±0.63	25.95±0.38	6.79±0.07	506.61±0.72	1.5±0.94
Open water	After	8.01±2.43	26.01±0.85	7.51±0.33	500.16±2.80	1.5±0.95

Data S1. Perception and willingness to pay survey conducted at the Hartbeespoort Dam.

Dear survey participant,

Thank you for participating in this survey. It is part of a publicly funded research project called MadMacs. For more information on MadMacs, please see the last page of this questionnaire. Your answers will help us with estimating the environmental quality and issues important to the local community around the Hartbeespoort Dam. We will ask you questions about your relationship to the area. All your answers are important – it is not necessary that you have specific knowledge on nature, water, tourism or the environment. There are no right and wrong answers.

Completing the survey takes about 10 minutes and will be anonymous. We follow the definitions of the Protection of Personal Information Act. If you have any questions regarding the study, please contact the interviewers (contact information on the last page).



Hartbeespoort Dam

0 0.5 1 2 3 4 Kilometers

N 1:60,000

MADMACS

Service Layer Credits: Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Your relationship to the area

The map on the previous page shows the Hartbeespoort Dam, which is our study area.

1. During the past 12 months, for what purpose have you been in the area? Multiple answers are possible.

a)	Short recreational visits (less than a day)	○
b)	Long recreational visits (more than a day)	○
c)	I live in the area	○
d)	I work in the area	○
e)	None of the above	○
f)	Other: ____	○

If you did not recreate in the area during the last 12 months, please jump to question 9. Otherwise, continue to question 2.

2. Please mark on the map on page 2 with an X which location you visit most often for recreation. <u>Please mark only one location.</u>

3. If the above location would not be accessible, would you have an alternative location for recreation? <u>Please choose only one answer.</u>

Yes, in the study area	Yes, in another area	No
○	○	○

4. Please tick the activities you typically do when visiting the area. Multiple answers are possible. Also indicate how many days you have done the activity in the last 12 months.

		I do this in the area	Number of days in the last 12 months
a)	Walking/hiking	○	____________________
b)	Running	○	____________________
c)	Cycling/mountainbiking	○	____________________
d)	Orienteering	○	____________________
e)	Enjoying the landscape and views	○	____________________
f)	Photographing, painting or drawing nature	○	____________________
g)	Playing golf	○	____________________
h)	Rock climbing	○	____________________
i)	Motorbiking	○	____________________
j)	Motorized boating	○	____________________
k)	Rowing, sailing, canoeing	○	____________________
l)	Watersports (like waterskiing)	○	____________________
m)	Hunting	○	____________________
n)	Fishing	○	____________________
o)	Swimming	○	____________________
p)	Managing my property	○	____________________

q)	Just relaxing	○	____________________ __
r)	Other:______________________________________	○	____________________ __

5. Do you own property within 10 km of the study area? Multiple answers are possible.

I own a house	I own a holiday home	I own farmland	I own a guesthouse	Other: _____________	I do not own property in the area
○	○	○		○	○

6. How far do you travel from your home to the part of the area where you recreate most often?

_____________ km

7. How do you usually travel when recreating there? <u>Please mark only one option.</u>

a)	Car	○
b)	Public transport	○
c)	Taxi	○
d)	Bicycle	○
e)	Motorcycle	○
f)	Private boat	○
g)	Walking	○
h)	Motorhome/caravan	○
i)	Other: ____________________	○

8. The Hartbeespoort Dam generates benefits to society. Please indicate how important the following benefits are to your own wellbeing.

		Very unimportant	Somewhat unimportant	Neither important, nor unimportant	Somewhat important	Very important	I don't know
a)	Source of drinking water	○	○	○	○	○	○
b)	Possibilities for recreational fishing	○	○	○	○	○	○
c)	Clean water for nature	○	○	○	○	○	○
d)	Habitats for plants and animals	○	○	○	○	○	○
e)	Swimming possibilities	○	○	○	○	○	○
f)	The fact that there is nature	○	○	○	○	○	○
g)	Educational possibilities	○	○	○	○	○	○
h)	Boating possibilities	○	○	○	○	○	○
i)	The beauty of the landscape	○	○	○	○	○	○
j)	Water storage to prevent floods	○	○	○	○	○	○
k)	Possibilities for watersports	○	○	○	○	○	○
l)	Water for irrigation	○	○	○	○	○	○

9. Please indicate your top three most important benefits from the list above. Write down the letter from the first column related to the benefit.

1. _________

2. _________

3. _________

Water hyacinth growth

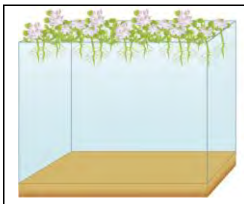
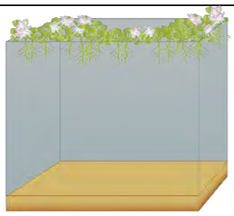
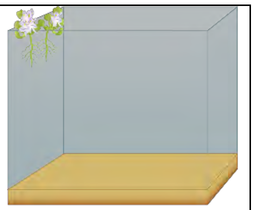
This part of the survey is about your opinion on water hyacinth growth. Water hyacinth (*Eichhornia crassipes*) is a water plant that develops very dense free-floating stands on the water surface in large parts of the Hartbeespoort Dam. We use the term mass development for this. Water hyacinth is native to South America, but when introduced in other areas, it often grows rapidly in water that contains many nutrients from human activity nearby. In South Africa, water hyacinth has previously been controlled by using herbicides and biological control, but this management practice is being replaced by mechanical removal.

The following questions focus on the growth of water hyacinth in the Hartbeespoort Dam and the different ways to manage this growth. We will focus on your perception and preferences on water hyacinth growth.

10. How do you personally perceive the current presence of water hyacinth in the Hartbeespoort Dam? <u>Please choose only one answer below.</u>

Very negative	Negative	Neutral	Positive	Very positive	I don't know
○	○	○	○	○	○

11. The pictures below show different levels of water hyacinth growth in the Hartbeespoort Dam. Image 1 shows the current level of water hyacinth growth. Please tick the pictures showing a level of growth you consider to be a nuisance, if any. You can select multiple pictures.

				
1. ○	2. ○	3. ○	4. ○	5. ○
I don't find the growth a nuisance. ○		I don't know. ○		

12. If you selected one or more of the above growth levels as a nuisance, what causes the nuisance? You can select multiple options.

a)	The plants make swimming less enjoyable	○
b)	The plants make it difficult for me to navigate a boat	○
c)	The plants make it difficult for me to do water sports	○
d)	The plants make it harder for me to fish	○
e)	I am worried about the effect it might have on biodiversity	○
f)	I dislike the way the dam looks with that many plants	○
g)	Other: ____	○
h)	I don't know	○

Currently, the water hyacinth in the Hartbeespoort Dam is removed on local scale by different groups. This removal mainly takes place around private jetties or where there is much recreation. The photo below shows how this removal can look.

A new large-scale removal program funded by an increase in municipal household waste

water levy and a tourist levy is possible, which will remove hyacinth in the total Hartbeespoort Dam instead of only in small selected locations. For residents, this will mean an increase in municipal household levy. For visitors, this levy will be paid once per year when visiting the area for at least one overnight stay.

On the following pages, we will show you four different levels of removal. On each page, the level of growth without a large-scale removal program is shown on the left side. Five local effects, for example possibilities for swimming and possibilities for boating are likewise shown.

13. For each highlighted level, please consider how much you would be willing to pay per year in increased levy to reach that level as compared to the current situation. If you are a resident of the area, the municipal household waste-water levy applies. If you are a visitor, the individual tourist levy applies. Bear in mind that an increase in tax would reduce your income and consumption possibilities. <u>Please mark only one option</u>

	Current situation
Level of growth	
Possibilities for swimming	Plants fill up the water in many parts, making it impossible to swim there.
Possibilities for boating	Rowing is hard. Engine rotors are very often clogged.
Possibilities for fishing	It's impossible to fish in many parts.
Changes in biodiversity	Low diversity in living environment for plants and animals.
Changes to the overall scenery	Much of the lake is completely filled up with plants.

With removal program			
			
Plants fill up the water in some parts, making it very hard to swim there.	Plant beds can be found in some parts that you have to swim around.	Plants beds can be found in some parts which you can swim through.	There are small plant beds in only a few parts which are easy to swim through.
Plants slow down rowing and regularly clog engine rotors.	Plants brush up against boats and sometimes clog engine rotors.	Occasionally plants brush up against boats.	Rowing and motorized boating is unimpeded.
Lines often get stuck on plants in many parts.	Lines sometimes get stuck on plants in some parts.	Occasionally lines get stuck on plants in a few small parts.	Fishing lines don't get stuck.
Slightly diverse living environment for plants and animals.	Very diverse living environment for plants and animals.	Very diverse living environment for plants and animals.	Low diversity in living environment for plants and animals.
Large beds are visible in many parts.	Some large beds are visible with space in between.	Some beds are visible along the shore.	There are only small beds visible in a few places along the shore.

FOR RESIDENTS. For the highlighted level of removal, I am willing to pay the following increase in annual household levy:

R 0	R 50	R 100	R 250	R 500	R 1.000	R 2.500	R 5.000	More than R 5.000	I don’t know
○	○	○	○	○	○	○	○	○	○

FOR VISITORS. For the highlighted level of removal, I am willing to pay the following increase in annual individual levy:

R 0	R 10	R 50	R 100	R 250	R 500	R 1.000	R 1.500	More than R 1.500	I don’t know
○	○	○	○	○	○	○	○	○	○

	Current situation	With removal program			
Level of growth					
Possibilities for swimming	Plants fill up the water in many parts, making it impossible to swim there.	Plants fill up the water in some parts, making it very hard to swim there.	Plant beds can be found in some parts that you have to swim around.	Plants beds can be found in some parts, which you can swim through.	There are small plant beds in only a few parts, which are easy to swim through.
Possibilities for boating	Rowing is hard. Engine rotors are very often clogged.	Plants slow down rowing and regularly clog engine rotors.	Plants brush up against boats and sometimes clog engine rotors.	Occasionally plants brush up against boats.	Rowing and motorized boating is unimpeded.
Possibilities for fishing	It's impossible to fish in many parts.	Lines often get stuck on plants in many parts.	Lines sometimes get stuck on plants in some parts.	Occasionally lines get stuck on plants in a few small parts.	Fishing lines don't get stuck.
Changes in biodiversity	Low diversity in living environment for plants and animals.	Slightly diverse living environment for plants and animals.	Very diverse living environment for plants and animals.	Very diverse living environment for plants and animals.	Low diversity in living environment for plants and animals.
Changes to the overall scenery	Much of the lake is filled up with plants.	Large beds are visible in many parts.	Some large beds are visible with space in between.	Some beds are visible along the shore.	There are only small beds visible in a few places along the shore.

FOR RESIDENTS. For the highlighted level of removal, I am willing to pay the following increase in annual household levy:

R 0	R 50	R 100	R 250	R 500	R 1.000	R 2.500	R 5.000	More than R 5.000	I don't know
○	○	○	○	○	○	○	○	○	○

FOR VISITORS. For the highlighted level of removal, I am willing to pay the following increase in annual individual levy:

R 0	R 10	R 50	R 100	R 250	R 500	R 1.000	R 1.500	More than R 1.500	I don't know
○	○	○	○	○	○	○	○	○	○

	Current situation	With removal program			
Level of growth					
Possibilities for swimming	Plants fill up the water in many parts, making it impossible to swim there.	Plants fill up the water in some parts, making it very hard to swim there.	Plant beds can be found in some parts that you have to swim around.	Plants beds can be found in some parts, which you can swim through.	There are small plant beds in only a few parts, which are easy to swim through.
Possibilities for boating	Rowing is hard. Engine rotors are very often clogged.	Plants slow down rowing and regularly clog engine rotors.	Plants brush up against boats and sometimes clog engine rotors.	Occasionally plants brush up against boats.	Rowing and motorized boating is unimpeded.
Possibilities for fishing	It's impossible to fish in many parts.	Lines often get stuck on plants in many parts.	Lines sometimes get stuck on plants in some parts.	Occasionally lines get stuck on plants in a few small parts.	Fishing lines don't get stuck.
Changes in biodiversity	Low diversity in living environment for plants and animals.	Slightly diverse living environment for plants and animals.	Very diverse living environment for plants and animals.	Very diverse living environment for plants and animals.	Low diversity in living environment for plants and animals.
Changes to the overall scenery	Much of the lake is filled up with plants.	Large beds are visible in many parts.	Some large beds are visible with space in between.	Some beds are visible along the shore.	There are only small beds visible in a few places along the shore.

FOR RESIDENTS. For the highlighted level of removal, I am willing to pay the following increase in annual household levy:

R 0	R 50	R 100	R 250	R 500	R 1.000	R 2.500	R 5.000	More than R 5.000	I don’t know
○	○	○	○	○	○	○	○	○	○

FOR VISITORS. For the highlighted level of removal, I am willing to pay the following increase in annual individual levy:

R 0	R 10	R 50	R 100	R 250	R 500	R 1.000	R 1.500	More than R 1.500	I don’t know
○	○	○	○	○	○	○	○	○	○

	Current situation	With removal program			
Level of growth					
Possibilities for swimming	Plants fill up the water in many parts, making it impossible to swim there.	Plants fill up the water in some parts, making it very hard to swim there.	Plant beds can be found in some parts that you have to swim around.	Plants beds can be found in some parts which you can swim through.	There are small plant beds in only a few parts, which are easy to swim through.
Possibilities for boating	Rowing is hard. Engine rotors are very often clogged.	Plants slow down rowing and regularly clog engine rotors.	Plants brush up against boats and sometimes clog engine rotors.	Occasionally plants brush up against boats.	Rowing and motorized boating is unimpeded.
Possibilities for fishing	It's impossible to fish in many parts.	Lines often get stuck on plants in many parts.	Lines sometimes get stuck on plants in some parts.	Occasionally lines get stuck on plants in a few small parts.	Fishing lines don't get stuck.
Changes in biodiversity	Low diversity in living environment for plants and animals.	Slightly diverse living environment for plants and animals.	Very diverse living environment for plants and animals.	Very diverse living environment for plants and animals.	Low diversity in living environment for plants and animals.
Changes to the overall scenery	Much of the lake is filled up with plants.	Large beds are visible in many parts.	Some large beds are visible with space in between.	Some beds are visible along the shore.	There are only small beds visible in a few places along the shore.

FOR RESIDENTS. For the highlighted level of removal, I am willing to pay the following increase in annual household levy:

R 0	R 50	R 100	R 250	R 500	R 1.000	R 2.500	R 5.000	More than R 5.000	I don’t know
○	○	○	○	○	○	○	○	○	○

FOR VISITORS. For the highlighted level of removal, I am willing to pay the following increase in annual individual levy:

R 0	R 10	R 50	R 100	R 250	R 500	R 1.000	R 1.500	More than R 1.500	I don’t know
○	○	○	○	○	○	○	○	○	○

14. Some of the five characteristics that will change due to an increase in removal might be more important to you than others. Please distribute 100 points over the different characteristics according to the importance they had when making your choices in the previous question.

a)	Possibilities for swimming	____ / 100
b)	Possibilities for boating	____ / 100
c)	Possibilities for fishing	____ / 100
d)	Changes to biodiversity	____ / 100
e)	Changes to aesthetics	____ / 100
	Total	100 / 100

15. Are there any other aspects, either negative or positive, about water hyacinth that you considered when deciding on your willingness to pay? If so, write them down here:

____
____

16. How certain are you about your willingness to pay for water hyacinth removal? Please mark only one option.

Very uncertain	Slightly uncertain	Slightly certain	Very certain	I don't know
○	○	○	○	○

17. How realistic do you find the suggested costs for water hyacinth removal? Please mark only one option.

Very unrealistic	Slightly unrealistic	Slightly realistic	Very realistic	I don't know
○	○	○	○	○

18. Please rate to what degree you agree with the following statement:
I believe that levy collected for a water hyacinth removal program will be efficiently spent. **Please mark only one option.**

Strongly disagree	Disagree	Agree	Strongly agree	I don’t know
○	○	○	○	○

19. If you chose no increase of tax, please indicate why you did so. Multiple answers are possible. If not, you can skip this question.

a)	I prefer to let the water hyacinth grow naturally without removing it	○
b)	I did not find an increase of tax for removal realistic	○
c)	I do not want to pay an extra tax on principle	○
d)	I do not have enough money to pay an extra tax	○
e)	I believe the money would end up in the wrong hands	○
f)	I believe we should spend money on solving the causes instead of fighting the symptoms	○
g)	Other: ____	○

Background information

20. What is your age?

____

21. What is your gender?

a)	Female	○
b)	Male	○

22. What is your nationality?

a)	South African	○
b)	Other: ______________________	○

23. In what kind of neighbourhood did you grow up?

a)	Rural area or village	○
b)	City, town or urban agglomeration	○

24. In what kind of neighbourhood do you currently live?

a)	Rural area or village	○
b)	City, town or urban agglomeration	○

25. What is the highest level of education you have received? <u>Please choose only one answer.</u>

a)	Primary school	○
b)	Secondary school	○
c)	Vocationary education	○

d)	University degree	○
e)	Other education: ______________________________	○

26. Are you currently employed? Please choose only one answer.

a)	Yes, I am employed	○
b)	I am unemployed	○
c)	I am retired	○
d)	I am a student	○
e)	I manage the household	○
f)	No, other reason	○

27. In which sector do you work (pensioners and unemployed: past work, students: future work)? Please only choose one answer.

		Public sector	Private sector
a)	Agriculture	○	○
b)	Forestry	○	○
c)	Building and construction	○	○
d)	Manufacturing industry	○	○
e)	Energy and mining	○	○
f)	Fishery	○	○
g)	Healthcare	○	○
h)	Education	○	○
i)	Other services (anything not producing material goods)	○	○
j)	Other:______________________	○	○

28. What is your monthly gross income level in Rand?

a)	No income	○
b)	Less than R 15 000	○
c)	R 15 000 – 19 999	○
d)	R 20 000 – 24 999	○
e)	R 25 000 – 29 999	○
f)	R 30 000 – 39 999	○
g)	R 40 000 – 59 999	○
h)	R 60 000 – 79 999	○
i)	R 80 000 – 99 999	○
j)	Over R 100 000	○

29. In what type of household do you live?

a)	Single	○
b)	Couple	○
c)	Couple with underaged children	○
d)	Other adult household (all over 18 yrs.)	○
e)	Other	○

30. Please indicate to what extent do you agree or disagree with the following statements in general.

		Strongly disagree	Disagree	Agree	Strongly agree	I don' t know
a)	We are approaching the limit of the number of people the earth can support	○	○	○	○	○
b)	Humans have the right to modify the natural environment to suit their needs	○	○	○	○	○
c)	When humans interfere with nature it often produces disastrous consequences	○	○	○	○	○
d)	Human ingenuity will insure that we do NOT make the earth unlivable	○	○	○	○	○
e)	Humans are severely abusing the environment	○	○	○	○	○
f)	The earth has plenty of natural resources if we just learn how to develop them	○	○	○	○	○
g)	Plants and animals have as much right as humans to exist	○	○	○	○	○
h)	The balance of nature is strong enough to cope with the impacts of modern industrial nations	○	○	○	○	○
i)	Despite our special abilities, humans are still subject to the laws of nature	○	○	○	○	○
j)	The so–called ''ecological crisis'' facing humankind has been greatly exaggerated	○	○	○	○	○
		Strongly disagree	Disagree	Agree	Strongly agree	I don' t know

k)	The earth is like a spaceship with very limited room and resources	○	○	○	○	○
l)	Humans were meant to rule over the rest of nature	○	○	○	○	○
m)	The balance of nature is very delicate and easily upset	○	○	○	○	○
n)	Humans will eventually learn enough about how nature works to be able to control it	○	○	○	○	○
o)	If things continue on their present course, we will soon experience a major ecological catastrophe	○	○	○	○	○

Thank you very much for taking the time to fill in this questionnaire. Below there is some room for additional comments. The final page gives some additional information on our research project.

About MadMacs

MadMacs (**Ma**ss **d**evelopment of aquatic **ma**crophyte**s**) is an international research project funded by Water JPI (www.waterjpi.eu) including the South African Water Research Commission, together with local partners and is a collaboration between the following research institutes and universities:

Norwegian Institute for Water Research, NIVA (Norway)

Norwegian University of Life Sciences, NMBU (Norway)

Rhodes University (South Africa)

Leibniz-Institute of Freshwater Ecology and Inland Fisheries, IGB (Germany)

University of Rennes, UMR ECOBIO (France)

Universidade Federal do Paraná, UFPR (Brazil)

Mass development of aquatic macrophytes (water plants) in rivers and lakes is today considered a worldwide problem and considerable resources are spent on macrophyte removal each year. In MadMacs, our objective is to evaluate the causes and consequences of macrophyte removal on ecosystem structure, functions and services and to provide consistent and comparable data from five countries across three continents. Our research will contribute to improved management of aquatic ecosystems.

This survey is developed by Kirstine Thiemer, PhD candidate at NIVA/NMBU and Bart Immerzeel, PhD candidate at NMBU, in collaboration with local partners at Rhodes University, Dr. Julie Coetzee and PhD candidate Keneilwe Sebola. Our aim is to estimate the benefits and disadvantages society derives from macrophytes, and to examine if these estimates change when macrophytes are removed. If you have any further questions to the questionnaire, please contact: kirstine.thiemer@niva.no or bart.immerzeel@nmbu.no and questions regarding water hyacinth in Hartbeespoort Dam, please contact: Julie.coetzee@ru.ac.za and keneilwe.sebola@gmail.com.

For more information on MadMacs, please have a look at our website by scanning the QR code below or by going to:
https://www.niva.no/en/projectweb/madmacs