The development of a spatio-temporal model for water hyacinth, *Eichhornia crassipes* (Martius) Solms-Laubach (Pontederiaceae), biological control strategies

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Declaration

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Abstract

The sustainable and cost-effective management of the notorious water hyacinth weed remains a challenge in South Africa. In this study, a reaction-diffusion model, consisting of a system of delayed partial differential equations, is developed to mathematically describe the population growth and dispersal of water hyacinth and the interacting populations of the various life stages of the *Neochetina eichhorniae* weevil as a biological control agent (BCA) in a temporally variable and spatially heterogeneous environment, subject to homogeneous Neumann boundary conditions on a bounded two-dimensional spatial domain. The primary objectives are to establish a spatio-temporal model which may be used to investigate the efficiency of different biological control release strategies, providing guidance towards the optimal magnitude, frequency, timing and distribution of BCA releases, and to evaluate the cost-effectiveness of local mass rearing programmes in biological control. Although previous studies have started to examine the influence of temperature on the population dynamics of the two species and the control of the weed under constant conditions, the model developed in this study is the first to evaluate the effect of introducing spatial dynamics. In addition, for the first time in research of water hyacinth management, different BCA release strategies are compared by means of mathematical modelling to provide practical recommendations for efficient and cost-effective biological control of water hyacinth in South Africa without having to conduct formal field experiments.

Numerical solutions emphasise the benefit of frequent releases of *N. eichhorniae* compared to a once-off release in the long term, as well as the advantage of more distributed releases along the edges of an infested water body. Furthermore, releases commencing in summer appear to be significantly more efficient and cost-effective than releases commencing in winter. The model is applied to a real-world release site in order to illustrate how the model may be utilised to provide guidance towards suitable BCA release strategies, which may minimise costs while maximising the benefit for a specific site.

Uittreksel

Die volhoubare en koste-effektiewe bestuur van die berugte waterhiasint onkruid bly 'n uitdaging in Suid-Afrika. In hierdie studie word 'n reaksie-diffusiemodel, wat bestaan uit 'n stelsel van vertraagde parsiële differensiaalvergelykings, ontwikkel om die bevolkingsaanwas en verspreiding van die waterhiasint en die interaktiewe bevolkings van die verskillende lewenstadiums van die *Neochetina eichhorniae*-kewer as 'n biologiese beheeragent in 'n dinamiese en ruimtelik-heterogene omgewing wiskundig te beskryf, onderhewig aan homogene Neumann-randwaardes op 'n begrensde, tweedimensionele ruimtelike gebied. Die primêre doelstellings is om 'n model tot stand te bring wat gebruik kan word om die doeltreffendheid van verskillende biologiese beheervrylatingstrategieë te ondersoek, om leiding te verskaf met betrekking tot die optimale omvang, frekwensie, tydsberekening en verspreiding van beheeragentvrylatings, en om die koste-effektiwiteit van plaaslike massakweekprogramme in biologiese beheer te evalueer. Alhoewel vorige studies begin het om die invloed van temperatuur op die bevolkingsdinamika van die twee spesies en die beheer van die onkruid onder konstante toestande te ondersoek, is die model wat in hierdie studie ontwikkel is die eerste om die effek van die bekendstelling van ruimtelike dinamika te evalueer. Bykomend, vir die eerste keer in navorsing van waterhiasintbestuur, is verskillende biologiese beheeragentvrylatingstrategieë met mekaar vergelyk met behulp van wiskundige modellering om praktiese aanbevelings vir doeltreffende en koste-effektiewe biologiese beheer van waterhiasint in Suid-Afrika te voorsien sonder om formele veldeksperimente uit te voer.

Numeriese oplossings beklemtoon die voordeel van gereelde vrylatings van *N. eichhorniae* in vergelyking met 'n eenmalige vrylating in die langtermyn, asook die voordeel van meer verspreide vrylatings langs die kante van 'n besmette waterliggaam. Verder vertoon vrylatings wat in die somer begin om aansienlik meer doeltreffend en koste-effektief te wees as vrylatings wat in die winter begin. Die model word toegepas op 'n werklike vrylatingsgebied om te illustreer hoe die model gebruik kan word om leiding te verskaf met betrekking tot geskikte biologiese beheeragentvrylatingstrategieë, wat kostes mag minimeer terwyl die voordeel gemaksimeer word vir 'n spesifieke scenario.

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  "He is the image of the invisible God, the firstborn over all creation. For by Him all things were created that are in heaven and that are on earth, visible and invisible, whether thrones or dominions or principalities or powers. All things were created through Him and for Him. And He is before all things, and in Him all things consist." – Colossians 1:15-17;

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List of Acronyms

BCA: Biological control agent

CPI: Consumer Price Index

DDE: Delay differential equation

FEM: Finite element method

GIS: Geographic information system

IBM: Individual-based model

PDE: Partial differential equation

SASRI: South African Sugarcane Research Institute

USA: United States of America

List of Reserved Symbols

The symbols listed below are reserved for a specific use, unless specified otherwise in a localised section where their meanings are apparent. Other symbols may be used throughout the thesis in an unreserved fashion.

Symbols in this thesis conform to the following font conventions:		
$\mathbf{A}$	Symbol denoting a **matrix**	(Boldface capitals)
$\mathcal{A}$	Symbol denoting a **set**	(Calligraphic capitals)
$\underline{a}$	Symbol denoting a **vector**	(Underlined lower case letters)

Symbol	Meaning
a	Allee-effect threshold for weevil reproduction
$A(\underline{\xi}, t)$	Population density of adults at position $\underline{\xi}$
$\alpha_E(\theta)$	Egg daily development rate at temperature θ
$\alpha_{L_1}(\theta)$	Young larval daily development rate at temperature θ
$\alpha_{L_2}(\theta)$	Old larval daily development rate at temperature θ
$\alpha_P(\theta)$	Pupal daily development rate at temperature θ
α_E^{max}	Maximum daily development rate of egg stage
$\alpha_{L_1}^{max}$	Maximum daily development rate of young larval stage
$\alpha_{L_2}^{max}$	Maximum daily development rate of old larval stage
α_P^{max}	Maximum daily development rate of pupal stage
$c_{L_2}(\theta)$	Daily rate of damage caused by old larvae at temperature θ
$c_{L_2}^{max}$	Maximum daily rate of damage caused by old larvae
c_{wa}	Value of water per litre
c_{we}	Cost of rearing and releasing a weevil
CB	Cost/benefit of a release strategy
$\mathbf{D}$	Diffusion coefficient matrix
$\mathcal{D}$	Two-dimensional spatial domain
d_A	Adult weevil diffusion coefficient
$d_{L_2}(\theta)$	Old larval diffusion coefficient at temperature θ
d_W	Water hyacinth diffusion coefficient
$e_n(\theta)$	Evaporation rate of open water at temperature θ
$e_W(W(\underline{\xi}, t))$	Evapotranspiration rate of water hyacinth at position $\underline{\xi}$
$E(\underline{\xi}, t)$	Population density of eggs at position $\underline{\xi}$
f	Release frequency
$f(n_{wa}, p_{wa})$	Water nutrient scaling function for the water hyacinth growth rate

$g(\theta)$	Temperature scaling function for the water hyacinth growth rate
$g(\underline{\xi}, t)$	Spatial averaging kernel for a two-dimensional unbounded spatial domain
$G(\underline{\xi}, \underline{x}, t)$	Spatial averaging kernel for a two-dimensional bounded spatial domain
h	Elevation of a location
$h_{c_{L_2}}(\theta)$	Temperature scaling function for old larval damage rate
$h_E(\theta)$	Temperature scaling function for egg development rate
$h_{L_1,L_2}(\theta)$	Temperature scaling function for larval development rates
$h_P(\theta)$	Temperature scaling function for pupal development rate
$h_q(\theta)$	Temperature scaling function for weevil oviposition rate
H	Plant density at which herbivore feeding is reduced by half
I	Number of new adult weevils released per position
J_{L_1}	Density-dependent scaling parameter for young larval mortality
K	Carrying capacity of water resource
l	Latitude of a location
$L_1(\underline{\xi}, t)$	Population density of young larvae at position $\underline{\xi}$
$L_2(\underline{\xi}, t)$	Population density of old larvae at position $\underline{\xi}$
m	Number of nodes in triangular mesh created in MATLAB
M	Number of time-stepping increments when solving the system in MATLAB
$\mu_A(\theta)$	Density-independent mortality rate for the adult stage at temperature θ
$\mu_{L_1}(\theta)$	Density-independent mortality rate for the young larval stage at temperature θ
$\mu_{L_2}(\theta)$	Density-independent mortality rate for the old larval stage at temperature θ
$\underline{n}$	Outward normal vector on the boundary
n_{wa}	Concentration of nitrogen in the water resource
$\underline{\xi}$	Position vector in spatial domain
p_{wa}	Concentration of phosphorus in the water resource
$P(\underline{\xi}, t)$	Population density of pupae at position $\underline{\xi}$
$q(\theta)$	Daily weevil oviposition rate at temperature θ
q_{max}	Maximum daily weevil oviposition rate
$r(\theta)$	Daily water hyacinth intrinsic growth rate at temperature θ
r_{max}	Maximum daily growth rate of water hyacinth
$R_A(\underline{\xi}, t)$	Rate of recruitment into adult stage at position $\underline{\xi}$
$R_{L_1}(\underline{\xi}, t)$	Rate of recruitment into young larval stage at position $\underline{\xi}$
$R_{L_2}(\underline{\xi}, t)$	Rate of recruitment into old larval stage at position $\underline{\xi}$
$\bar{R}_{L_2}(\underline{\xi}, t)$	Weighted average of R_{L_2} at position $\underline{\xi}$ at an earlier time
$R_P(\underline{\xi}, t)$	Rate of recruitment into pupal stage at position $\underline{\xi}$
s	A point in time (in days)
$S_{L_1}(\underline{\xi}, t)$	Density-dependent through stage survival rate for young larvae at position $\underline{\xi}$
$\sigma_E(\theta)$	Density-independent through stage survival probability for eggs at temperature θ
$\sigma_{L_1}(\theta)$	Density-independent through stage survival probability for young larvae at temperature θ
$\sigma_{L_2}(\theta)$	Density-independent through stage survival probability for old larvae at temperature θ
$\sigma_P(\theta)$	Density-independent through stage survival probability for pupae at temperature θ
σ_E^{max}	Maximum probability of surviving through the egg stage

$\sigma_{L_1}^{max}$	Maximum probability of surviving through the young larval stage
$\sigma_{L_2}^{max}$	Maximum probability of surviving through the older larval stage
σ_{P}^{max}	Maximum probability of surviving through the pupal stage
t	Time (in days)
$t_E(\theta)$	Development duration of egg stage at temperature θ (in days)
$t_{L_1}(\theta)$	Development duration of young larval stage at temperature θ (in days)
$t_{L_2}(\theta)$	Development duration of old larval stage at temperature θ (in days)
$t_P(\theta)$	Development duration of pupal stage at temperature θ (in days)
t_E^{max}	Maximum duration of egg stage (in days)
$t_{L_1}^{max}$	Maximum duration of young larval stage (in days)
$t_{L_2}^{max}$	Maximum duration of old larval stage (in days)
t_P^{max}	Maximum duration of pupal stage (in days)
θ	Temperature (in °C)
θ_d	Dew point temperature (in °C)
θ_E^{max}	Maximum temperature for egg development
θ_E^{min}	Minimum temperature for egg development
θ_E^{opt}	Optimum temperature for egg development
θ_h^{max}	Maximum temperature for water hyacinth growth
θ_h^{min}	Minimum temperature for water hyacinth growth
θ_h^{opt}	Optimum temperature for water hyacinth growth
θ_{L_1,L_2}^{max}	Maximum temperature for larval development
θ_{L_1,L_2}^{min}	Minimum temperature for larval development
θ_{L_1,L_2}^{opt}	Optimum temperature for larval development
θ_P^{max}	Maximum temperature for pupal development
θ_P^{min}	Minimum temperature for pupal development
θ_P^{opt}	Optimum temperature for pupal development
θ_q^{max}	Maximum temperature for oviposition
θ_q^{min}	Minimum temperature for oviposition
θ_q^{opt}	Optimum temperature for oviposition
$\underline{u}$	Solution of the system of PDEs
$\mathbf{U_n}$	History matrix for the time dependent results of the n^{th} PDE in MATLAB
$W(\underline{\xi}, t)$	Biomass density of water hyacinth material at position $\underline{\xi}$
$\underline{x}$	Position vector in spatial domain
$X(\underline{\xi}, t)$	Function which regulates releases at position $\underline{\xi}$

CHAPTER 1

Introduction

Contents

The Amazonian water hyacinth, *Eichhornia crassipes* (Martius) Solms-Laubach (Pontederiaceae), has since the 1880s spread its roots across the USA and eventually the world, where it is now notorious for being one of the world's, as well as South Africa's, worst aquatic weeds. Initially distributed for its ornamental value, water hyacinth now rules water masses in tropical and warm regions of the world by forming dense impenetrable layers across the surfaces, as illustrated in Figure 1.1. Invasive alien plants have globally been recognised as the second largest threat to biodiversity [20]. Man and animal suffer severely under its reign. Natural habitat is abducted. Ecosystems are threatened as native plants are being displaced. Travelling on water and fishing are hampered. Water sports areas are limited. Irrigation systems are blocked. Hydro-electric turbine intakes are obstructed. Water loss rates drastically increase due to the higher evapotranspiration rate of water hyacinth, leading to higher water supply costs. Water quality is reduced. Health risks arise with the plants providing breeding grounds for mosquitoes and other disease carriers. Communities relying on invaded water bodies for transport and basic needs are devastatingly affected [31, 38, 69].

FIGURE 1.1: *Water hyacinth blankets the Kuilsriver in Cape Town, June 2015.*

Since the early 1900s, several initiatives to counteract this invasive alien plant species' growth have been investigated. Chemical, mechanical and manual control methods proved both very expensive and ineffective, especially for large infested water bodies. These concerns motivated a more serious consideration of the use of biological control methods [38].

1.1 Background

Water hyacinth, existing in still or slow-moving fresh water, is a floating water plant which reproduces by budding and/or the spreading of seeds. Budding entails the process of growing long shoots or the breaking off of parts of the plant that develop into new plants. The plant also produces thousands of seeds several times a year after flowering. Seeds can produce flowers as early as 10 - 15 weeks after it started to grow in warm, shallow water or moist silt. Wind, water streams, boats, birds and other animals may unintentionally assist in spreading the plant into other areas. Water hyacinth has an exponentially high growth rate, especially under ideal conditions, such as tropical weather, warm temperatures and water with high nutrient levels (particularly nitrogen and phosphorous). It can double its size in the matter of a week. Seeds can still reproduce after 15 - 20 years of remaining in water sediments. These qualities make it extremely difficult to control this determined weed [37, 69].

1.1.1 History of water hyacinth control globally

Research conducted during the past few decades have investigated possible uses of the plant, such as a fertilizer, fodder, paper and fibre source, or for mineral nutrient removal from polluted water. Eradicating the weed therefore involves a potential conflict of interests. However, these uses seldom develop into sustainable activities and the cost of water hyacinth to communities far outweighs any benefits [38].

One of the more successful methods of control is biological control. Natural enemies are sought in the weed's native land and put through quarantine where their host specificity is assessed. If proven to be host specific, they are certified for release as biological control agents (BCAs) for the specific weed. Candidate species are then released in the new habitat where they attack the weed by feeding on it, thereby contributing to the suppression of the plant population. In its natural habitat, water hyacinth is attacked by a large number of arthropods. Study of the ecology of some of these as possible BCAs began in Argentina in 1961. The first natural enemies were released as BCAs in the USA in early 1970s. Since then several agents have been released in 33 countries [38]. While mechanical and herbicidal control are viewed as short-term or immediate control options, biological control outranks other methods by offering a more sustainable, environment-friendly, long-termed and possibly more affordable solution to the problem, even for large or inaccessible areas [31, 32].

Different biological control methods have been developed. *Classical biological control* consists of releasing the host specific BCAs that survived quarantine directly in the new habitat [38]. This process consists of a once-off release of BCAs and yields a relatively small number of agents to be released at any one time. Even though successful biological control of water hyacinth has been achieved, this method takes a long time to be effective. Another biological control approach, where BCAs that have been cleared from quarantine are taken to a *mass rearing* facility, has evolved. With the use of mass rearing technology, the BCAs can be reared in large numbers before they are released. As a result, more BCAs may be frequently released to speed up biological control [12].

1.1.2 History of water hyacinth control in South Africa

In South Africa, water hyacinth was first documented in 1908 on the Cape Flats and was introduced into KwaZulu-Natal at about the same time, supposedly as an ornamental aquatic plant for garden ponds and aquaria. Since then it has spread to water bodies all over the country. In Figure 1.2, the distribution of the weed in South Africa in 2002 is given. In 2002, this invasive alien plant was already widespread throughout the country, impacting rivers and water bodies in six provinces [31]. A warning of what was likely to happen with water hyacinth was printed as early as 1913 [37].

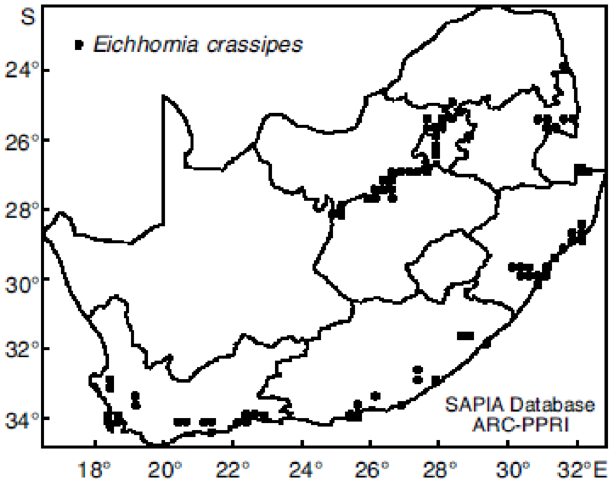

FIGURE 1.2: *Distribution of water hyacinth,* Eichhornia crassipes, *in South Africa in 2002 [31].*

Available control methods include mechanical control, physical removal, application of herbicides and the importation and release of BCAs [38]. Since the 1970s, South African control options have largely focussed on the use of herbicides, consisting of target-specific chemical pesticides used to kill or control unwanted plants [64]. Opposed to this, is these early years, biological and integrated control[1] have received much less effort and investment, despite the fact that these methods proved highly successful in other parts of Africa and the world. Currently, the main focus of integrated control in South Africa is a combination of biological and herbicidal control. With the exception of cables spanned across rivers to collect the weed, no large scale mechanical control is practised at this stage [38].

One of the *Working for Water* (now known as *Natural Resource Management Programmes of the South African Department of Environment Affairs*) funded mass rearing centres for weed BCAs in South Africa is based at the South African Sugarcane Research Institute (SASRI) in Mount Edgecombe in KwaZulu-Natal [69]. Aquatic weed BCAs are reared on their host plants in portable pools (see Figure 1.3). Mass rearing and re-releases are aimed at establishing the full suite of natural enemies at all sites throughout the country, to ensure that inappropriate release methods used previously were not the cause of non-establishment [32]. Another mass rearing facility is situated at the *Invasive Species Unit* in Westlake, Cape Town. Currently, the Cape Town unit is mainly focusing on rearing *Megamelus scutellaris* Berg (Hemiptera: Delphacidae) as BCAs for water hyacinth due to resource constraints. The unit is collecting about 50 000 *M. scutellaris* per month which need to be distributed between four water hyacinth infested sites in the area [52, 60]. Weekly releases of BCAs have commenced in September 2014 [36], however,

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[1] Integrated control involves the use of two or more control methods to achieve better control of invasive alien species.

little to no success could be observed by June 2015.

FIGURE 1.3: *Mass rearing centre for weed BCAs at SASRI, KwaZulu-Natal.*

The biological control of water hyacinth in South Africa currently relies on six established agents, the largest number in all countries involved in such programmes against water hyacinth, of which the popular *Neochetina eichhorniae* Warner (Coleoptera: Curculionidae) weevil species is considered in this study (see Figure 1.4). After years of thorough research, these agents can now be easily and relatively cheaply distributed worldwide [38].

FIGURE 1.4: *The* N. eichhorniae *adult weevil.*

Biological control in South Africa has been effective in certain areas such as the New Year's Dam in the Eastern Cape (see Figure 1.5), but remains hampered by certain restrictions [31, 32]. Firstly, *unsuitable climatic conditions* like cold winters and frequent frost may restrict some of the species to become abundant and control the weed. Successful biological control of water hyacinth elsewhere in the world highly correlates with tropical or subtropical climates. Secondly, *high nitrogen and phosphorus levels* in infested waters allow the weed to thrive and reproduce rapidly. BCAs are often unable to suppress the resulting sudden and massive growth of the host plant. Measures to limit the plant growth rate, such as the upgrading of waste-water treatment works and investigation into industrial effluent (and therefore nutrient control), is an ongoing process. Finally, *flooding, herbicide application and mechanical removal programmes* regularly remove the natural enemy populations as well as the water hyacinth infestations, limiting the success of biological control. When cleared or treated water bodies are re-infested after these removals, the enemies are absent, resulting in rapid and abundant growth of the weed [31, 32, 81].

FIGURE 1.5: *New Year's Dam, South Africa, where* N. eichhorniae *was released in 1990 and by 2000 had reduced the infestation to 10% cover. In 1997 (left), the dam was more then 90% covered by water hyacinth. In 2003 (right), water hyacinth covered less than 10% of the dam [20, 49].*

1.1.3 Costs and benefits of biological control

The global phenomenon of ecosystems being invaded by alien plants is a serious environmental problem that threatens the sustainable use of benefits derived from such ecosystems [20, 76]. More than 9 000 plant species have been introduced to the South African ecosystem of which more than 160 species rank as serious pest weeds, although many more may become weeds in the future [56, 73, 76]. In 2000, Le Maitre *et al.* [43] reported that an estimated 10.1 million hectares of South Africa and Lesotho had been invaded to some degree by a wide range of alien plants, mainly trees and woody shrubs, with undoubtedly significant impacts, yielding substantial costs. According to their research, the Western Cape was the most heavily invaded at about a third of the total area at that stage, followed by Mpumalanga, KwaZulu-Natal and the Northern Province [43]. In 2011, Pimentel [56] reported an estimated annual environmental loss of just more than US$1 billion per year for all weeds in South Africa, equal to 2.5% of the 2009 South African gross domestic product.

Relatively little research has been done on the economic aspects and consequences of invasions. Van Wilgen *et al.* [76] reviewed what was known of the economic consequences of alien plant invasions in South Africa in 2001. Economic arguments by Le Maitre *et al.* [42], Van Wilgen *et al.* [77] and Van Wilgen *et al.* [80] have been used to successfully launch the largest environmental management programme in Africa, namely the *Working for Water* programme [76, 79]. In addition to the obvious environmental and economic advantages, invasive plant control programmes in South Africa have leveraged further benefits (mainly through engaging unemployed people in labour-intensive clearing, follow-up and rehabilitation projects) for the expensive control programmes from the government's poverty relief budget [76]. These benefits justified the spending of more than US$100 million by the South African government on the *Working for Water* programme between 1995 and 2000. Biological control of invasive species is a solution that appears to offer considerable benefits, which far outweigh the costs. Biological control is considered as one of the best and most cost-effective interventions for addressing the problem for most invasive alien plant species in South Africa [56, 76]. Most of the benefits of control are derived from restricting the invasive species' spread and reducing their densities, thereby avoiding or reducing future negative impacts. The challenge is to justify the expenditure that will avoid or reduce these losses [56].

South Africa is regarded as a water-scarce, drought prone region. Water shortages may have a significant influence on economic development and productivity, highlighting the imperative need to manage water as a national asset and for overall social benefit [51]. Water hyacinth is known to degrade aquatic ecosystems and to change river flows [76]. The loss of water due to excessive evapotranspiration from water hyacinth, which averages about 3.7 (2.6 to 6.6) times that of evaporation from open water surfaces [54, 71], accounts for the largest part of the economic consequences of the weed in South Africa. Consequently, the management of water hyacinth in South Africa is vital given its impact on water loss. However, few studies have quantified the impact of this weed economically and ecologically and even fewer studies have quantified the benefits of its control [20]. The only alternative sources of water are through recycling and desalination, both of which are very expensive. Besides the gains to be obtained from the effective control of alien plants in terms of water conservation and quality, there are many other advantages. These include the conservation of biodiversity, increased catchment stability, a greater potential for ecotourism, reduction in health risks, an increase in quality of life for communities relying on invaded water bodies for basic needs and direct job creation through the control programmes [42].

The need to validate the continued funding for clearing, controlling and researching of alien plants serves as motivation for recent studies around the economic impacts of alien invasive plants in South Africa [20, 73]. Turpie [73] noted that only a few studies have investigated aquatic alien plants such as water hyacinth and that most studies have focused on terrestrial or riparian invaders, despite the fact that aquatic weeds have equally severe negative effects on the environment and economy [20].

The most widely used economic approach to determine the feasibility of biological control programmes is the cost-benefit analysis [20]. However, limited resources in South Africa have meant that scientists have concentrated their efforts on the identification, screening, release and establishment of BCAs, without further investigations of the effects on a large scale, making cost-benefit studies the exception rather than the norm [78]. Cost-benefit studies involve quantifying the effects of biological control efforts by comparing the benefits with the costs of the programmes. This includes the full financial costs accumulated to control the alien invasive species, accounting for costs associated with research and technology, with salaries of biological control practitioners according to their time dedicated to the programme, with maintenance and monitoring, as well as with administration and travelling expenses [20]. These costs vary amongst projects. The start-up costs for biological control programmes are usually relatively high, with subsequent costs generally decreasing over time [20, 52]. The benefits of the programme will be determined by quantifying the benefits associated with preventing or reducing invasions [20]. Each site may have its own risks and consequences associated with water hyacinth infestations. Research has shown that as much as 70% of benefits obtained relate to water, thereby emphasising how biological control programmes of invasive species greatly contribute towards water conservation [78].

Water hyacinth's impacts on water resource utilisation [31] and biodiversity [11, 47] have been investigated, but its impact on water loss through extensive transpiration created by its dense mats has not been studied in South Africa, except for a case study presented by Fraser *et al.* [20] earlier this year, where they quantified the benefit/cost ratio of water saving due to the biological control of water hyacinth on the New Year's Dam, Alicedale, South Africa. Fraser *et al.*'s cost-benefit study, which considered the costs of the programme and the loss of water from evapotranspiration due to water hyacinth, highlighted significant social and economic benefits for the local community of Alicedale [20], even though they used an aggregated approach. The economic evaluation of biological control programmes allows for the efficient allocation of scarce resources between competing control and management programmes [20]. The future funding of control programmes will depend on the demonstration of its full socio-economic worth, which, in turn, will depend on how efficiently its resources have been allocated. Until now, the total economic benefits have not been adequately described in economical terms, nor has there been any prioritisation strategy in place to ensure that the benefits of the control programmes' current activities are maximised [73].

1.2 Problem description

The sound and cost-effective management of the water hyacinth weed remains a challenge in South Africa [81]. Managers of water hyacinth control programmes in South Africa may benefit from a thorough analysis of the options for control. The success of biological control alone in other parts of Africa raises questions as to why it has not been as successful in South Africa. Unsuitable climatic conditions like cold winters may restrict some of the species to become abundant and control the weed. Many of the management decisions that have been taken in the past have been taken in the absence of clear guidelines with regard to the relative results of different control options. Critical assessments of the approaches may therefore assist managers in making better-informed decisions in the use of control options [81]. More research is needed to determine the optimal effort for biological control. In Australia, for example, research has indicated the marginal value of extra funds for weed control and where and how additional releases of BCAs are economically justified to speed up control [73]. At the moment, managers of biological control programmes in South Africa are releasing as many BCAs as possible at a time. The cost of rearing these agents makes it worth the while to investigate the releasing process in order to determine whether there exists a release strategy that would yield optimum results [12].

The Cape Town *Invasive Species Unit* has started with weekly releases of BCAs (*M. scutellaris*) at four water hyacinth infested sites in September 2014 [36]. BCAs are released by hand at the edges of the infested water bodies. Upon a field visit during June 2015, no BCA establishment or influence could be observed at the Kuilsriver site. Suggestions towards more effective release strategies for different temperatures may aid in improving the control of water hyacinth. Byrne *et al.* [8] concurs with the hypothesis that flawed release procedures contribute to the variable success of biological control programmes for water hyacinth.

In this study, mathematical modelling is used to investigate the efficiency and cost-effectiveness of different BCA release strategies to water hyacinth management for different temperatures and climates in South Africa. Model simulations may aid in improving the control of water hyacinth by providing suggestions towards more effective release strategies for specific sites. Additionally, mathematical modelling may be used to indicate prior to release that a specific agent may not be able to develop or establish under a certain temperature threshold and that a different agent should be considered for that area, saving on costly in-field experimentation. Previous models have started to examine the influence of temperature on the population dynamics of the two species and the control of the weed under constant conditions [74, 91, 93, 94], but the effect of introducing spatial dynamics is yet to be investigated.

1.3 Scope and objectives

The scope of the research will only consider biological control of water hyacinth in South Africa. This narrows the temperature range that will be taken into account down to the applicable possible temperatures in this country. The main contribution is the development of a mathematical model which is able to describe the water hyacinth and *N. eichhorniae* population growth, dispersal and interaction in various scenarios. The scope is limited to the *N. eichhorniae* weevil species and how it can be optimally utilised as BCA in South Africa. The primary objectives of this study are to:

Objective I: Perform a literature survey of the life cycles of the water hyacinth and the *N. eichhorniae* weevil, as well as the impact which they have on each other. This should provide the necessary biological background to formulate a realistic mathematical model of the population growth and interaction of the two species.

Objective II: Perform a literature survey of

a) mathematical models previously formulated to describe the interaction between water hyacinth and the *N. eichhorniae* weevil;

b) spatio-temporal modelling approaches which may be adopted to model the dispersal along with the population growth of the two species.

Objective III: Construct a model to mathematically describe the population growth and dispersal of water hyacinth and the interacting populations of the various life stages of the *N. eichhorniae* weevil as BCA in a temporally variable and spatially heterogeneous environment by

a) constructing suitable equations;

b) determining suitable parameters and parameter values for the growth and dispersal of the two species by means of model calibration[2];

c) validating the parameter values and mathematical content.

The spatio-temporal model may be used to investigate the efficiency of different release strategies for various temperatures and water hyacinth distributions, providing guidance towards the optimal magnitude, frequency, timing and distribution of BCA releases.

Objective IV: Develop a cost-benefit function which may be utilised to

a) evaluate the cost-effectiveness of local mass rearing programmes in biological control, determining whether the benefit of a faster decrease in water loss due to greater and more frequent BCA releases is worth the expenses pertaining to the rearing and releasing of more BCAs;

b) provide guidance towards the most cost-effective release strategy of BCAs in the short and long term.

Objective V: Apply the model presented in Objective III to a real-world release site in order to illustrate how the model may be utilised to provide guidance towards suitable magnitudes, frequencies, timing and distributions of BCA releases for a specific site.

Objective VI: Provide direction for possible future studies.

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[2] Calibration is the process of fitting the model to the observed data by adjusting the parameters [39]

1.4 Thesis organisation

This introductory chapter forms the first of seven chapters contained in this thesis. Chapter 2 provides the basic biological background of water hyacinth and the *N. eichhorniae* weevil, which is necessary in order to understand the assumptions made during the construction of the model in subsequent chapters.

Chapter 3 provides the reader with the mathematical background with respect to the modelling of water hyacinth and *N. eichhorniae* weevil population growth and interaction, together with the shortcomings of current modelling approaches. The chapter also provides a discussion on the main modelling approach adopted in this study.

Chapter 4 comprises of a detailed description of the construction of the spatio-temporal model used to mathematically describe the population dynamics of the water hyacinth and weevil system in a temporally variable and spatially heterogeneous environment, as well as detailed discussions and derivations of the model input and output parameters, including the derivation of a cost-benefit function which may be used to determine the most cost-effective release strategy for a specific scenario. An elaborate description of the implementation of the model in Matlab 9.0 is also provided, followed by various model validation tests.

The main purpose of Chapter 5 is to investigate the efficiency and cost-effectiveness of different water hyacinth BCA release strategies for both short-term and long-term scenarios by means of numerical simulation of the model presented in Chapter 4 in order to be able to provide guidance towards the optimal timing, frequency, distribution and magnitude of BCA releases. Chapter 5 closes with sensitivity analyses, ascertaining the robustness of the model output.

In Chapter 6, the model is applied to a real-world release site in order to illustrate how the model may be utilised to provide guidance towards suitable magnitudes, frequencies, timing and distributions of BCA releases, which will minimise costs and maximise the benefit for a specific site. Practical site-specific recommendations for efficient and cost-effective BCA release strategies are provided.

Finally, Chapter 7 contains a brief summary of the work presented in this study, as well as an overview of the main contributions of the study with respect to the mathematical modelling of biological control strategies for water hyacinth. The chapter concludes with suggestions for possible future work to further this research.

CHAPTER 2

Biological literature survey

Contents

In this chapter, the necessary biological background of the water hyacinth and the *N. eichhorniae* weevil is provided. In order to model biological control strategies for water hyacinth and to understand the assumptions made during the construction of the model, it is necessary to investigate the life cycles of the plant and its enemies as well as the way they influence each other.

2.1 Origin and distribution of water hyacinth

In 1823, the German naturalist C. von Martius discovered the species while carrying out botanical surveys in Brazil. He named it *Pontederia crassipes*. Sixty years later, it was included in the *Eichhornia* genus. The reason for the world-wide distribution of this weed is generally accepted to be due to its ornamental value or as animal feed while totally ignorant of the plant's invasive capabilities and the enormous negative ecological impact it would have on fresh water ecosystems. The native range of *E. crassipes* is spread throughout South America and parts of central America [37].

In North America, water hyacinth is believed to have been introduced in 1884 at the Cotton States Exposition in New Orleans, Louisiana. Since its introduction to Louisiana, it has spread to about 50% of the states in the USA [37].

Asia was invaded towards the end of the 19th century via Japan and Indonesia where the weed grew in rice fields and as an ornamental plant in botanical gardens. In India it first appeared in Bengal at the beginning of 1890. It has also established in Taiwan and China as early as 1901 as a good fodder plant [37].

Water hyacinth was first noticed in Australia in Brisbane, Sydney and Grafton in the 1890s and has since spread to all mainland states. In 1962, it expanded its territory to Papua New Guinea. New Zealand, Bangladesh and many islands in the Pacific Ocean [37].

Europe has been affected by water hyacinth through Portugal since 1939. JF Potter commented in *The Environmentalist* that water hyacinth has also been observed in the wild in Britain and quoted: "Invasive species, particularly those associated with aquatic habitats, are outcompeting many of Britain's native plants and the law is doing nothing to stop them…" [58].

In recent times, the lack of relevant legislation or the enforcement thereof, the lack of general public awareness or the lack of political will-power to step in have assisted in allowing the weed to disperse. Africa has been particularly affected by the introduction and spread of water hyacinth [37].

2.2 The life cycle of water hyacinth (*Eichhornia crassipes*)

Floating on water surfaces or anchoring itself with long, feather-like roots, water hyacinth exists in still or slow-moving fresh water and presents beautiful light blue or violet flowers (see Figure 2.1). The upper petal has a characteristic dark blue patch with a yellow centre. Flowers grow together in flower spikes in clusters of eight to ten flowers, with each flower measuring about 5 cm in diameter. Adult plants are normally 10 - 20 cm high, but can extend to one meter when growing together in dense mats. The leaves are rounded and shiny, dark-green in colour, with distinctive upright or bulbous petioles [37, 69].

FIGURE 2.1: *Water hyacinth flowers.*

Water hyacinth, growing in ideal conditions, has an incredible mechanism to outgrow any native species occurring in the system. The presence of excess nitrogen and phosphorus in water bodies encourages an even faster growth of the plant. It can reproduce in two ways: vegetatively and sexually.

- The main method of reproduction is *vegetatively* [3, 10, 37, 54]. The "mother" plant produces new plants from stolons (see Figure 2.2). Winds, currents and wave actions help to spread the plant to other areas [37]. Given enough space and favourable growing conditions, the number of plants may double at an average rate of once every two weeks (range 11 – 18 days, depending on the weather). From ten adult plants, a total of about 655 360 daughter plants may thus be produced in a single growing season of eight months (32 weeks). The edge of the surface mat may extend by 60 cm per month under good growing conditions [54]. Other studies report that the surface area may increase by an average of 8% per day, doubling the surface mat in as little as a week (every 6.2 – 9 days) [37].

- *Sexual* reproduction is known to be limited. In an extensive survey performed by Barrett [3], only 45.9% of the flowers sampled produced capsules. The ovary of one plant may produce up to 500 ovules, with an average of 44.2 and a maximum of 50 seeds per capsule [3, 54]. Up to 900 000 capsules have been observed in an area of 0.405 ha [54], equating to about 40 million seeds. Seeds are produced several times a year following flowering. Plants may flower throughout the year, given the climate and environmental conditions are suitable [37]. Flowering season in North America, however, only lasts for five to nine months [3]. Pollination by insects rarely occurs, but when the plant starts to wilt, self-pollination is common. Water hyacinth seeds may remain dormant for up to twenty years until the correct climatic conditions arise for it to germinate. Seeds only germinate in warm, shallow water or on moist sediments. Out of nineteen water hyacinth populations surveyed by Barrett [3], seed production occurred in all of them, but only three of the populations produced seedlings, occurring only on saturated soil at the edges of the water hyacinth populations. Very few seeds germinate on the mat, as they may either be lost in plant debris or sink. Further tests indicate that when appropriate field conditions occur, a seed germination rate of as high as 87.5% is possible. Flowering may occur ten to fifteen weeks after germination. Experiments performed by Penfound and Earle [54], however, suggested that the life cycle from seed to seed is a much slower process in nature since none of their sampled plant succeeded in completing the life cycle in five months. If suitable ecological conditions for seed germination and seedling establishment occur, sexual reproduction could be a potential problem resulting in the re-infestation of cleared areas [3].

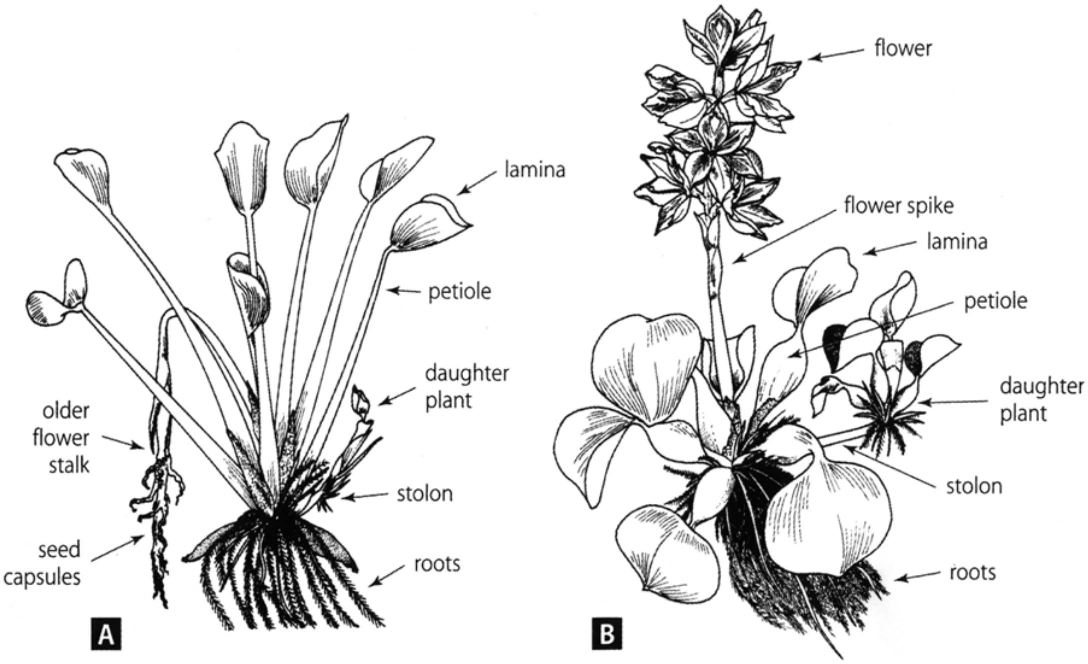

FIGURE 2.2: *Water hyacinth plants with (A) slender petioles and (B) bulbous petioles [38].*

2.3 The life cycle of the mottled water hyacinth weevil (*N. eichhorniae*)

The *Neochetina* genus of semi-aquatic weevils uses plants in the Pontederiaceae family as hosts for development. Specifically, the *Neochetina eichhorniae* weevil develops exclusively on water hyacinth, *E. crassipes* [10]. A generalised life cycle of the *N. eichhorniae* weevil may be seen in Figure 2.3. A more detailed discussion of the weevil's various life stages is given below.

Eggs: Slender, soft, single eggs are laid under the epidermal layers of the young central leaves. Under temperatures of 25 – 30°C, females lay between 5 and 7.3 eggs per day. A female can lay a total of approximately 300 eggs in her lifetime. Eggs need high temperatures to develop normally and will not hatch at temperatures under 15°C [18, 38].

Larvae: Larvae develop through three instars. Newly hatched, they tunnel through the lower parts of the petioles and find themselves in the crown of the plant where they dig small pockets and feed on new buds. As the plant grows, the more matured instar larvae, now established in the older outer leaves, sometimes make their way back to younger leaves where their feeding causes severe damage. Their development rates depend highly on the quality of the plant and the temperature [38].

Wilson [91] observed that third instar larvae (referred to as old larvae) are able to move between connected plants, while Wilson *et al.* [92] observed that first and second instar larvae (referred to as young larvae) do not move from the petioles in which they were laid, let alone between plants. Young larvae are thus assumed to be immobile. Wilson *et al.* [92] further noted that the survival of first and second instar larvae declines as larval density increases, but third instar larvae are not affected by density dependence[1]. It is assumed that the greater mobility of the old larvae makes them less subject to competition for food and/or to be affected by plant mortality [92]. Density dependence in insects has been reported more frequently for larval stages than for adult, egg or pupal stages as larvae originate from within the plant and their growth may become limited by food quality or quantity [91]. In accordance with this, Wilson *et al.* [92] argued that the density dependence operating in *N. eichhorniae* occurs through an interaction between young larvae and leaf longevity. Disruption of water hyacinth leaf dynamics will consequently have a significant effect on the weevils and may reduce the level of control imposed on the plant [92].

Pupae: Fully grown larvae exit the crown and make their way down to the living roots where they pupate under water [17]. They build a cocoon out of pieces of root hair and attach it to larger established roots. They can remain in the cocoon for several months [38].

Adults: Adults are nocturnal and hide themselves during the day near the crown of the plant to protect themselves against severe heat which may reduce egg production and even cause death. They start feeding on the outside of the plant within 24 hours of their appearance whereafter the production of eggs commences about six days later. Maximum feeding and oviposition occur at 30°C and *N. eichhorniae* typically produce three or four generations per year [17, 18, 65]. The male and female ratio is generally close to one [26, 38], although in South Africa females seem to dominate on healthy plants while there is an excess of males on unhealthy plants [38]. Adult life span ranges from 28 to 88 days with an average of 57.8 ± 9.6 days, depending on temperature, although life spans of between three and four months have been recorded [38, 65].

Movement behaviour of adults: During certain seasons or under specific physiological con-

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[1] Density dependence occurs when the per capita growth rate of a population is dependent on its own density. Either the mortality rate at some stage of the life cycle increases or the reproduction or input rate decreases as density increases [62].

ditions, adults may develop flight muscles and be able to fly [16]. This seems to be quite rare and the exact factors influencing wing muscle development remain difficult to pinpoint. Previous attempts by Stark and Goyer [65] to stimulate adults to fly in laboratory experiments proved unsuccessful, although reports of large numbers of *N. eichhorniae* flying at night to bright lights in Louisiana during July 1980 confirmed the existence of cases where the weevils are able to fly [65]. The wide distribution of *N. eichhorniae* in North America in the 1980s further suggested that they are strong fliers [7].

Buckingham and Passoa [7] discovered during a study in Florida in 1982–1983 that some *N. eichhorniae* weevils exposed to temperatures ranging $21 - 32$°C in laboratory experiments developed flight muscles. The percentage weevils with developed flight muscles was directly related to temperature and time period. No flight muscles developed at 37.8°C and the muscles were also underdeveloped during winter with an assumed lower threshold of about 18.3°C. Fifty percent of the considered newly emerged *N. eichhorniae* weevils held at 26.7°C developed flight muscles after 13 days. The development of flight muscles in field-collected weevils were more variable due to the variation within the population in the number of new weevils that had not previously flown or already lost their wing muscles. Flight muscles and eggs were almost always mutually exclusive for individuals. Under certain conditions female adults may switch from egg production to flight muscle development or *vice versa* [7].

The phenomenon of wing muscles regenerating and degenerating, similar to the related rice water weevil, *Lissorhoptrus oryzophilus* Kuschel, where flight muscles develop in spring prior to migration to new sites and degenerate soon after arrival as females begin to oviposit [48], offers a ready explanation for the previous failure of researchers to observe flight in the weevils. Weevils without flight muscles cannot be forced to fly. The influence of weevil density, sex, source location and food quality on flight muscle development proved to be both insignificant and inconsistent [7]. Grodowitz *et al.* [26] reported a case of possible immigration of adult weevils to a study site in Texas from nearby (60 m) areas infested with water hyacinth, supporting high numbers of *N. eichhorniae* weevils from 1987 to 1988.

Experiments with herbicide treatment of water hyacinth, which limits the weevil's food supply and forces them to either migrate or die, indicate that herbicides may speed up wing muscle development of weevils already developing muscles due to seasonal factors, but will not stimulate such development of older weevils not already in the process of wing muscle development [7, 30]. If conservation of the weevils is desired, herbicides should thus be applied when the greatest number of newly emerged weevils are present [7]. Haag [30] also suggests that it may be possible to time field herbicide applications to coincide with periods of time during which the weevils may potentially develop flight muscles and migrate to unsprayed areas of healthy plants.

During aquarium trials with herbicide application to water hyacinth, Haag [30] further discovered that even if flight muscles are absent, adult weevils are able to crawl from sprayed, decaying plants to adjacent healthy plants, if available, at least over a distance of 4 m. Dispersal experiments on unsprayed 1 m by 4 m water hyacinth mats indicated that weevils distributed themselves randomly throughout the weed mat in a course of one month. There was no apparent preference by weevils for any particular area of the weed mat and weevils were close to uniformly distributed throughout the considered area after the one month period [30].

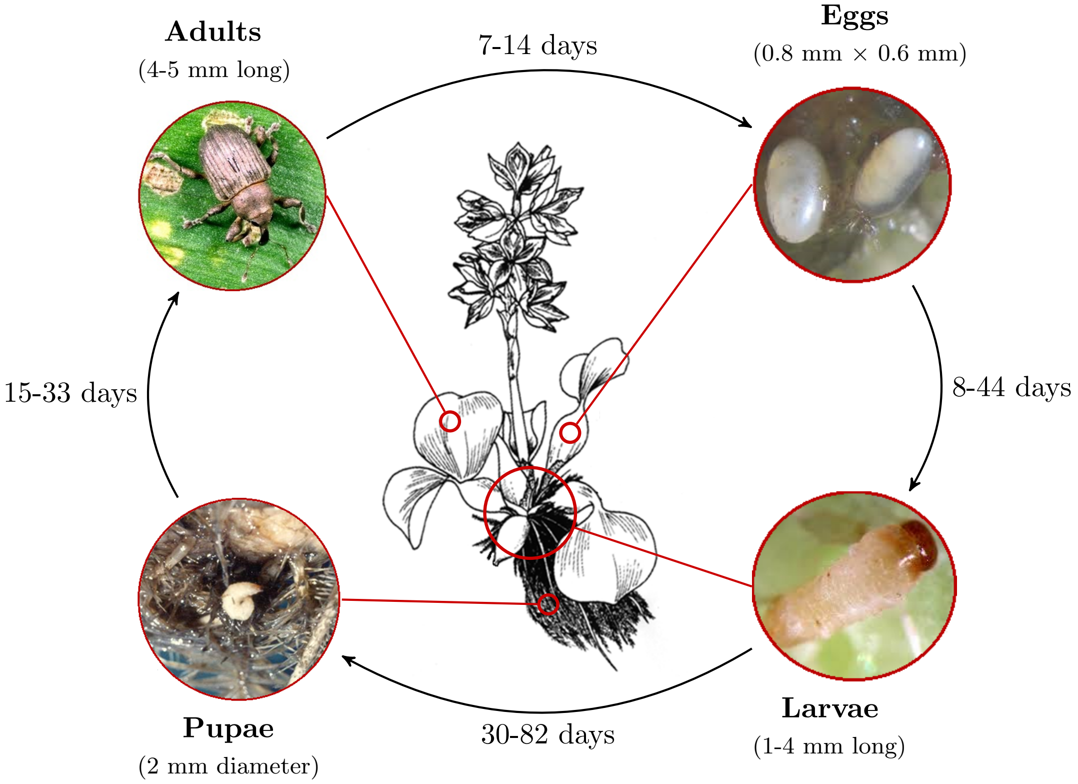

FIGURE 2.3: *Life cycle and development duration for each stage of the* N. eichhorniae *weevil and its occurrence on different organs of the water hyacinth [38, 91].*

2.4 The impact of *N. eichhorniae* weevils on water hyacinth

FIGURE 2.4: *Leaf feeding scars caused by* N. eichhorniae *adults.*

Both the *N. eichhorniae* larvae and adults feed on water hyacinth. Adult beetles feed externally on the epidermal layers of the leaves leaving behind its trademark of small, semi circular scars, as may be seen in Figure 2.4. These feeding scars do not usually penetrate the leaves, unless a scar on one side of the leaf is aligned with a scar on the opposite surface of the leaf [65]. Heavy feeding by adults on the lamina causes leaves to dry out and curl [26]. The larvae's tunnelling into the petioles and the crown of the plant does extensive damage [9, 17, 18], causing the petioles to become thin and fragile and plants to become waterlogged until they eventually sink and die [38, 82]. Some trapped larvae and pupae attached to roots will sink and drown with dying plants [91].

In the long term, herbivore pressure from the weevils results in a reduction of production of flowers, leaves, daughter plants and plant biomass and reduces the overall vigour of plants [10, 38, 69]. Especially the larval damage that hinders the production of new daughter plants, interfering with vegetative reproduction, has a definite effect on the water hyacinth productivity [25, 26]. At 1 kg of plant biomass/m^2 the water surface can still be completely covered by water hyacinth [91]. Dense mats of water hyacinth eventually start to break up as plants die and sink, with patches of water becoming visible between the plants. New areas of growth and small plants are affected first by BCAs, leaving behind a stand of plants with more uniform size and structure. As the sizes of the mats decrease over time, it becomes easier to eliminate them. However, feeding is assumed to be reduced when there is open water between plants. Although the adult weevils are strong swimmers and mobile [19, 94], they tend not to move between open water bodies [91]. Some plants may thus temporally escape attack and low plant densities are given a chance to increase again [9, 82, 91]. It would therefore be expected that the reduction of water hyacinth populations in a large water body would be relatively less and slower than in a similar smaller water body [94].

During a field study in southern Louisiana in 1980, Goyer and Stark [25] noted that due to the extremely high reproductive rate of water hyacinth and lags in the weevil population, the plants grew much faster than weevils could incur damage and plants re-covered open water surfaces until weevil populations increased again. A cycle may develop wherein high weevil populations and resultant low plant populations alternate. A cumulative effect over several seasons of weevil damage may be necessary to decrease water hyacinth mats [25].

The speed and efficiency with which control is achieved depends, amongst other factors, on the number of insects released and their distribution through the infested areas [38, 69]. Plant growth may limit the effectiveness of biological control at low weevil densities [9]. DeLoach and Cordo [17] performed a two-year field study in Argentina from 1972 to 1974 and found that the weevils damaged the plant throughout the year, but maximum damage by larvae tunnelling inside the petioles occurred during summer and was lowest during spring. Although *N. eichhorniae* is the most popular of the introduced host-specific biological control agents, its effectiveness is reduced by floods, frost, physical removal of plants and herbicide sprays [69].

2.5 Chapter summary

In this chapter, a review of the origin and the global spread of water hyacinth has been given together with the necessary biological background information of the water hyacinth weed and the *N. eichhorniae* weevil, consisting of the life cycles of the plant and insects, the movement behaviour, as well as the way they influence each other. Understanding the biology of the two species is important in order to formulate a realistic mathematical model of the population dynamics.

CHAPTER 3

Mathematical literature survey

Contents

> *"If the Lord Almighty had consulted me before embarking on creation, I should have recommended something simpler."*
>
> – Alfonso X of Castile (1221 – 1284)

The increasing use of mathematical models in population biology, whether dealing with a human population, a population of an endangered species and/or bacterial or viral growth, has helped in understanding the dynamic processes involved in the field and in making practical recommendations. The study of population change has a very long history. In 1202, an exercise in an arithmetic book written by Leonardo of Pisa involved building a mathematical model for a growing rabbit population. Many examples followed in later decades, for example, the well known Lotka-Volterra equations for describing predator-prey interactions in ecology[1] [50, 66]. Mathematical models have also been applied to competition interactions, renewable resource management, evolution of pesticide resistant strains, ecological and genetically engineered control of pests, multi-species societies and plant-herbivore interactions [50].

In this chapter the mathematical background with respect to modelling water hyacinth population growth and interaction models of water hyacinth and the *N. eichhorniae* weevil is discussed and methods which may be used to describe spatial dynamics are provided.

3.1 Differential equations and predator-prey systems

Differential equations relate unknown functions of variables with their derivatives. These equations may be used when the relationship between the varying quantities of the solutions (ex-

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[1] Ecology refers to the study of the interrelationship between species and their environment.

pressed as the set of functions that satisfies the equations) and their rates of change over time (expressed as the functions' derivatives) are known or assumed [85]. Differential equations thus come in handy where changes are noticed in real-world problems and predictions about future behaviour, on the basis of how current values change, are required [66].

Consider the situation where one species, the prey, has an unrestricted supply of food and the other species, the predator, feeds on the prey. An example of this is where rabbits represent the prey and foxes the predators. When species interact, the population dynamics of each species are affected. Predator-prey relationships such as these may be modelled as a pair of linked differential equations. This will yield a model of two dependent variables where both are functions of time. Let $R(t)$ be the number of rabbits (prey) and $F(t)$ the number of foxes (predators) at time t. In the absence of predators, the abundant supply of food will support exponential growth of the prey, that is,

$$\frac{\mathrm{d}R(t)}{\mathrm{d}t} = \beta R(t),$$

where β is a positive constant. In the absence of prey, the predator population will decline at a rate proportional to itself, that is,

$$\frac{\mathrm{d}F(t)}{\mathrm{d}t} = -\delta F(t),$$

where δ is a positive constant. In the case where both species are present, the primary cause of death among the prey is being eaten by a predator, while the birth and survival rates of the predators depend on the availability of food, that is, the prey. It is assumed that the two species encounter each other at a rate that is proportional to both populations, that is, proportional to the product $R(t)F(t)$. The more there are of either population, the more encounters there are likely to be. The system of two differential equations governing this scenario is given by

$$\frac{\mathrm{d}R(t)}{\mathrm{d}t} = \beta R(t) - aR(t)F(t) \quad \text{and} \tag{3.1}$$

$$\frac{\mathrm{d}F(t)}{\mathrm{d}t} = -\delta F(t) + bR(t)F(t), \tag{3.2}$$

where a and b are positive constants. The term $-aR(t)F(t)$ decreases the natural growth rate of the prey and the term $bR(t)F(t)$ increases the natural growth rate of the predators [50, 66]. Equations (3.1) and (3.2) are known as the *predator-prey equations* or the *Lotka-Volterra equations*. A solution of this system of equations is a pair of functions $R(t)$ and $F(t)$ that describe the populations of prey and predators as functions of time. Because $R(t)$ and $F(t)$ occur in both equations, the system is coupled and the equations have to be solved simultaneously [66].

Another population modelling approach comprises of the use of individual-based models (IBMs), also referred to as agent-based models, which incorporate a high degree of complexity of individuals and of interactions among individuals. IBMs simulate populations or systems of populations as discrete individual organisms, where each individual has a unique set of attributes and behaviours. In contrast to traditional differential equation population models, which are described in terms of top-down population parameters (such as birth and death rates), IBMs are bottom-up models in which population-level behaviours emerge from the interactions among independent individuals with each other and their environment [15]. Although a lot can be learned from IBMs, it is time consuming to track every microscopic birth and death event. Moreover, the ecological signal may be hard to discern beneath the stochastic variation, as well as difficult to analyse mathematically. An approach that deals with the dynamics of large-scale variables like population density, such as the differential equation population model described in this section, may be preferred [41].

In this study, two-species population density models are considered. More specifically, plant-herbivore interactions, which resemble predator-prey interactions to a certain extent, however, with one species being static, are considered.

3.2 Time delays and stage-structured models

Population models as discussed in §3.1 assume that births occur instantaneously and do not account for possible time delays due to, for example, a gestation period, the time it takes for eggs to hatch or the time to reach maturity. Discrete delay involves the evaluation of a population exactly a certain number of time units ago [24]. As shown in Nicholson's blowflies equation, such discrete time delays can be incorporated by using a delay differential equation[2] (DDE) of the form

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = -\delta N(t) + \beta N(t-\tau)e^{-aN(t-\tau)},$$

where δ, β, a and τ are positive constants, with δ representing the per capita daily death rate, β the maximum per capita daily reproduction rate, $1/a$ the size at which the population reproduces at its maximum rate and τ the generation time, or the time taken from birth to maturity [4, 5, 24]. This equation was first proposed by Gurney *et al.* [27] to mathematically describe the population of the Australian sheep-blowfly, *Lucilia cuprina* Wiedemann (Diptera: Calliphoridae) .

Age or stage-structured models make use of time delays. Gurney *et al.* [28] developed a set of coupled ordinary DDEs to describe an age-structured population in which the life-history of a species is divided into age classes of arbitrary duration, assuming that all individuals in a particular age class have the same birth and death rates. By adding age or stage-structure, a model is able to account for more biological detail of a species, making it a more realistic representation. The proposed model in [28] is given by

$$\begin{aligned}\frac{\mathrm{d}N_i(t)}{\mathrm{d}t} &= R_i(t) - R_i(t-\tau_i)P_i(t) - \delta_i(t)N_i(t),\\ \frac{\mathrm{d}P_i(t)}{\mathrm{d}t} &= P_i(t)\left[\delta_i(t-\tau_i) - \delta_i(t)\right],\end{aligned} \tag{3.3}$$

where N_i is defined as the number of individuals in age class i, R_i the rate of recruitment into class i, P_i the through age class survival rate of class i, τ_i the duration of age class i and δ_i the per capita death rate of class i. System (3.3) is linked to the set of algebraic equations given by

$$R_i(t) = \begin{cases} \sum_{i=1}^{Q} \beta_i(t)N_i(t) + I_1(t) & i = 1\\ R_{i-1}(t-\tau_{i-1})P_{i-1}(t) + I_i(t) & i = 2,\ldots,Q, \end{cases} \tag{3.4}$$

where $I_i(t)$ is defined as the rate at which individuals aged exactly a_i are added to age class i at time t, β_i the reproduction rate of class i and Q the total number of age classes of the species under consideration [28]. The system is to be solved subject to the initial conditions

$$N_i(t) = R_i(t) = I_i(t) = 0, \ \text{for} \ -\max(\tau_i) \le t \le 0 \quad \text{and} \quad P_i(0) = \int_{-\tau_i}^{0} \delta_i(x)\mathrm{d}x, \ \forall i.$$

The formalisation is also described in [29].

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[2] A delay differential equation is a differential equation in which the derivative of the unknown function at a certain time depends on the values of the function at previous times [84].

3.3 Partial differential equations and reaction-diffusion systems

Partial differential equations (PDEs) is one of the major mathematical tools used to model and analyse spatio-temporal processes in ecology. PDEs that are sufficiently realistic to describe ecological systems are usually more difficult to solve than ordinary differential equations, but they offer the significant advantage of incorporating temporal and spatial processes simultaneously in equations governing population dynamics. Although PDE models understandably cannot describe all ecological aspects, they are useful to lend insight into many fundamental population processes such as dispersal, ecological invasions and the effect of habitat geometry and size [34].

In the classical applications of PDE models to population ecology and dispersal, organisms are assumed to have Brownian random motion, the rate of which is invariant in time and space. In a two-dimensional environment, this leads to the classical diffusion model

$$\frac{\partial u(\xi_1,\xi_2,t)}{\partial t} = d\left(\frac{\partial^2 u}{\partial \xi_1^2} + \frac{\partial^2 u}{\partial \xi_2^2}\right),$$

where $u(\xi_1,\xi_2,t)$ represents the concentration of organisms at spatial coordinates (ξ_1,ξ_2) at time t and d the diffusion coefficient that measures the dispersal rate of the organisms in $\frac{\text{distance}^2}{\text{time}}$ [34, 50]. This approach is known as *Fickian diffusion* where the flux of material is proportional to the gradient of the concentration of the material [50].

Reaction-diffusion equations, a special class of PDEs, are frequently used to model interaction in biology, geology, physics and ecology. These systems are mathematical models describing the movement or change in concentration of one or more substances distributed in an environment. The change in concentration results from two processes, namely *local reactions* and *diffusion*. The local reactions process consists of the production and decay of the substances as well as the particles (individuals) of the different substances interacting with each other, while diffusion causes the particles to spread out across the spatial domain without involving external forces. Reaction-diffusion systems are generally of the form

$$\frac{\partial \underline{u}(\underline{\xi},t)}{\partial t} = \underline{f}(\underline{\xi},t,\underline{u}) + \nabla\cdot[\mathbf{D}(\underline{\xi},t)\nabla\underline{u}(\underline{\xi},t)], \tag{3.5}$$

where the components of the vector $\underline{u}(\underline{\xi},t)$ denote the densities of the substances at location $\underline{\xi}$ at time t, where $\underline{\xi} = [\xi_1,...,\xi_m]^T \in \mathcal{D}$, where $\mathcal{D}$ is a closed spatial domain. Furthermore, $\underline{f}$ contains expressions describing the interaction between the different particles, while $\mathbf{D}(\underline{\xi},t) = \text{diag}\{d_1(\underline{\xi},t),...,d_m(\underline{\xi},t)\}$ denotes the diffusion matrix where $d_i(\underline{\xi},t)$ is the diffusion coefficient of substance i, indicating how effectively particles diffuse from a high to a low concentration area in $\mathcal{D}$ at location $\underline{\xi}$ at time t. The first term of the reaction-diffusion equation in (3.5) governs all the local reactions of the different particles and the second term governs the diffusion of the substances [40, 57, 75, 90].

3.3.1 Derivation of reaction-diffusion equations

The reactions process, where the number of particles at any location $\underline{\xi}$ may change over time due to birth, death or chemical reaction, is considered first. It is assumed that the rate of change in the density of substance i as a result of local reactions is $f_i(\underline{\xi},t,u_1....,u_m)$ [61]. The net growth of substance i inside any region $\mathcal{V}$ which is a subset of $\mathcal{D}$ is then given by

$$\int_{\mathcal{V}} f_i(\underline{\xi},t,u_1....,u_m)\mathrm{d}v.$$

Secondly, the way that the particles move due to the diffusion process, is based on the natural phenomenon that substances move from high density areas to low density area. This movement is known as the *flux* of the population density. The flux is a vector which always points to the most rapid decreasing direction or most negative gradient of the population density vector, $u_i(\underline{\xi}, t)$. This principle is known as *Fick's law* and may be denoted as

$$\underline{J}_i(\underline{\xi}, t) = -d_i(\underline{\xi}, t)\nabla u_i(\underline{\xi}, t), \tag{3.6}$$

where $\underline{J}_i(\underline{\xi}, t)$ denotes the flux vector of the population density of substance i and $d_i(\underline{\xi}, t)$ the diffusion coefficient as defined above [87]. The total out flux of substance i is thus given by

$$\int_{\partial\mathcal{V}} \underline{J}_i(\underline{\xi}, t) \cdot \mathrm{d}\underline{s},$$

where $\partial\mathcal{V}$ is the boundary of $\mathcal{V}$ and $\mathrm{d}\underline{s}$ is a unit vector orthogonal to $\partial\mathcal{V}$ and points outwards [50, 57, 61].

According to the *general conservation equation*, which states that the rate of change in the density of a substance in any subset $\mathcal{V} \in \mathcal{D}$ equates to the rate of flow of the substance across the boundary of $\mathcal{V}$ plus the amount of that substance created in $\mathcal{V}$ [50], the total rate of change in the density of substance i in any subset $\mathcal{V} \in \mathcal{D}$ is given by

$$\frac{\partial}{\partial t}\int_{\mathcal{V}} u_i(\underline{\xi}, t)\mathrm{d}v = \int_{\mathcal{V}} f_i(\underline{\xi}, t, u_1 ...., u_m)\mathrm{d}v - \int_{\partial\mathcal{V}} \underline{J}_i(\underline{\xi}, t) \cdot \mathrm{d}\underline{s}. \tag{3.7}$$

Furthermore, the *divergence theorem*[3] [61] states that

$$\int_{\partial\mathcal{V}} \underline{J}_i(\underline{\xi}, t) \cdot \mathrm{d}\underline{s} = \int_{\mathcal{V}} \nabla \cdot \underline{J}_i(\underline{\xi}, t)\mathrm{d}v. \tag{3.8}$$

Substituting equations (3.6) and (3.8) into (3.7), and interchanging the order of differentiation and integration, obtains

$$\int_{\mathcal{V}} \frac{\partial}{\partial t} u_i(\underline{\xi}, t)\mathrm{d}v = \int_{\mathcal{V}} \big(f_i(\underline{\xi}, t, u_1 ...., u_m) + \nabla \cdot [d_i(\underline{\xi}, t)\nabla u_i(\underline{\xi}, t)]\big)\, \mathrm{d}v.$$

Since the region $\mathcal{V}$ was chosen arbitrarily, the differential equation

$$\frac{\partial u_i(\underline{\xi}, t)}{\partial t} = f_i(\underline{\xi}, t, u_1 ...., u_m) + \nabla \cdot [d_i(\underline{\xi}, t)\nabla u_i(\underline{\xi}, t)]$$

holds for any $(\underline{\xi}, t)$ and is known as the *reaction-diffusion equation*, corresponding to equation (3.5) [61]. In the case of no local reactions occurring, the equation is simplified to the *diffusion equation* denoted by

$$\frac{\partial \underline{u}(\underline{\xi}, t)}{\partial t} = \nabla \cdot [\mathbf{D}(\underline{\xi}, t)\nabla \underline{u}(\underline{\xi}, t)].$$

3.3.2 Partial differential equations in ecology

Ecological invasions have been formally modelled via reaction-diffusion equations since the early 1950s. These mathematical models have been successfully used to describe the historical range

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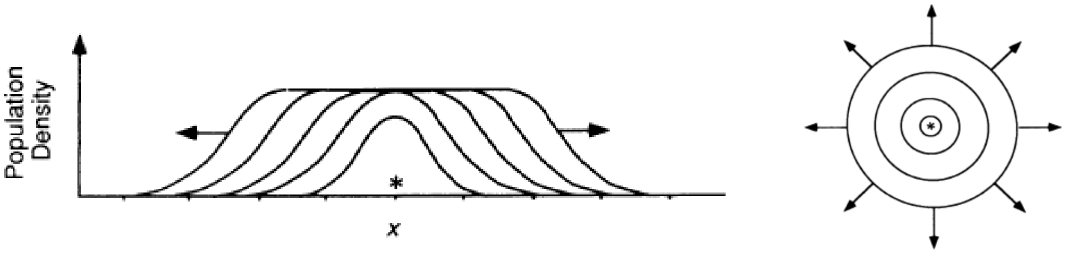
[3] The divergence theorem states that the outward flux of a vector field through a closed surface is equal to the volume integral of the divergence over the region inside the surface [86].

expansion of several animal species over the last few decades [34]. The classic reaction-diffusion model of ecological importance is the Fisher model, which represents logistic population growth of a single species, where population growth is regulated by density-dependent mortality, plus Brownian random dispersal. In a two-dimensional environment, this leads to the model given by

$$\frac{\partial u(\xi_1,\xi_2,t)}{\partial t} = ru(1-\frac{u}{K}) + d\left(\frac{\partial^2 u}{\partial \xi_1^2}+\frac{\partial^2 u}{\partial \xi_2^2}\right),$$

where r denotes a population's intrinsic growth rate and K the carrying capacity [34]. These models, where populations disperse outward and reproduce, produce travelling waves of species that spread out from their initial point of invasion at a constant velocity and shape into previously unoccupied areas (see Figure 3.1).



(a) (b)

FIGURE 3.1: *An example of the population growth and dispersal of an invasive species in one dimension (a) and two dimensions (b). Arrows indicate the direction of dispersal. The lines that are further from the initial point of invasion (*) are later in time [34].*

The concept of modelling population reproduction together with dispersal has also been applied to interacting species, generally restricted to pairwise interactions. An example of this is the application to two-species predator-prey interactions, using a Lotka-Volterra predator-prey model with diffusion terms in two dimensions, which yields a system of coupled PDEs given by

$$\begin{aligned}\frac{\partial u(\xi_1,\xi_2,t)}{\partial t} &= d_u\left(\frac{\partial^2 u}{\partial \xi_1^2}+\frac{\partial^2 u}{\partial \xi_2^2}\right) + ru(1-\frac{u}{K}) - \alpha_{uv}uv,\\ \frac{\partial v(\xi_1,\xi_2,t)}{\partial t} &= d_v\left(\frac{\partial^2 v}{\partial \xi_1^2}+\frac{\partial^2 v}{\partial \xi_2^2}\right) - \delta v + \alpha_{vu}uv,\end{aligned}$$

where u and v denote the densities of the two species, d_u and d_v the species-specific diffusion rates, δ the per capita mortality rate of predators in the absence of prey, α_{uv} the rate at which predators consume prey, α_{vu} the rate at which predators convert prey into new predators [34].

Reaction-diffusion models have also been used to successfully model the spread of plant populations [55], even though the redistribution or invasion or colonisation of plant populations in space takes place through seeds or offshoots forming and not through individuals physically moving from one position in space to another. When the plant growth rate is large enough, reaction-diffusion models succeed to model this spread. For populations where the stages of dispersal and reproduction are clearly distinguished and occur at discrete intervals, reaction-diffusion models appear to give unrealistic representations of the population dynamics. In these cases, another type of mathematical model based on integro-difference or integro-differential equations may yield a more realistic description [55].

3.4 Modelling time delay and diffusion simultaneously

In recent years, some progress has been made towards the modelling and analysis of ecological systems involving both time delay and diffusion. When incorporating diffusion into a time-delay model, a diffusion term is often simply added to the corresponding delayed ordinary differential equation model, however, there are modelling difficulties with this approach. The difficulty is that diffusion and time delays, even though they are associated with space and time respectively, are not independent of each other, since individuals have not been at the same point in space at previous times [22, 24].

Britton [6] was the first to address this difficulty for a delayed Fisher equation on an infinite spatial domain. He suggested that to account for the drift of individuals to their present position from all possible positions at previous times, the delay term has to involve a *weighted spatial averaging* over the entire domain, the weighting to be properly derived using probabilistic arguments and the assumptions made about the motion of the individuals. Gourley and Kuang [21] used a weighted spatial averaging technique (also used by [63]) to formulate and study a delay reaction-diffusion model of the spread of bacteriophage infection on an infinite one-dimensional domain. Gourley and So [23] illustrated how to correctly model and analyse such delay-induced spatial averaging on a *finite spatial domain* in one dimension. This introduces additional difficulties in that the individuals, as well as having been drifting around in the past, may also have been interacting with the domain's boundaries.

This modelling technique will be explained at the hand of Gourley and Kuang's [22] derivation of a reaction-diffusion extension of Aiello and Freedman's [1] stage-structured model for single species in a *finite spatial domain* with homogeneous Neumann boundary conditions, where they used the Britton approach. The techniques described may be carried over to the case of an n-dimensional spatial domain [2, 24]. Consider Aiello and Freedman's system given by

$$\begin{aligned} \frac{\mathrm{d}u_i(t)}{\mathrm{d}t} &= \alpha u_m(t) - \gamma u_i(t) - \alpha \mathrm{e}^{-\gamma\tau} u_m(t-\tau), \\ \frac{\mathrm{d}u_m(t)}{\mathrm{d}t} &= \alpha \mathrm{e}^{-\gamma\tau} u_m(t-\tau) - \beta u_m^2(t), \end{aligned} \tag{3.9}$$

where α, β, γ and τ are positive constants and u_i and u_m denote the densities of immature and mature individuals of the population, respectively. The parameter α denotes the birth rate, γ the death rate of immatures and β the death rate of mature individuals. The delay τ denotes the time from birth to maturity. The birth rate of immatures, $\alpha u_m(t)$, is proportional to the number of mature individuals present at a time and the mortality of immatures is denoted by $\gamma u_i(t)$. Death of matures is modelled by a quadratic term, as in the logistic equation. The term $\alpha \mathrm{e}^{-\gamma\tau} u_m(t-\tau)$ represents the rate at which individuals, who were born at time $t-\tau$ and are still alive now, leave the immature stage and enter the mature stage. The term $\mathrm{e}^{-\gamma\tau}$ thus represents the through-stage survival rate [2, 22].

When motion is allowed for, the derivation of the time-delayed term in system (3.9) has to be altered to take proper account of the motion. If immatures move, individuals are expected to enter the mature population stage at a point in space different from where they were born. The re-deriving of the time-delayed term depends on the assumptions being made about the motion and also on the spatial domain. Gourley and Kuang [22] considered the case of an infinite as well as a finite spatial domain, of which the latter is applicable to this study. The additional possible interactions of individuals with the boundaries of the domain make the bounded case slightly more difficult to model. For simplicity's sake, the authors assumed individuals to perform an unbiased random walk, modelling motion in terms of Fickian diffusion as described in Murray

[50]. Under this assumption, diffusion is approximated by adding Laplacian diffusion terms to the original system in (3.9) and re-deriving the delay term as described below.

For the case of a finite one-dimensional spatial domain $0 \leq x \leq \pi$ with homogeneous Neumann boundary conditions, the immature and mature population densities are now denoted by $u_i(x,t)$ and $u_m(x,t)$, respectively. Such boundary conditions model a closed environment with reflecting boundaries, *i.e.* individuals cannot leave the domain. Gourley and Kuang [22] argued that the delayed term, $\alpha \mathrm{e}^{-\gamma\tau} u_m(t-\tau)$, appearing twice in system (3.9), may be replaced by

$$\int_0^\pi G(x,y,\tau)\mathrm{e}^{-\gamma\tau}\alpha u_m(y,t-\tau)\mathrm{d}y, \tag{3.10}$$

where the total rate of entering the mature stage at time t and position x follows from

$$\begin{aligned} \alpha u_m(y,t-\tau) &= \text{number born at } y, \\ \mathrm{e}^{-\gamma\tau}\alpha u_m(y,t-\tau) &= \text{number born at } y \text{ and still alive now}, \\ G(x,y,\tau)\mathrm{e}^{-\gamma\tau}\alpha u_m(y,t-\tau) &= \text{number born at } y, \text{ still alive and now at } x, \end{aligned}$$

and the integral totals up the contributions from all parts of the domain. Expression (3.10) allows for the fact that an individual that enters the mature stage at position x will most likely have been born at some other point y. The population is evaluated at time $t-\tau$ and is averaged in space in a way that explicitly involves τ through the fact that the function $G(x,y,t)$ is evaluated at time $t=\tau$ [24]. Note that the delay effect only involves the population exactly τ time units ago as this is the only population contributing to the current growth rate. The spatial distribution kernel $G(x,y,t)$ in (3.10) is the solution of

$$\frac{\partial G}{\partial t} = d_i \frac{\partial^2 G}{\partial x^2}, \quad 0 < x < \pi, \tag{3.11}$$

subject to homogeneous Neumann boundary conditions and initial conditions given by

$$\frac{\partial G}{\partial x} = 0 \ \text{ at } \ x = 0, \pi \quad \text{ and } \quad G(x,y,0) = \delta(x-y), \tag{3.12}$$

where $d_i > 0$ is the diffusion rate of the immature species. It should be noted that the function $G(x,y,t) > 0$ for all x, y if $t > 0$ and satisfies (3.11) and (3.12) with x and y interchanged. Although an explicit expression for $G(x,y,t)$ exists in the one-dimensional case, it is only necessary to know that the function G is the solution of equation (3.11) subject to (3.12). This observation indicates that this method may still be applied in higher space dimensions where $G(x,y,t)$ becomes $G(\underline{x},\underline{y},t)$ and there may no longer exist an explicit expression for it [24].

The diffusion version of system (3.9) in a finite one-dimensional spatial domain $0 \leq x \leq \pi$ may thus be given by

$$\begin{aligned} \frac{\partial u_i}{\partial t} &= d_i \frac{\partial^2 u_i}{\partial x^2} + \alpha u_m - \gamma u_i - \alpha \mathrm{e}^{-\gamma\tau}\bar{u}_m(x,t), \\ \frac{\partial u_m}{\partial t} &= d_m \frac{\partial^2 u_m}{\partial x^2} + \alpha \mathrm{e}^{-\gamma\tau}\bar{u}_m(x,t) - \beta u_m^2, \qquad t > 0, \quad 0 < x < \pi, \end{aligned}$$

where

$$\bar{u}_m(x,t) = \int_0^\pi G(x,y,\tau)u_m(y,t-\tau)\mathrm{d}y,$$

with boundary conditions

$$\frac{\partial u_m}{\partial x}(0,t) = \frac{\partial u_m}{\partial x}(\pi,t) = 0, \qquad t > 0,$$

and initial conditions

$$u_m(x,t) = \phi(x,t) \quad \text{for} \ (x,t) \in [0,\pi] \times [-\tau, 0].$$

Note that if $u_m(x,s) \geq 0$ for all $x \in [0,\pi]$ and $s \leq t$, then $\bar{u}_m(x,t) > 0$. This follows from the positivity of G. Note also that G satisfies

$$\int_0^\pi G(x,y,t)\mathrm{d}y = 1, \qquad \forall t \geq 0.$$

Thus $\bar{u}_m$ is a weighted average of u_m at an earlier time [22].

3.5 Modelling water hyacinth population growth and weevil interaction

Wilson *et al.* [93] have modelled water hyacinth population growth (excluding weevil interaction) using a logistic model

$$\frac{\mathrm{d}P}{\mathrm{d}t} = rP\left(1 - \frac{P}{K}\right), \tag{3.13}$$

where P denotes the biomass density of water hyacinth plant material (kg/m^2), r the intrinsic daily growth rate of the plant and K the carrying capacity (kg/m^2). At low plant densities, the population will increase at its intrinsic growth rate. As the density of plants approaches the carrying capacity, the rate of increase in water hyacinth population tends linearly to zero (see Figure 3.2). If the density is above the carrying capacity, the population will decrease to K [93].

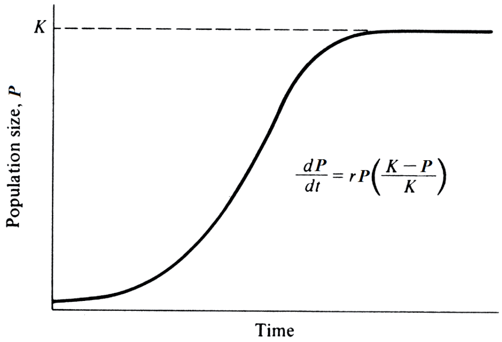


Figure 3.2: *Water hyacinth population (biomass) plotted against time.*

The logistic model succeeds in accurately predicting water hyacinth growth under different abiotic conditions in a spatially homogeneous environment, although predictions of the change in coverage over time cannot be made as information on the spatial dynamics is lacking [91].

Wilson *et al.* [94] presented a plant–herbivore model to investigate the introduction of the *N. eichhorniae* weevil as a BCA for water hyacinth in a spatially homogeneous environment. The model is given by

$$\frac{\mathrm{d}P}{\mathrm{d}t} = rP\left(1 - \frac{P}{K}\right) - c_1A\left(1 - e^{-d_1P}\right) \tag{3.14}$$

$$\frac{\mathrm{d}A}{\mathrm{d}t} = A\left(-a + c_2\left(1 - e^{-d_2P}\right)\right), \tag{3.15}$$

where the first term of equation (3.14) represents the logistic growth of the plant as described in (3.13), the second term of equation (3.14) represents the plant's interaction with the weevil and equation (3.15) represents the population growth of the weevil, dependant on the density of the plant. Here A denotes the weevil population, $-a + c_2$ the maximum rate of increase for the weevil population when there are many plants ($e^{-d_2 P}$ is approximately zero) and a the maximum rate of decline for the weevil population, when there are few plants ($e^{-d_2 P}$ is approximately 1) [94]. This model does not include the different stages of the weevil's life cycle. It is assumed that all weevils have the same effect on the plant, while in reality late larval stages are the most damaging. To account for this, a time delay was added to the growth of the weevil population [94]. Under these conditions, the plant-weevil system undergoes large amplitude cycles, as shown in Figure 3.3.

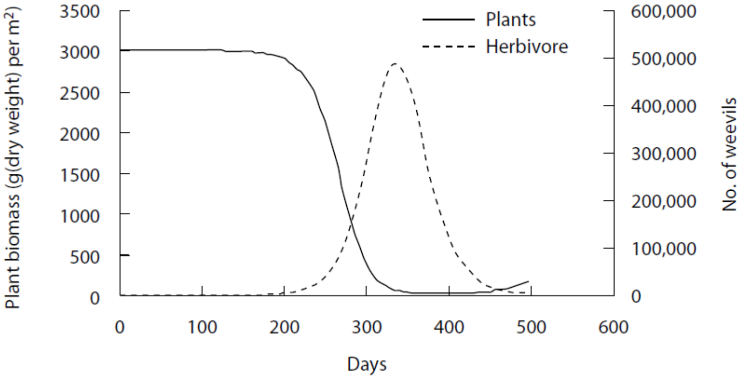


FIGURE 3.3: *Plant-herbivore model output with a time delay added to the growth of the weevil population [94].*

In order to improve the realism, Wilson [91] developed and investigated temporal models where stage structure has been added to the weevil population, formulated as a system of coupled DDEs, making use of techniques similar to descriptions in §3.2. The model which gave predictions closest to field observation in terms of the level and stability of control, is given by

$$\begin{aligned}
\frac{\mathrm{d}W}{\mathrm{d}t} &= rW\left(1-\frac{W}{K}\right) - c_{L_2}L_2\left(\frac{W}{W+H}\right),\\
\frac{\mathrm{d}L_1}{\mathrm{d}t} &= qA(t-t_E)\,\sigma_E - \mu_{L_1}L_1 - J_{L_1}\frac{L_1}{W}L_1 - qA(t-t_E-t_{L_1})\,\sigma_E\sigma_{L_1}S,\\
\frac{\mathrm{d}L_2}{\mathrm{d}t} &= qA(t-t_E-t_{L_1})\,\sigma_E\sigma_{L_1}S - \mu_{L_2}L_2 - qA(t-t_E-t_{L_1}-t_{L_2})\,\sigma_E\sigma_{L_1}S(t-t_{L_2})\,\sigma_{L_2},\\
\frac{\mathrm{d}A}{\mathrm{d}t} &= qA(t-t_E-t_{L_1}-t_{L_2}-t_P)\,\sigma_E\sigma_{L_1}S(t-t_{L_2}-t_P)\,\sigma_{L_2}\sigma_P - \mu_A A,\\
\frac{\mathrm{d}S}{\mathrm{d}t} &= SJ_{L_1}\left(\frac{L_1(t-t_{L_1})}{W(t-t_{L_1})} - \frac{L_1(t)}{W(t)}\right),
\end{aligned}$$

where the state variable W denotes the biomass density of water hyacinth, while L_1, L_2 and A denote the density of young larvae, old larvae and adult weevils, respectively. These three development stages with density-dependent processes were considered sufficient to represent the weevil population. The final state variable, S, denotes the density-dependent through stage survival rate for young larvae. Furthermore, r denotes the intrinsic growth rate of the plant, K the carrying capacity, c_{L_2} the rate of damage caused by the older larvae and H the plant density at which herbivore feeding is reduced by half. Parameter, q denotes the weevil oviposition rate, t_i the development duration of stage i of the weevil's life cycle, σ_i the density-independent through stage survival probability for stage i, μ_i the daily density-independent mortality rate for stage i and J_{L_1} the density-dependent scaling parameter for young larvae [91]. The models presented by Wilson [91] exclude spatial dynamics and predict that, given stable conditions, water hyacinth will always be controlled. However, from field observations, this prediction is known to be incorrect. The models appear to overemphasise the effect of the weevils on water hyacinth growth and in some way fail to capture an important aspect of water hyacinth and weevil interaction [93]. The research done by Wilson [91] provides support for some important assumptions in the modelling of water hyacinth and weevil interaction and highlights the lack of information on certain important parameter values.

Van Schalkwyk and Potgieter [74] built on Wilson [91] and Wilson *et al.*'s [93, 94] work by developing a model to compare different biological control release strategies for water hyacinth in terms of cost-effectiveness in a spatially homogeneous environment. In contrast to Wilson's [91] model, a more detailed temperature dependence was incorporated in the model, as well as a term making more frequent releases of BCAs possible. In addition, a different approach towards the modelling of mortality and maturation through the stages of the weevil's life cycle was followed and the output of the model was translated by a cost function to reflect the total cost, in terms of mass rearing expenses and water loss, for a specific release strategy. Van Schalkwyk and Potgieter's [74] mean-field model predicted that once-off and frequent BCA releases will be able to drive water hyacinth populations to complete extinction and clear an entire water body of any size in less than 150 days, subject to constant temperature conditions, ranging from 20°C to 35°C. Low frequency releases proved to be more cost-effective than high frequency releases, while once-off releases appeared to be more efficient and cost-effective than frequent releases over a time period of 300 days. However, over an extended period of time, the weed would grow back, and re-releases will be required. Sensitivity analyses indicated that the most cost-effective strategy will be to release BCAs during the time of the year when the climate is optimal (30°C) for maximum weevil development. Furthermore, the average plant population density appeared to be more sensitive when the number of BCAs released was decreased than when it was increased. In order to minimise the average plant population density, accounting for cases where BCAs may struggle to adapt in a new habitat or a disaster hits and a lot of them die, it was recommended to release a slightly larger number of BCAs than the optimal number.

A limitation of the respective models developed by Wilson [91] and Van Schalkwyk and Potgieter [74], is the assumption that BCAs are uniformly distributed throughout an area, where in a real-life scenario, BCAs are released at the edges of an infested water body and take time to spread out. This mean-field approximation may have indicated faster control of water hyacinth than in reality. In order to improve on realism, spatial dynamics may be added to the model in order to give a more realistic representation of the impact of the *N. eichhorniae* weevil on water hyacinth populations, using modelling techniques derived from §3.3 and §3.4. Furthermore, the model may be expanded to incorporate fluctuating temperatures over a period of time. It is unrealistic to assume a constant temperature over a period of time. More thorough investigations of the costs and benefits of biological control release strategies may also add to the validity and generality of conclusions drawn from the model. Van Schalkwyk and Potgieter [74] considered a fixed cost per BCA pertaining to a specific mass rearing facility, whereas, in reality, the cost of biological control does not necessarily follow a linear relationship with the number of BCAs used. Furthermore, the benefit of water saving as a result of the control of water hyacinth was measured in terms of the cost of water for household consumption, whereas modified representative value estimates for water usage, based on its use as serviced (treated and generally supplied in bulk to the consumers) or unserviced water (generally supplied directly from a river, storage reservoir or canal system for irrigation or other bulk use), may be considered as more realistic unit-price estimates for water [56].

3.6 Chapter summary

In this chapter, a review of general population modelling approaches together with a discussion on reaction-diffusion theory, which is the main modelling approach adopted in this study to describe spatial dynamics in a heterogeneous environment, and its application in ecology, has been given. The chapter concluded with a review of the mathematical background with respect to the modelling of water hyacinth population growth and interaction with the *N. eichhorniae* weevil as a BCA specifically, as well as the limitations of current spatially implicit modelling approaches.

CHAPTER 4

The spatio-temporal model

Contents

In this chapter, a reaction-diffusion model for a temporally variable and spatially heterogeneous environment, consisting of a system of coupled delay partial differential equations, is developed to mathematically describe the spatio-temporal dynamics of water hyacinth populations and the interacting populations of the various life stages of the *N. eichhorniae* weevil as a BCA on an isolated and bounded spatial domain. The temporal mean-field model developed by Wilson [91] is not realistic in the context of assuming that weevils are uniformly distributed throughout an area while in reality BCAs are released by hand along the edges of an infested water body. A spatially explicit model is therefore required to model the distribution of water hyacinth and the weevils in a heterogeneous environment. After various model assumptions are discussed in §4.1, the development and mathematical formulation of the reaction-diffusion model is given in §4.2, followed by detailed discussions and, in some cases, derivations of the model input and output parameters in §4.3 and §4.4, respectively. An elaborate description of the implementation of the model in Matlab 9.0 is given in §4.5. Finally, simulations are performed in order to validate the model output by means of testing various model responses and comparing the model output to real-world data in §4.6.

4.1 Model assumptions

In order to translate the biological background information provided in Chapter 2 to a mathematical model that represents the population dynamics of the water hyacinth and weevil species, a number of simplifying assumptions, as discussed in §4.1.1 – §4.1.9, are made.

4.1.1 Stage-structure

For the purpose of this study, the weevil population is subdivided into different stages, while the water hyacinth population is only considered at its mature stage to evaluate the influence of the weevils on an established water hyacinth population. The *N. eichhorniae* weevil population is represented by five development stages: eggs, young larvae (first and second instar larvae), old larvae (third instar larvae), pupae and adults. All individuals within each of these stages may be regarded as functionally identical by having the same per capita vital rates. Individuals enter a stage by developing from the previous stage or by reproduction from the mature stage and leave a stage through death or maturation (see Figure 4.1). The number of eggs laid at a specific time is considered as a cohort and the model keeps track of how each cohort matures through the weevil life stages.

By adding the stage-structure, the model accounts for more biological detail of the weevils and allows for the explicit modelling of processes pertaining only to specific development stages, making it a more realistic representation. The number of equations necessary to represent the weevil population is limited to the number of development stages that have density-dependent processes (mortality, feeding or fecundity). In this study, similar to the temporal model developed by Wilson [91], the two larval stages and the adult stage are considered sufficient to represent the weevil population.

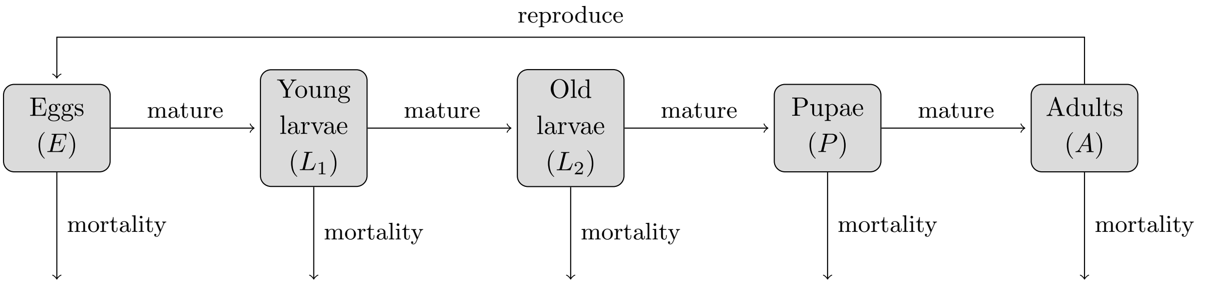


FIGURE 4.1: *Diagram of the* N. eichhorniae *weevil's development stages as used in model development.*

4.1.2 Plant growth

Several factors affecting the growth of the water hyacinth are not included in the model as it is difficult to quantify. These factors include frost, diseases, saltiness of water, wind, humidity, water currents, floods, light and carbon dioxide concentration [37, 91]. Constant nitrogen and phosphorus levels are assumed throughout the study.

4.1.3 Damage factor

While both the *N. eichhorniae* larvae and adults feed on water hyacinth, it is assumed that only the old larvae cause actual damage to the plant. In addition to the removal of biomass, tunnelling of larvae into the petioles and the crown of the plant can cause nutrient deficiency as well as provide a route of entry for disease-causing micro-organisms. The movement of larvae between leaves and the crown of the plant may also lead to flooding of old larval tunnels and a reduction in plant buoyancy [91]. Larval feeding thus causes more damage than just the removal of plant biomass.

Since adults can remove over 50% of the laminar area, it is possible that adult feeding reduces the plant's rate of photosynthesis. Moreover, adults prefer to feed on the youngest leaves and so damage may disrupt leaf development. Still, this does not directly affect the rhizome or the meristem, both of which can be damaged by larval feeding. In most cases, adult feeding appears to be much less destructive to water hyacinth and is thought to be negligible compared to damage caused by old larvae [18, 91].

Other aspects of the weevil life are unlikely to cause much damage. Oviposition scars may provide a route for pathogen entry, but the risk from this should be much less than the tunnelling scars caused by mobile larvae. Pre-pupae are not particularly destructive, as only a few root hairs are required to create the pupal cocoons [91].

4.1.4 Ovipositing

The adult male and female ratio is assumed to be 1 in the released weevil populations as well as the generations to follow. Therefore, the oviposition rate may be determined as an average rate per weevil. Adult weevils are assumed to start laying eggs immediately after they enter the system, via a release or maturation from immature stages, and continue to oviposit at a constant rate throughout their lifetime. The oviposition rate is adjusted accordingly to allow females to lay the approximated maximum amount of eggs during their lifetime when exposed to favourable temperature conditions.

4.1.5 Reproduction

When adult density within a considered area decreases below a minimum threshold, it is assumed that they will not be able to reproduce any longer. There has to be a large enough number of adults within a reachable range of each other for reproduction to occur. This is the typical case of an Allee-effect [68].

4.1.6 Density dependence

From experiments and personal observations, Wilson [91] found it reasonable to assume that due to adult weevil mobility, the female weevils will oviposit regardless of density, resulting in density-independent oviposition and egg survival rates for any realistic density of adults per plant. Due to the relative mobility of old larvae, the through stage survival rates of the old larval and pupal stages of the weevil's life cycle are also assumed to be unaffected by density. Density-dependent mortality is only added to the young larval population as Wilson [91] found that most density-dependent effects occur before damage is caused to the plant. At high larval densities, young larvae may have a higher probability of being stranded in dead and dying petioles [91]. It is assumed that adults have abundant supplies of any limiting nutrient.

4.1.7 Dispersal

The presented spatio-temporal model assumes that individuals in the mobile instars of the weevil's life cycle perform an unbiased random walk. This assumption concurs with previous studies which found that weevils randomly disperse throughout a water hyacinth mat without any apparent preference for particular areas of the plants [30], or influence by external forces causing attraction or repulsion. During each time unit, a proportion of old larvae and adult weevils are assumed to leave the location at which they emerged or from where they were released to inhabit neighbouring sites within their range of motion. This motion can be modelled in terms of *Fickian diffusion* and is approximated by using the Laplacian operator.

The water hyacinth dispersal is also described by *Fickian diffusion* as weed mats randomly expand to neighbouring sites. Dispersal will only occur within the spatial domain as it is assumed that neither plant nor weevil enters or exits the domain as a result of the assumed land use categories surrounding the considered water body.

4.1.8 Domain

For the purpose of this study, the spatial domain is assumed to be an isolated water body infested with water hyacinth to its carrying capacity, surrounded by land use categories considered unsuitable habitat for water hyacinth or *N. eichhorniae* weevils. It is thus assumed that neither plant nor weevil enters or exits the domain. The spatial domain is considered heterogeneous as the plant density may vary for different locations, resulting in variant per capita growth rates for the BCAs.

4.1.9 Releases

Adult weevils are released by hand from small plastic containers at the accessible edges of an infested water body and take time to disperse to neighbouring sites. In some cases, boats may be used for releases on larger water bodies where there are sufficient open water areas for boats to move. Releases are assumed to occur once off or at a constant rate over the period of release. The distribution of the releases is up to the field workers performing the releases and may be influenced by the accessibility to the infested area and the number of BCAs available for release.

4.2 Model formulation and notation

Let $W(\underline{\xi}, t)$ denote the biomass density of water hyacinth material (in kg/unit^2) at location $\underline{\xi} = [\xi_1, \xi_2]^T \in \mathcal{D}$ at time t, where $\mathcal{D}$ is a closed, two-dimensional spatial domain, and $E(\underline{\xi}, t)$, $L_1(\underline{\xi}, t)$, $L_2(\underline{\xi}, t)$, $P(\underline{\xi}, t)$ and $A(\underline{\xi}, t)$ denote the densities of eggs, young larvae, old larvae, pupae and adult weevils at location $\underline{\xi}$ at time t, respectively. Similar to the modelling approach for a variable survival rate used in previous studies [28, 91], let $S_{L_1}(\underline{\xi}, t)$ denote the density-dependent through stage survival rate for young larvae at location $\underline{\xi}$ at time t. All other development stages are assumed to have density-independent per capita death rates, yielding constant survival rates. Time delays are modelled as differences from the current time t and subscripts indicate the stage involved, *e.g.* the development duration of the egg stage is denoted by t_E. The time spent in each stage of the weevil's life cycle is temperature-dependent.

4.2.1 A spatial implementation of the Wilson model

In order to model the spatial dynamics of the water hyacinth and weevil system in a bounded two-dimensional spatial domain, diffusion terms are added to the applicable ordinary delay differential equations in the temporal model presented by Wilson [91]. Let the diffusion coefficients d_W, $d_{L_2}(\theta)$ and d_A be a measure of how effectively water hyacinth, old larvae and adult weevils disperse to neighbouring locations, respectively, invariant in time and space. The change in the population density of the young larval population per time unit at a certain location is assumed equal to the local reactions occurring at that location with no dispersal occurring. In addition, an Allee-effect and a term allowing for frequent releases of adult weevils are included, a more detailed temperature dependence is incorporated, as well as slight changes to the modelling of the through stage survival probabilities.

A provisional reaction-diffusion model for the interacting species, formulated as a system of coupled delay partial differential equations, is given by

$$\frac{\partial W(\underline{\xi},t)}{\partial t} = d_W \nabla^2 W(\underline{\xi},t) + r(\theta)W(\underline{\xi},t)\left(1-\frac{W(\underline{\xi},t)}{K}\right) - c_{L_2}(\theta)L_2(\underline{\xi},t)\left(\frac{W(\underline{\xi},t)}{W(\underline{\xi},t)+H}\right), \tag{4.1}$$

$$\begin{aligned}\frac{\partial L_1(\underline{\xi},t)}{\partial t} &= q(\theta)A\big(\underline{\xi},t-t_E(\theta)\big)\,\sigma_E(\theta)\left(\frac{A(\underline{\xi},t-t_E(\theta))-a}{A(\underline{\xi},t-t_E(\theta))}\right) - \left(\mu_{L_1}(\theta)+\frac{J_{L_1}}{W(\underline{\xi},t)}L_1(\underline{\xi},t)\right)L_1(\underline{\xi},t)\\ &\quad - q(\theta)A\big(\underline{\xi},t-t_E(\theta)-t_{L_1}(\theta)\big)\,\sigma_E(\theta)S_{L_1}\big(\underline{\xi},t\big),\end{aligned} \tag{4.2}$$

$$\begin{aligned}\frac{\partial L_2(\underline{\xi},t)}{\partial t} &= d_{L_2}(\theta)\nabla^2 L_2(\underline{\xi},t) + q(\theta)A\big(\underline{\xi},t-t_E(\theta)-t_{L_1}(\theta)\big)\,\sigma_E(\theta)S_{L_1}\big(\underline{\xi},t\big) - \mu_{L_2}(\theta)L_2(\underline{\xi},t)\\ &\quad - q(\theta)A\big(\underline{\xi},t-t_E(\theta)-t_{L_1}(\theta)-t_{L_2}(\theta)\big)\,\sigma_E(\theta)S_{L_1}\big(\underline{\xi},t-t_{L_2}(\theta)\big)\,\sigma_{L_2}(\theta),\end{aligned} \tag{4.3}$$

$$\begin{aligned}\frac{\partial A(\underline{\xi},t)}{\partial t} &= d_A\nabla^2 A(\underline{\xi},t) - \mu_A(\theta)A\big(\underline{\xi},t\big) + IX\big(\underline{\xi},t\big)\\ &\quad + q(\theta)A\big(\underline{\xi},t-t_E(\theta)-t_{L_1}(\theta)-t_{L_2}(\theta)-t_P(\theta)\big)\sigma_E(\theta)S_{L_1}\big(\underline{\xi},t-t_{L_2}(\theta)-t_P(\theta)\big)\sigma_{L_2}(\theta)\sigma_P(\theta),\end{aligned} \tag{4.4}$$

$$\frac{\partial S_{L_1}(\underline{\xi},t)}{\partial t} = S_{L_1}\big(\underline{\xi},t\big)\,J_{L_1}\left(\frac{L_1(\underline{\xi},t-t_{L_1}(\theta))}{W(\underline{\xi},t-t_{L_1}(\theta))} - \frac{L_1(\underline{\xi},t)}{W(\underline{\xi},t)}\right), \tag{4.5}$$

where $\nabla^2 \equiv \frac{\partial^2}{\partial {\xi_1}^2} + \frac{\partial^2}{\partial {\xi_2}^2}$ denotes the Laplacian operator for diffusion, θ the temperature (°C), $r(\theta)$ the daily intrinsic growth rate of the plant at temperature θ and K the carrying capacity (kg/unit^2) of the water resource. Furthermore, $c_{L_2}(\theta)$ denotes the rate of damage caused by the older larvae at temperature θ and H the plant density at which herbivore feeding is reduced by half. Parameters $r(\theta), K, c_{L_2}(\theta), H, q(\theta)$ and J_{L_1} were obtained from Wilson [91].

In equations (4.2) – (4.4), $q(\theta)$ denotes the rate of oviposition of viable eggs at temperature θ, $t_i(\theta)$ the development duration in days of stage i of the weevil's life cycle at temperature θ and $\sigma_i(\theta)$ the density-independent through stage survival probability for stage i at temperature θ.

In equation (4.2), the rate of recruitment into the young larval stage at location $\underline{\xi}$ at time t is equal to the number of eggs maturing at the corresponding location and time. The number of eggs maturing is the number of eggs laid at location $\underline{\xi}$ and $t_E(\theta)$ days ago – the number of adults present at that location $t_E(\theta)$ days ago multiplied by the oviposition rate – multiplied by the probability of surviving through the egg stage. An Allee-effect, resulting in a decrease of the young larval population growth rate at low adult weevil densities, is added to this term. Once the adult population within a considered area of 1 m^2 falls below the minimum threshold for reproduction, a, the negative instantaneous growth rate of the young larvae leads to the extinction of the population. The Allee-effect may cause slower spread and decreased establishment likelihood of the BCAs, thus influencing the efficacy and cost of biological control. Expected spatial ranges, distributions and patterns of species may be altered when an Allee-effect is present [68], making this an important effect to consider.

The number of young larvae maturing to the next stage at location $\underline{\xi}$ at time t is equal to the number of eggs laid at location $\underline{\xi}$ and $t_E(\theta)+t_{L_1}(\theta)$ days ago, represented by $q(\theta)A(\underline{\xi},t-t_E(\theta)-t_{L_1}(\theta))$, multiplied by the probability of surviving through the egg stage and the probability of surviving through the young larvae stage. The number of old larvae entering the system at location $\underline{\xi}$ at time t is equal to the number of young larvae maturing at that location and time. The same logic is followed for individuals entering other stages and maturing from immature stages.

Assuming a given young larva competes equally with all other young larvae for limited resources, Gurney *et al.* [28] suggested to reflect this limitation by choosing a per capita young larval death rate which varies linearly with young larval population. In line with Wilson's application of this modelling approach [91], the young larval density-dependent mortality rate is given by $\frac{J_{L_1}}{W(\underline{\xi},t)}L_1(\underline{\xi},t)$, where J_{L_1} denotes the density-dependent scaling parameter for young larvae which is equal to the number of kilogrammes of plant material per young larva at which the young larval population growth rate is zero. In equations (4.2) – (4.4), $\mu_i(\theta)$ denotes the daily density-independent mortality rate for stage i ($i = L_1$, L_2 or A) of the weevil's life cycle at temperature θ.

Finally, I denotes the number of new adult weevils released per location at any time and

$$X(\underline{\xi},t) = \begin{cases} 1 & \text{if adults are released at location } \underline{\xi} \text{ at time } t \\ 0 & \text{otherwise.} \end{cases} \tag{4.6}$$

A limitation of the time-delayed modelling approach is that time lags allow weevil populations to still exist for a period of time at a specific location after the plant has been driven to extinction at that point in space, as density dependence in terms of limiting resources is only added to the young larval stage. There is a delayed density dependence effect on the other weevil development stages. In the long term, these delayed effects become negligible and the model still succeeds in providing good estimates of the overall population dynamics.

A further limitation in the modelling approach presented above is that, due to the spatial dispersal of old larvae, the maturation rate out of the old larval stage at time t at location $\underline{\xi}$ in equation (4.3) should depend on the old larval recruitment rate at time $t - t_{L_2}(\theta)$ at other spatial points. Individuals will have entered the system at various locations in $\mathcal{D}$ and will have moved around, being at point $\underline{\xi}$ on maturing to the next stage. A sufficient expression should therefore be derived for the old larval distributed maturation delay term.

Another shortcoming in this model is the prolonged delay before the limitation on the young larval growth rate, as a result of the Allee-effect, has an influence on the growth rates of the subsequent stages of the weevil population. Due to through-stage transition always being calculated from adults, the model allows the populations of the other weevil stages to continue to grow at their usual rates based on the number of adults that were present at previous times, regardless of whether young larval production was limited or not, which should, from a biological point of view, directly affect the population growth rate of subsequent weevil life stages.

4.2.2 The final model

In this section, a different approach towards the modelling of the recruitment and maturation terms for the weevil population is followed and a sufficient expression for the old larval maturation term is derived.

Let $R_i(\underline{\xi},t)$ denote the rate of recruitment into stage i of the weevil's life cycle at location $\underline{\xi}$ at time t. The rate of recruitment into the young larval stage at location $\underline{\xi}$ at time t is equal to the number of eggs maturing at the corresponding location and time, limited by an Allee-effect, as explained in §4.2.1. The rate of maturation out of the young larval stage at location $\underline{\xi}$ at time t, which is equal to the recruitment rate into the old larval stage at location $\underline{\xi}$ at time t, is simply the recruitment rate into the young larval stage at time $t - t_{L_1}(\theta)$ multiplied by the probability of surviving through the young larval stage. The same logic is followed for the recruitment and maturation rates of the other weevil development stages, except for the maturation rate out of the old larval stage where diffusion is involved. The time-delay term for the rate of maturation out of the old larval stage must be derived in a different way. This is necessary because an old larva can move during the period between entering the system and maturing to the next stage and is therefore expected to enter the pupal stage at a different point in space from where it originally emerged. The recruitment rates used in the model are given by

$$R_{L_1}\big(\underline{\xi},t\big) = q(\theta)A\big(\underline{\xi},t-t_E(\theta)\big)\,\sigma_E(\theta)\left(\frac{A\big(\underline{\xi},t-t_E(\theta)\big)-a}{A\big(\underline{\xi},t-t_E(\theta)\big)}\right), \tag{4.7}$$

$$R_{L_2}\big(\underline{\xi},t\big) = \begin{cases} R_{L_1}\big(\underline{\xi},t-t_{L_1}(\theta)\big)\,S_{L_1}\big(\underline{\xi},t\big) & \text{if } R_{L_1}\big(\underline{\xi},t-t_{L_1}(\theta)\big)>0 \\ 0 & \text{otherwise,} \end{cases} \tag{4.8}$$

$$\begin{aligned} R_P\big(\underline{\xi},t\big) &= \{\text{a weighted average of } R_{L_2} \text{ at an earlier time}\}\,\sigma_{L_2}(\theta) \\ &= \bar{R}_{L_2}\big(\underline{\xi},t\big)\,\sigma_{L_2}(\theta), \end{aligned} \tag{4.9}$$

$$R_A\big(\underline{\xi},t\big) = R_P\big(\underline{\xi},t-t_P(\theta)\big)\,\sigma_P(\theta), \tag{4.10}$$

with parameters defined similar to the descriptions in §4.2.1. In equation (4.8), young larvae are only able to mature to the old larval stage if a positive amount of young larvae entered the system $t_{L_1}(\theta)$ days ago.

These modifications lead to the refined reaction-diffusion model given by

$$\frac{\partial W(\underline{\xi},t)}{\partial t} = d_W\nabla^2W(\underline{\xi},t) + r(\theta)W(\underline{\xi},t)\left(1-\frac{W(\underline{\xi},t)}{K}\right) - c_{L_2}(\theta)L_2(\underline{\xi},t)\left(\frac{W(\underline{\xi},t)}{W(\underline{\xi},t)+H}\right), \tag{4.11}$$

$$\frac{\partial L_1(\underline{\xi},t)}{\partial t} = R_{L_1}\big(\underline{\xi},t\big) - \left(\mu_{L_1}(\theta)+\frac{J_{L_1}}{W(\underline{\xi},t)}L_1(\underline{\xi},t)\right)L_1(\underline{\xi},t) - R_{L_2}\big(\underline{\xi},t\big), \tag{4.12}$$

$$\frac{\partial L_2(\underline{\xi},t)}{\partial t} = d_{L_2}(\theta)\nabla^2L_2\big(\underline{\xi},t\big) + R_{L_2}\big(\underline{\xi},t\big) - \mu_{L_2}(\theta)L_2(\underline{\xi},t) - R_P\big(\underline{\xi},t\big), \tag{4.13}$$

$$\frac{\partial A(\underline{\xi},t)}{\partial t} = d_A\nabla^2A\big(\underline{\xi},t\big) + R_A\big(\underline{\xi},t\big) - \mu_A(\theta)A\big(\underline{\xi},t\big) + IX\big(\underline{\xi},t\big), \tag{4.14}$$

$$\frac{\partial S_{L_1}(\underline{\xi},t)}{\partial t} = S_{L_1}(\underline{\xi},t)\,J_{L_1}\!\left(\frac{L_1(\underline{\xi},t-t_{L_1}(\theta))}{W(\underline{\xi},t-t_{L_1}(\theta))} - \frac{L_1(\underline{\xi},t)}{W(\underline{\xi},t)}\right), \tag{4.15}$$

linked to the set of algebraic equations (4.7) – (4.10).

Since the state variables $W(\underline{\xi},t), L_1(\underline{\xi},t), L_2(\underline{\xi},t)$ and $A(\underline{\xi},t)$ represent population densities, they are set to be non-negative real numbers for obvious reasons. The density-dependent survival rate, $S_{L_1}(\underline{\xi},t)$, is assumed to have a lower bound of *zero* and an upper bound equal to the density-independent through stage survival rate for young larvae, $\sigma_{L_1}(\theta)$.

Based on Gourley and Kuang's [22] formulation of a bounded one-dimensional single-species diffusive-delay population model, the time-delayed maturation term for the old larval stage where there is diffusion is derived for the model in a closed, two-dimensional spatial domain $\mathcal{D}$ with homogeneous Neumann boundary conditions. For simplicity's sake, studies in literature only demonstrate the derivation of the delay term for a one-dimensional domain [22, 24], only mentioning that it should be possible to carry out numerical simulations in higher space dimensions.

In algebraic equation (4.9), the weighted average of R_{L_2} at an earlier time is given by

$$\bar{R}_{L_2}\big(\underline{\xi},t\big) = \int_{\mathcal{D}} G(\underline{\xi},\underline{x},t_{L_2}(\theta))R_{L_2}\big(\underline{x},t-t_{L_2}(\theta)\big)\,\mathrm{d}\underline{x}, \tag{4.16}$$

where $\underline{x}$ is another point in space. Old larvae will have emerged at various locations ($\underline{x}$) in domain $\mathcal{D}$ and may have moved around, being at point $\underline{\xi}$ on maturing to the pupal stage. The quantity $\bar{R}_{L_2}\big(\underline{\xi},t\big)\sigma_{L_2}(\theta)$ gives the rate at which old larvae mature into the pupal stage at location $\underline{\xi}$ and time t, having taken $t_{L_2}(\theta)$ days to mature. The spatial averaging kernel $G(\underline{\xi},\underline{x},t)$ is the solution of

$$\frac{\partial G}{\partial t} = d_{L_2}(\theta)\nabla^2 G, \tag{4.17}$$

subject to homogeneous Neumann boundary conditions and initial conditions given by

$$G(\underline{\xi},\underline{x},0) = \delta(\underline{\xi}-\underline{x}), \tag{4.18}$$

where δ is the Dirac delta function and ∇^2 the Laplacian computed with respect to the first argument of $G(\underline{\xi},\underline{x},t)$. The Dirac delta function, $\delta(\underline{\xi}-\underline{x})$, has the value 0 for all $\underline{\xi} \neq \underline{x}$ and 1 for $\underline{\xi} = \underline{x}$. Furthermore, function $G(\underline{\xi},\underline{x},t) > 0$ for all $t > 0$. If $R_{L_2}\big(\underline{\xi},s\big) \geq 0$ for all $\underline{\xi} \in \mathcal{D}$ and $s \leq t$, then $\bar{R}_{L_2}\big(\underline{\xi},t\big) \geq 0$. This follows from the positivity of G. It can also be noted that

$$\int_{\mathcal{D}} G(\underline{\xi},\underline{x},t)\mathrm{d}\underline{\xi} = \int_{\mathcal{D}} G(\underline{\xi},\underline{x},t)\mathrm{d}\underline{x} = 1, \qquad \forall t \geq 0.$$

Although the explicit expression of the spatial averaging kernel $G(\underline{\xi},\underline{x},t)$ is difficult to compute (or unknown) for the bounded two-dimensional case, literature indicates that it is only necessary to know that the function G is the solution of equation (4.17) subject to (4.18) [2, 24].

According to Gourley and Kuang [21], the existence of solutions to one-dimensional delay reaction-diffusion systems, similar to the one described in equations (4.11) – (4.15), which is already more complex due to being in two dimensions, have yet to be established. It is therefore assumed that a solution to the presented model exists and the focus in the rest of the thesis is turned towards how the model may be applied to optimise water hyacinth biological control release strategies.

Boundary conditions

Since water hyacinth cannot exist on land and the *N. eichhorniae* weevils are host–specific BCAs, only able to survive on water hyacinth, it is assumed that neither plant nor weevil enters or exits the domain. System (4.11) – (4.15) is therefore subject to homogeneous Neumann boundary conditions given by

$$\underline{n} \cdot (\mathbf{D} \otimes \nabla \underline{u}) = \underline{0}, \quad \forall \underline{\xi} \in \partial\mathcal{D}, \tag{4.19}$$

where $\underline{n}$ is the outward normal vector on the boundary, $\mathbf{D}$ the diffusion coefficient matrix, $\underline{u}$ the solution of the system and $\partial\mathcal{D}$ the boundary of $\mathcal{D}$.

Initial conditions

Initially, the water hyacinth density is assumed to be at carrying capacity ($K = 70$ kg/m^2) throughout the entire domain under consideration ($\mathcal{D}$) and all weevil stages are assumed absent prior to BCA releases. A certain amount of adult weevils will be released at specific locations at the edges of the domain at time $t = 0$. The initial conditions for system (4.11) – (4.15) are thus given by

$$\begin{aligned}
W(\underline{\xi},t) &= K, && \text{for } t \leq 0, && \forall \underline{\xi} \in \mathcal{D} \\
L_1(\underline{\xi},t) &= 0, && \text{for } t \leq 0, && \forall \underline{\xi} \in \mathcal{D} \\
L_2(\underline{\xi},t) &= 0, && \text{for } t \leq 0, && \forall \underline{\xi} \in \mathcal{D} \\
A(\underline{\xi},t) &= 0, && \text{for } t < 0, && \forall \underline{\xi} \in \mathcal{D} \\
A(\underline{\xi},0) &= \begin{cases} I & \text{if } \; X(\underline{\xi},0) = 1 \\ 0 & \text{otherwise} \end{cases} \\
S_{L_1}(\underline{\xi},t) &= \sigma_{L_1}(\theta), && \text{for } t \leq 0, && \forall \underline{\xi} \in \mathcal{D},
\end{aligned} \tag{4.20}$$

where K, I and $\sigma_{L_1}(\theta)$ are assumed to be positive real numbers.

4.3 Model input parameters

The values of the parameters used in the model described in §4.2 have all been obtained, derived or estimated from previous studies [7, 18, 30, 38, 72, 91, 92, 93], with the exception of the threshold for the Allee-effect, a.

4.3.1 Intrinsic growth rate of water hyacinth

The growth rate of water hyacinth, $r(\theta)$, is given by

$$r(\theta) = r_{max} f(n_{wa}, p_{wa}) g(\theta),$$

where r_{max} denotes the maximum daily growth rate of the plant, f and g are scaling factors between 0 and 1, n_{wa} and p_{wa} denote the concentration of nitrogen and phosphorus in the water (mg/ℓ), respectively, and θ the water temperature (°C) [93]. Wilson *et al.* [93] proposed that the growth rate of water hyacinth increases linearly with temperature above the threshold and up to an optimum and decreases linearly with temperatures above that. He also described the relationship between the concentration of limiting nutrients and the growth rate of water hyacinth as a hyperbolic function [93]. In line with the parameter values used in studies by Tucker and DeBusk [72] and Wilson *et al.* [93], constant low nitrogen and phosphorus concentrations, yielding a scaling factor of $f(n_{wa}, p_{wa}) = 0.875$ for the effect of the water nutrient level, are assumed, together with a parameter value of $r_{max} = 0.11$/day. The water hyacinth daily growth rate, $r(\theta)$, measured at different temperatures, is then as given in Figure 4.2.

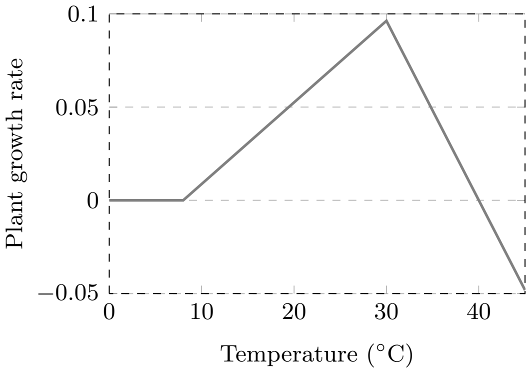


FIGURE 4.2: *Water hyacinth daily growth rate, $r(\theta)$, measured at different temperatures [93].*

4.3.2 Development duration of the life stages of the weevil

Similar to Wilson's [91] approach, time lags are used to account for the time it takes for the weevil to develop from one stage in its life cycle to the next. At time $t = 0$, following a release, there are only adult weevils present in the system. It is assumed that the adults immediately start laying eggs, leading to young larvae entering the system after $t_E(\theta)$ days. Old larvae are expected to start appearing $t_{L_1}(\theta)$ days thereafter. Similar to most temperature-dependent development studies [8], Wilson [91] suggested that the daily development rate of each stage increases linearly with temperature up to an optimum (θ_i^{opt}) and decreases linearly with temperatures above that up to a maximum temperature (θ_i^{max}). Assuming the minimum and maximum development durations provided by Wilson [91], the development rate, $\alpha_i(\theta)$, with $i = E, L_1, L_2$ or P, is given by

$$\alpha_i(\theta) = \alpha_i^{max} h_i(\theta),$$

where α_i^{max} denotes the maximum daily development rate of stage i and $h_i(\theta)$ denotes the temperature function presented by Wilson [91], given by

$$h_i(\theta) = \begin{cases} \frac{\theta - \theta_i^{min}}{\theta_i^{opt} - \theta_i^{min}} & \text{if} \quad \theta_i^{min} < \theta \leq \theta_i^{opt} \\ \frac{\theta_i^{max} - \theta}{\theta_i^{max} - \theta_i^{opt}} & \text{if} \quad \theta_i^{opt} < \theta < \theta_i^{max} \\ 0 & \text{otherwise.} \end{cases} \tag{4.21}$$

The development rate of a stage will be *zero* for all temperatures below θ_i^{min} or above θ_i^{max}. The average development duration (in days) of each stage, $t_i(\theta)$, is then given by

$$t_i(\theta) = \begin{cases} \frac{1}{\alpha_i(\theta)} & \text{if} \quad \frac{1}{\alpha_i(\theta)} < t_i^{max} \quad \text{and} \quad \alpha_i(\theta) > 0 \\ t_i^{max} & \text{if} \quad \frac{1}{\alpha_i(\theta)} \geq t_i^{max} \quad \text{and} \quad \alpha_i(\theta) > 0 \\ \infty & \text{if} \quad \alpha_i(\theta) = 0. \end{cases}$$

The assumed development durations of immature stages at different temperatures are given in Table 4.1.

	Development duration (in days)			
Temperature (°C)	Eggs (t_E)	Young larvae (t_{L_1})	Old larvae (t_{L_2})	Pupae (t_P)
16	44	47	35	33
20	24	47	25.87	29.85
25	12	28.85	14.42	19.90
30	8	20	10	14.93
35	16	40	20	29.85
39	44	47	35	33

TABLE 4.1: *Average development duration of weevil life stage, measured at different temperatures.*

4.3.3 Oviposition rate

Wilson [91] found the effect of temperature on the oviposition rate to appear similar to the effect of temperature on the development rates. The oviposition rate of viable eggs, $q(\theta)$, is therefore assumed to be given by

$$q(\theta) = q_{max} h_q(\theta),$$

where q_{max} denotes the maximum number of eggs laid per adult per day. The temperature function, $h_q(\theta)$, is assumed similar to the temperature function given in equation (4.21), but using different minimum (θ_q^{min}), optimum (θ_q^{opt}) and maximum (θ_q^{max}) temperatures for oviposition.

4.3.4 Rate of damage caused by old larvae

Wilson [91] suggested that the rate of damage caused by old larvae, $c_{L_2}(\theta)$, is affected by temperature in the same way as the oviposition rate and development rates. Some studies found no significant effect of low water nutrient concentrations ($0.1 - 4$ mg/l) on the damage rate [92] and that the weevil consumption rate may increase exponentially with increasing water nutrient levels [91]. Since a constant low water nutrient concentration of less that 2 mg/l is assumed in this study, the interaction between the water nutrient concentration and the damage rate is assumed to be negligible. The rate of damage used in this study is given by

$$c_{L_2}(\theta) = c_{L_2}^{max} h_{c_{L_2}}(\theta),$$

where $c_{L_2}^{max}$ denotes the maximum rate of damage caused by old larvae and $h_{c_{L_2}}(\theta)$ is assumed similar to the temperature function given in equation (4.21), but using the same minimum, optimum and maximum temperatures as for ovipositing [91].

4.3.5 Through stage survival probabilities

The density-independent through stage survival probability for weevil development stage i is denoted by $\sigma_i(\theta)$. Provided the maximum probability of surviving through stage i, σ_i^{max}, attained from Wilson [91], the temperature dependent probability of surviving through stage i used in this study is assumed to be

$$\sigma_i(\theta) = \sigma_i^{max} h_i(\theta).$$

The temperature function, $h_i(\theta)$, is assumed similar to the temperature function given in equation (4.21). The change in the survival probabilities $\sigma_i(\theta)$ as a result of changes in temperature is shown in Figure 4.3.

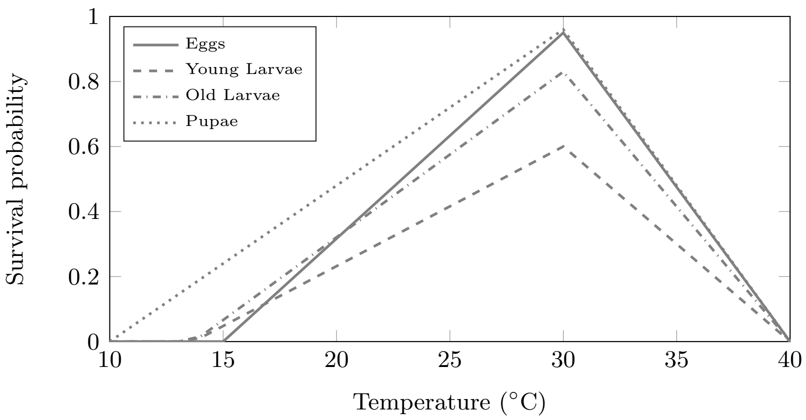


FIGURE 4.3: *Through stage survival probabilities, measured at different temperatures.*

4.3.6 Stage-specific mortality rates

The daily density-independent mortality rate, $\mu_i(\theta)$, for weevil development stage i ($i = L_1$ or L_2), is a function of temperature and is given by

$$\mu_i(\theta) = \begin{cases} -\frac{\ln(\sigma_i(\theta))}{t_i(\theta)} & \text{if} \quad \sigma_i(\theta) > 0 \\ 1 & \text{otherwise.} \end{cases} \tag{4.22}$$

This expression is derived from the well known relationship between the through stage survival probability and the density-independent mortality rate given by

$$\sigma_i(\theta) = \exp\{-t_i(\theta)\mu_i(\theta)\},$$

where $\sigma_i(\theta)$ is a constant [28, 91]. Since parameter values for the through stage survival probabilities could be obtained from literature, but not the mortality rates, the inverse relationship is used to determine the mortality rates as described in equation (4.22).

As temperature deviates from the optimal temperature for weevil survival and development, both the numerator and the denominator of the daily mortality rate are adjusted. The value of the survival probability, $\sigma_i(\theta)$, decreases with deviations from the optimal temperature, leading to an increase in the negative natural logarithm term and thus an increase in the numerator, while the value of the development duration, $t_i(\theta)$, in the denominator also increases with temperature deviations. The overall change in the daily mortality rate $\mu_i(\theta)$ as a result of changes in temperature is shown in Figure 4.4.

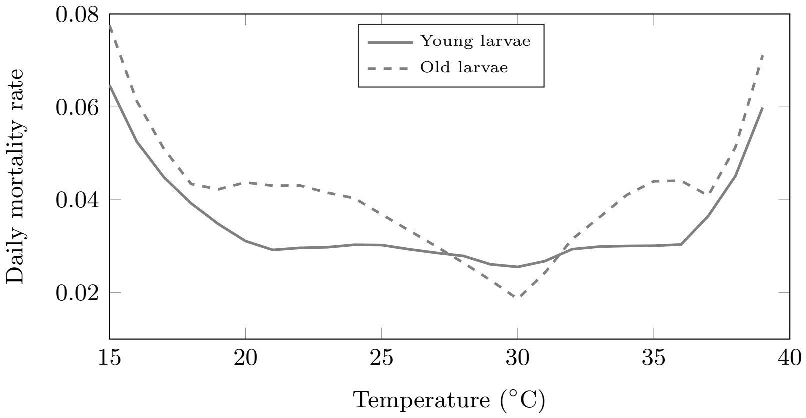


FIGURE 4.4: *Stage-specific daily mortality rates, measured at different temperatures.*

Furthermore, the temperature-dependent daily mortality rate for adult weevils, $\mu_A(\theta)$, is assumed to be the inverse of adult life expectancy, measured at different temperatures. The average adult life span, $t_A(\theta)$, at different temperatures was obtained from previous studies in literature [7, 18, 91] and is given in Table 4.2, together with the corresponding mortality rates ($1/t_A(\theta)$). This data is used as collocation points for the adult mortality function.

The temperature-dependent mortality function for adult weevils is determined by assuming linear relationships between adjacent collocation points given in Table 4.2. Adult mortality is assumed to be independent of density due to adult mobility. The daily adult mortality rate is

	Temperature							
	-5°C	0°C	5°C	20°C	25°C	30°C	35°C	40°C
Average adult life span (in days)	0 [18]		60 [18]	70 [91]	88 [91]	60 [91]	12 [91]	0 [91]
Daily adult mortality rate	1	0.0273 [18]	0.0167	0.0143	0.0114	0.0167	0.0833	1

TABLE 4.2: *Average adult life span and corresponding daily mortality rates, measured at different temperatures.*

thus given by

$$\mu_A(\theta) = \begin{cases} 1 & \text{if} \quad \theta \leq -5 \\ -0.194555\theta + 0.0273 & \text{if} \quad -5 < \theta \leq 0 \\ -0.002122\theta + 0.0273 & \text{if} \quad 0 < \theta \leq 5 \\ -0.000166\theta + 0.0175 & \text{if} \quad 5 < \theta \leq 20 \\ -0.000588\theta + 0.0260 & \text{if} \quad 20 < \theta \leq 25 \\ 0.001066\theta - 0.0151 & \text{if} \quad 25 < \theta \leq 30 \\ 0.013333\theta - 0.3833 & \text{if} \quad 30 < \theta \leq 35 \\ 0.183333\theta - 6.3333 & \text{if} \quad 35 < \theta \leq 40 \\ 1 & \text{if} \quad \theta > 40. \end{cases}$$

The change in the adult mortality rate $\mu_A(\theta)$ as a result of changes in temperature is shown in Figure 4.5.

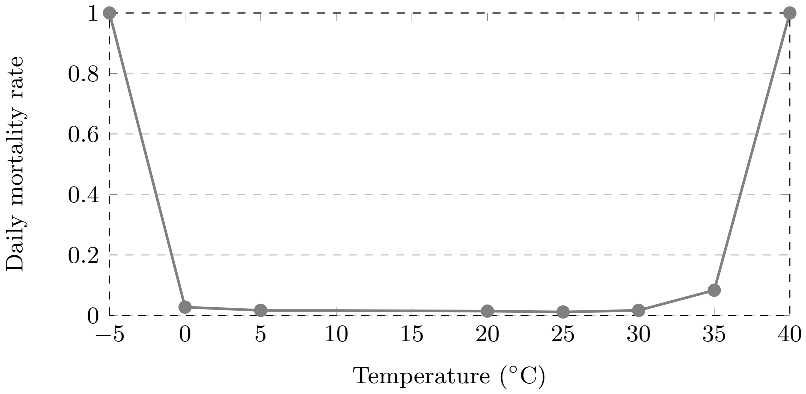


FIGURE 4.5: *Daily adult mortality rates measured at different temperatures.*

No losses from predators are assumed for the weevil populations. Although instances of birds attacking adults or fish feeding upon pupae have been observed, weevils are unlikely to have any specialist natural enemies in their introduced ranges [91]. These sources of mortality may reduce the effectiveness of weevils in controlling water hyacinth, but these exceptional scenarios are too unpredictable and variable to model.

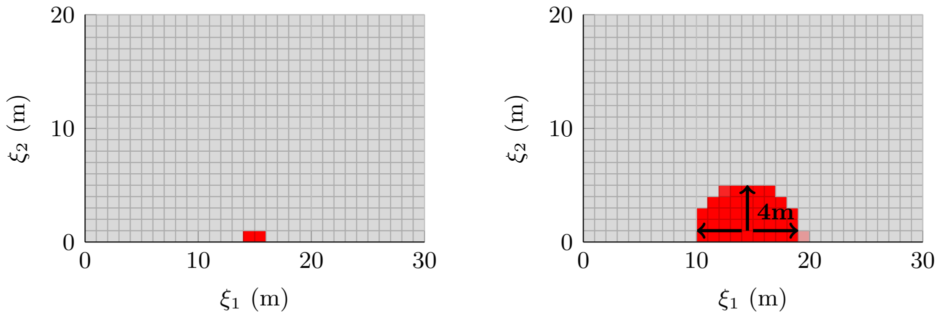
4.3.7 Diffusion coefficients

Crank [14] defines the diffusion coefficient as the rate of transfer of the diffusing substance across a unit area of a section, divided by the space gradient of concentration at the section. At the time of this study, information regarding the effectiveness with which old larvae and adult weevils disperse between neighbouring locations was limited. Suitable parameter values for the diffusion coefficients for the *N. eichhorniae* weevils and water hyacinth were therefore determined by means of reverse engineering[1], using the limited information available on the respective dispersal patterns from previous studies.

1. *Old larvae.* Wilson [91] observed the probability of third instar larvae moving between plants to be $p = 0.065$, assuming larvae move randomly between plants independent of plant size or nutrients. If plants are not in contact, larvae cannot move between plants [91]. The possible range of movement and the rate of dispersal were not available. The diffusion coefficient for old larvae, $d_{L_2}(\theta)$, is thus assumed to be equal to the movement probability divided by the number of days spent in the old larval stage in order to determine a daily rate. The old larval diffusion coefficient (in m^2/day) is thus temperature dependent and given by

$$d_{L_2}(\theta) = \frac{0.065}{t_{L_2}(\theta)}.$$

2. *Adults.* By means of dispersal experiments, Haag [30] determined that even in the absence of flight muscles, adult weevils are able to move between adjacent plants over a distance of at least 4 m in a course of one month. Information about adult movement over longer distances is still lacking. It is therefore assumed that adult weevils travel a maximum distance of 4 m per month. By means of reverse engineering, a diffusion coefficient of $d_A = 0.09$ m^2/day was obtained. In Figure 4.6, the dispersal of adult weevils released within a 1 m^2 area at the edge of an infested water body at time 0, with $d_A = 0.09$ m^2/day, is shown as obtained from the simulation output.



(a) *Initial population.* (b) *Dispersal after one month.*

FIGURE 4.6: *Adult weevil dispersal over one month with the derived diffusion coefficient of* $d_A = 0.09$ *m*^{2}*/day.*

3. *Water hyacinth.* As reported in Chapter 2, literature indicates that the water hyacinth surface area may increase by an average of 8% per day under good growing conditions [37]. A diffusion coefficient of $d_W = 0.08$ m^2/day reflects this assumed daily surface expansion. Figure 4.7 illustrates the population growth of the weed with the obtained diffusion rate without the influence of the BCAs. The red line indicates the carrying capacity of the water body. Once the plant density at a certain location reaches the carrying capacity, local reactions can no longer contribute to the population growth at that location, but the mat continues to expand sideways through diffusion. The model therefore yields realistic results for water hyacinth growth.

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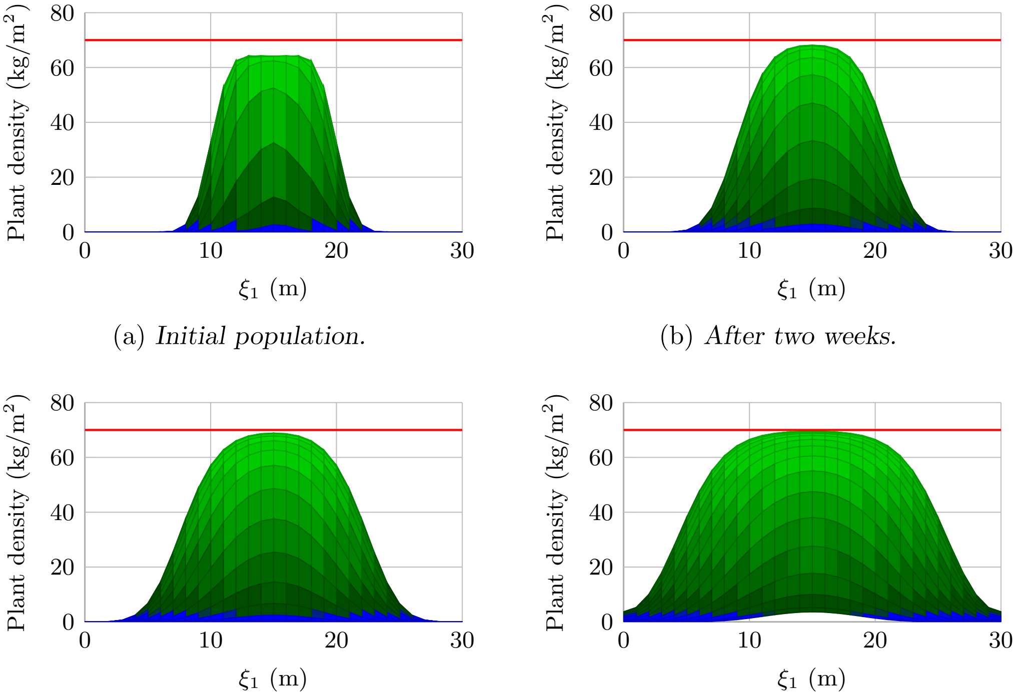
[1] The process of analysing an operation, extracting knowledge from it and reproducing something that would yield a similar outcome [64].



(a) *Initial population.*

(b) *After two weeks.*

(c) *After four weeks.*

(d) *After eight weeks.*

FIGURE 4.7: *Water hyacinth population growth over eight weeks without BCA releases.*

4.3.8 Temperature data

Temperature data was obtained from the weather website, WeatherSpark, where reports summarise typical weather for a region based on historical records from 1994 to 2012 [83]. For simplicity's sake, a constant mean temperature is assigned to each month. The monthly mean maximum temperatures and dew point temperatures at the Cape Town International Airport weather station, which will be used in this study, unless otherwise stated, are given in Figure 4.8. The dew points will be needed for evaporation rate calculations later in the study. Since *N. eichhorniae* weevils only develop at sufficiently high temperatures, only the mean maximum temperatures are considered. It is assumed that during each day, weevils will be exposed to temperatures around the mean maximum temperature of the applicable month for a sufficient period of time to allow for daily weevil development to occur at a rate based on the mean maximum temperature.

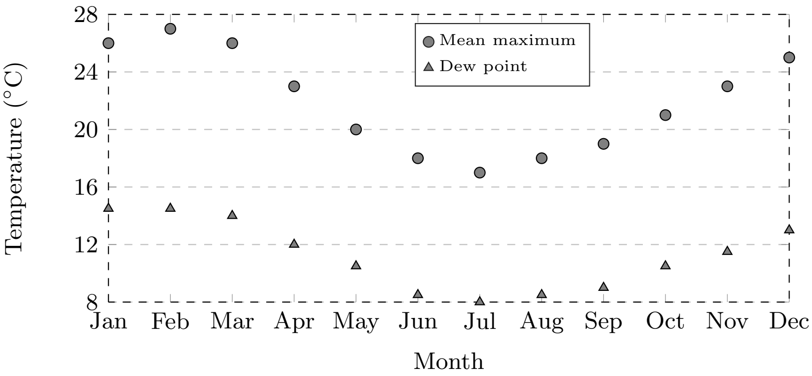


FIGURE 4.8: *Monthly mean maximum and dew point temperatures for the Cape Town region [83].*

4.3.9 Parameterisation

The parameter values and ranges given in Table 4.3 are assumed in this study.

Parameter	Description	Estimated Value (Range)	References
K	carrying capacity of water resource	70 kg/m^2	[93]
H	plant density at which herbivore feeding is reduced by half	0.2 kg/m^2	[91]
$c_{L_2}^{max}$	max rate of damage caused by old larvae/day	0.0951 kg/L_2	[91]
J_{L_1}	density-dependent mortality scaling parameter	0.0054 kg/L_1	[91]
q_{max}	max oviposition rate of viable eggs/day	4.4 eggs/adult	[91]
θ_h^{min}	min temperature for water hyacinth growth	8°C	[93]
θ_h^{opt}	optimum temperature for water hyacinth growth	30°C	[93]
θ_h^{max}	max temperature for water hyacinth growth	40°C	[93]
θ_q^{min}	min temperature for oviposition	10°C	[91]
θ_q^{opt}	optimum temperature for oviposition	30°C	[18, 38, 91]
θ_q^{max}	max temperature for oviposition	40°C	[91]
θ_E^{min}	min temperature for egg development	15°C	[38]
θ_E^{opt}	optimum temperature for egg development	30°C	[91]
θ_E^{max}	max temperature for egg development	40°C	[91]
θ_{L_1,L_2}^{min}	min temperature for larval development	13.7°C	[91]
θ_{L_1,L_2}^{opt}	optimum temperature for larval development	30°C	[91]
θ_{L_1,L_2}^{max}	max temperature for larval development	40°C	[91]
θ_P^{min}	min temperature for pupal development	10°C	§4.3.2
θ_P^{opt}	optimum temperature for pupal development	30°C	§4.3.2
θ_P^{max}	max temperature for pupal development	40°C	§4.3.2
α_E^{max}	max daily development rate for eggs	0.125	§4.3.2
$\alpha_{L_1}^{max}$	max daily development rate for young larvae	0.05	§4.3.2
$\alpha_{L_2}^{max}$	max daily development rate for old larvae	0.1	§4.3.2
α_P^{max}	max daily development rate for pupae	0.067	§4.3.2
$t_E(\theta)$	duration from oviposition to hatching of eggs	8-44 days	[91]
$t_{L_1}(\theta)$	duration of young larval stage	20-47 days	[91]
$t_{L_2}(\theta)$	duration of older larval stage	10-35 days	[91]
$t_P(\theta)$	duration of pupae stage	15-33 days	[91]
t_E^{max}	max duration from oviposition to hatching of eggs	44 days	[91]
$t_{L_1}^{max}$	max duration of young larval stage	47 days	[91]
$t_{L_2}^{max}$	max duration of older larval stage	35 days	[91]
t_P^{max}	max duration of pupae stage	33 days	[91]
σ_E^{max}	max probability of surviving the egg stage	0.95	[91]
$\sigma_{L_1}^{max}$	max probability of surviving the young larval stage	0.6	[91]
$\sigma_{L_2}^{max}$	max probability of surviving the older larval stage	0.83	[91]
σ_P^{max}	max probability of surviving the pupal stage	0.96	[91]

TABLE 4.3: *Model parameters and their corresponding values assumed in this study.*

4.4 Model output parameters

In this section, a cost-benefit function is derived in order to estimate the strengths and weaknesses of alternative biological control release strategies. The model output provides the densities of all the considered populations at every location at every time increment, which may be averaged over space and/or time for each population, as well as the total cost/benefit of each BCA release strategy. The average plant population size may be used to indicate the extent to which BCAs succeeded in suppressing weed populations for a specific release strategy, area and its temperature conditions over a period of time, while the cost-benefit function may be used to determine the most cost-effective release strategy for the specific scenario.

4.4.1 Release strategy

The decision variables for a release strategy are the number of weevils per release, I, the frequency of releases (defined as the number of days between two consecutive releases), f, the timing (specified as the starting season of releases) and the distribution of releases. Releases are assumed to occur once-off or at a constant rate of weekly, two weekly or four weekly over the period of release. A release may be concentrated at one point of an infested area or distributed among multiple accessible locations of the water body. An optimal release strategy is defined as a strategy which maximises the benefit. In order to maximise the total benefit, water hyacinth infestation has to be minimised together with the cost of releasing BCAs. The optimal strategy for a specific scenario is obtained by means of simulation.

4.4.2 Cost-benefit function

In order to estimate the cost-effectiveness of a release strategy, a cost-benefit function, which considers the daily cost of BCA releases and the daily benefit of water saved, is constructed. Even though there are many other advantages to effective control of water hyacinth, like the conservation of biodiversity, increased catchment stability, a greater potential for ecotourism and job creation through control programmes [42], only the gains to be obtained in terms of water are considered in this study. The amount of water saved is measured in terms of evapotranspiration from the plants. Significant amounts of water are being lost through water hyacinth infestations since the evapotranspiration rate from the plant averages about 3.7 (2.6 to 6.6) times that of evaporation from open water surfaces [54, 71], making it worth the while to investigate the benefit of the control of the weed in terms of water saving. The value of water saved will increase as water hyacinth densities are reduced by BCAs. The cost-benefit function will be used during analyses in the next chapter to determine whether the increase in the value of water saved due to a faster suppression of water hyacinth population densities as a result of greater amounts of BCAs being released, is worth the costs pertaining to the rearing and releasing of more BCAs. The cost/benefit, CB, of a release strategy is given by

$$\begin{aligned} CB &= \sum_t \sum_{\mathcal{D}} [\text{daily value of water saved}] - \sum_t \sum_{\mathcal{D}} [\text{daily cost of BCA releases}] \\ &= \sum_t \sum_{\mathcal{D}} \left[c_{wa} \left(e_W \left(K \right) - e_W \left(W(\underline{\xi}, t) \right) \right) \right] - \sum_t \sum_{\mathcal{D}} \left[c_{we} I X(\underline{\xi}, t) \right], \end{aligned}$$

where c_{wa} denotes the value of water per litre, c_{we} the cost of rearing and releasing a weevil and $e_W \left(W(\underline{\xi}, t) \right)$ the evapotranspiration rate of water hyacinth at location $\underline{\xi}$. When water hyacinth population density is suppressed below carrying capacity K, water is being saved. In the case where the total value of water saved is greater than the total cost pertaining to BCA releases, the release strategy yields an overall benefit. The cost-benefit function may be used to determine the break-even cost per BCA at which the cost of rearing and releasing BCAs will be justified by the amount of water saved. Such a break-even cost may serve as a target value for mass rearing programmes.

The relationship between the plant evapotranspiration rate and the density of the plant is assumed to be as illustrated in Figure 4.9. When the plant density is equal to 0 kg at location $\underline{\xi}$, the evapotranspiration rate is equal to the evaporation rate of open water at that location. At low plant densities, an increase in plant density will result in a high rate of increase in the plant evapotranspiration rate. The rate of increase in the plant evapotranspiration rate will decrease as the plant approaches carrying capacity at a certain location, where the plant evapotranspiration rate will be 3.7 times the normal evaporation rate of open water. The evapotranspiration rate of water hyacinth at location $\underline{\xi}$ at time t is, therefore, assumed to be given by $e_W\big(W(\underline{\xi},t)\big) = e_n(\theta) + (1-0.37)e_n(\theta)\ln\big(W(\underline{\xi},t)+1\big)$, where $e_n(\theta)$ denotes the evaporation rate of open water at temperature θ.

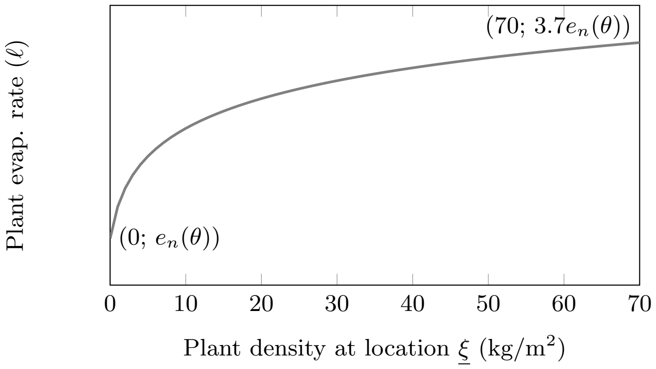


FIGURE 4.9: *Plant evapotranspiration rate for different plant densities.*

A formula for estimating the evaporation rate of open water surfaces like lakes, requiring only temperature and location data, was obtained from Linacre [44]. The assumed formula for the daily evaporation rate (in ℓ/m^2) from open water at temperature θ is given by

$$e_n(\theta) = \frac{700(\theta + 0.006h)/(100-l) + 15(\theta - \theta_d)}{80-\theta}, \tag{4.23}$$

where h denotes the elevation (meters) of the considered location, l the latitude (degrees), θ the mean temperature and θ_d the mean dew point [44]. When simulations are performed for areas within the Cape Town region, an elevation of $h = 42$ m and a latitude of $l = 34°$S are used. The average temperatures given in §4.3.8 are used as the values for parameters θ and θ_d. Substituting these parameter values into equation (4.23), the monthly average evaporation rates for open water for the Cape Town region, given in Table 4.4, were obtained.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Average $e_n(\theta)$ (ℓ/m^2/day)	8.35	8.99	8.49	7.22	5.95	5.42	5.05	5.42	5.81	6.49	7.35	8.14

TABLE 4.4: *Monthly average evaporation rates for open water for the Cape Town region.*

The costs pertaining to the rearing and release of BCAs are site specific and will depend on the mass rearing facility involved. For the sake of generality, the model will primarily be used to provide target values for c_{we}. When real-world case studies are investigated, the value of c_{we} will be determined for a specific scenario. Unit-price estimates for water are normally based on modified representative value estimates for water usage, assuming that the value of water is derived from its use [56]. As a rule, the two broadly defined water-use categories are *serviced* and *unserviced* water. The primary distinction is that the cost of the serviced water includes the treatment and delivery costs in addition to the costs of capturing and storing the water. In a study where the value of water losses due to invasive alien plants in South Africa was estimated, Pimentel [56] reported that about 64% of the total surface water supplied to consumers in South Africa is sold as unserviced water with a marginal value of R0,00014/ℓ in 2011 Rand, while the remaining 36% is supplied as serviced water which is sold at R0,0052/ℓ. In 2011, Pimentel [56] took the weighted average value of water as R0,0018/ℓ for South Africa in his ecological and economic analysis. By means of inflation adjustment[2], using the South Africa Consumer Price

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[2] The adjustment of prices to be measured in a constant currency over time by dividing monetary values by a price index and thereby removing the effect of inflation.

Index (CPI), the value was adjusted to 2016 Rand values. Considering this as a proxy value for water, the value of water saved, c_{wa}, is assumed to be equal to R0,00235/ℓ in 2016 Rand.

4.5 Software implementation

The model was implemented in MATLAB 9.0 (R2016a) where the system of delayed PDEs in a bounded two-dimensional spatial domain is solved using tools from the PDE toolbox and its built-in functions [70]. Various difficulties encountered during the implementation process are discussed below.

1. *System formulation.* Firstly, the equations had to be put in the correct form in order to be able to use the tools from MATLAB's PDE toolbox to solve the system of PDEs, since the toolbox does not have the option for solving nonlinear parabolic PDEs. For each equation, the linear part is put on the left-hand side and the nonlinear part on the right-hand side of the equation. Similar to an approach used by Howard [35], the nonlinearity is taken as a driving term from the previous time step and the remaining linear equations are decoupled so that five single equations are solved rather than a system. Provided the initial conditions, solution times, boundary conditions, mesh parameters and various PDE coefficients are supplied, the built-in `parabolic` function produces the solution to the *finite element method*[3] formulation of the PDE problem. The `parabolic` function creates finite element matrices corresponding to the problem internally and calls `ode15s` to solve the resulting system of ordinary differential equations.

2. *Time lags.* Since the built-in functions do not allow for time lags, history matrices containing the solutions to the system at all previous time increments are constructed to determine the partial derivative of a function where the solution at a certain time depends on the values of the function at previous times.

3. *Spatial averaging.* Spatial averaging for the old larval stage, involving both time delay and diffusion, had to be implemented. An explicit expression for the spatial averaging kernel $G(\underline{\xi}, \underline{x}, t_{L_2}(\theta))$ in equation (4.16) in the bounded two-dimensional case does not exist. Therefore, the expression for the spatial averaging kernel for the *un*bounded case is used in the implementation and the effect of each reflecting boundary (homogeneous Neumann boundary conditions) is accounted for manually. Following an approach used by Powell [59], the effect of reflecting boundaries is simulated by creating artificial populations of dispersers on the outsides of the boundaries, which, when they disperse back toward the original grid, will add to the original population the individuals that "reflected" from the boundaries. This is accomplished by first reflecting the data of the original grid over each boundary, storing the reflections together with the original grid (nine grids in total) in an artificial grid and considering the new grid as an infinite domain. Spatial averaging is then performed over the entire new grid. Finally, the original grid is extracted to obtain the population of interest. The effect of what happens at each boundary of the original grid is illustrated in Figure 4.10, with a reflecting boundary at 0. The red line resembles the initial population at time 0, blue the dispersal of the original population after a certain time period, green the dispersal of the reflected population and magenta the final population of interest, which is the population after dispersal, taking the reflecting boundaries into

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[3] The finite element method (FEM) is a numerical technique for finding approximate solutions to PDEs when finding their solutions by analytical means is impossible. FEM subdivides a large problem into smaller, simpler parts and approximates a solution to the problem by minimising an associated error function [67, 88].

account. The final population distribution (magenta) is the sum of the original (blue) and reflected (green) population densities for each location within the original grid.

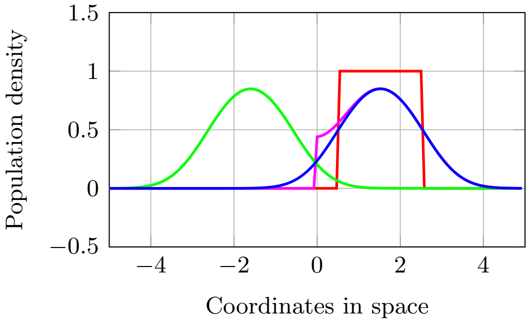


FIGURE 4.10: *Illustration of how the effect of a reflecting boundary is accounted for in the model.*

The recruitment rate, $R_{L_2}(\underline{x}, t - t_{L_2}(\theta))$, is considered as the initial population for the old larval stage. The individuals disperse randomly according to the distribution g. Derived from the one-dimensional unbounded expression provided in [21, 22] and similar to an expression used by [59], the spatial averaging Gaussian kernel g for the two-dimensional unbounded case is given by

$$g(\underline{\xi}, t_{L_2}(\theta)) = \frac{1}{4\pi d_{L_2}(\theta) t_{L_2}(\theta)} e^{-(\xi_1^2+\xi_2^2)/4 d_{L_2}(\theta) t_{L_2}(\theta)}, \tag{4.24}$$

with parameters as defined in §4.2. The final population distribution after $t_{L_2}(\theta)$ days is given by

$$\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} g(\underline{\xi}, \underline{x}, t_{L_2}(\theta)) R_{L_2}(\underline{x}, t - t_{L_2}(\theta))\,\mathrm{d}\underline{x} = R_{L_2}(\underline{\xi}, t - t_{L_2}(\theta)) * g(\underline{\xi}, t_{L_2}(\theta)), \tag{4.25}$$

where the latter operation is called the convolution. Algorithm 4.1 describes the spatial averaging process.

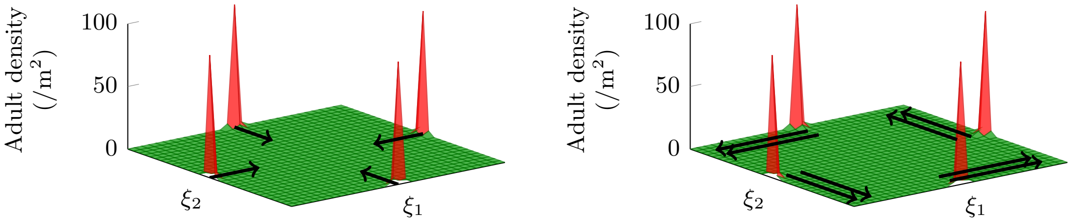
Algorithm 4.1: Spatial averaging for old larval stage

Input : Distribution of old larvae as they enter the stage at an earlier time, mesh coefficients, development duration of old larval stage, old larval diffusion rate.
Output: Distribution of old larvae ready to mature at current time.

```
Create two-dimensional $a \times b$ grid of geometry;
Create triangular mesh of grid;
Set $R_{L_2}(i, t - t_{L_2}(\theta))$ as initial population for each node $i$ of the grid;
Define expression g given in Eq. (4.24) for spatial averaging kernel over entire mesh;
Normalise kernel using the built-in trapz function;          // g/trapz(trapz(g))
Perform Fast Fourier Transform of g in 2 dimensions for convolution in Eq. (4.25);   // fft2(g)
Create reflections of the original grid data over each boundary;
Store the reflected grids together with the original grid in a new $3a \times 3b$ grid in their
  corresponding positions;
Perform dispersal on the entire $3a \times 3b$ grid;
Extract the original grid's data;
```

4. *Frequent releases.* Implementing frequent releases for the spatially explicit domain proved to be more challenging than for the spatially implicit case, especially concerning the locations of releases. Releases cannot occur at constant points in the spatial domain as after a period of time the plant may not exist at those points anymore, making it senseless to continue releases at the original points. To account for this, the function of the variable

$X(\underline{\xi}, t)$ in equation (4.14), indicating whether or not a release occurs at location $\underline{\xi}$ at time t, is implemented by executing two separate procedures. The first procedure determines the *time increments* at which releases are permitted (1 if permitted, 0 otherwise) and the second procedure validates the *locations* of releases (1 for a valid location, 0 otherwise). Concerning the latter procedure, an algorithm was constructed to search for the closest points to the original points of release where there exist sufficient plant densities for releases. The search may be conducted either straight in the direction of the centre of the domain (Figure 4.11(a)), or first to the right of the original points of release before it proceeds to the next row towards the centre of the domain, where it again will search to the right and so the process will continue until it reaches the centre of the domain (Figure 4.11(b)). Figure 4.11 illustrates an example of adult releases at the midpoints of each of the four edges of a square domain, with arrows indicating the two options for the directions in which the algorithm may proceed when searching for feasible points of release at each edge of the geometry once plant densities become insufficient at the original points of release. Since there was not a significant difference in the outcome between the two search options, the search straight to the centre of the domain was implemented in the interest of multiple releases per edge, where BCAs are already distributed along an edge and releases to the sides of the original positions become redundant.



(a) *To the centre of the domain.* (b) *First to the right of every point.*

FIGURE 4.11: *The two options for the direction in which searches for feasible points of release may be conducted when frequent releases are involved.*

Algorithm 4.2 demonstrates the procedure being followed for obtaining feasible points of release for the case illustrated in Figure 4.11(a), where BCAs will be released every f days at each of a four edges of a square domain.

Algorithm 4.2: Frequent releases

Input : Water hyacinth population density, mesh coefficients.
Output: Coordinate points of additions to adult population.

```
for every edge of the grid do
    for every node in the median column/row perpendicular to the edge do
        Determine plant density;
        if plant density $> 0$ then
            Allow addition to adult population at the current node;
            Terminate execution of the loop;
        end
    end
end
```

In the main algorithm where the system of PDEs is solved (Algorithm 4.3), a release is implemented as an addition of I to the right-hand side of the adult weevil population equation if both the required constraints are met at the considered time and location.

In light of these difficulties, let equations (4.11) – (4.15), governing the change in $W(\underline{\xi}, t)$, $L_1(\underline{\xi}, t)$,

$L_2(\underline{\xi}, t)$, $A(\underline{\xi}, t)$ and $S_{L_1}(\underline{\xi}, t)$, respectively, be the five PDEs being solved in the main procedure (Algorithm 4.3), assuming parameters and variables as defined in §4.2. Let $\mathbf{U_n}$ be the history matrix for the time-dependent results of the n^{th} PDE.

Algorithm 4.3: Solving the system of PDEs

Input : Total running time, starting month, Allee-effect threshold, magnitude of releases, frequency of releases, points of release, initial conditions.

Output: Solutions to the PDEs at every node for every time increment.

```
Create two-dimensional grid of geometry;
Assign boundary conditions given in Eq. (4.19) to edges;
Create triangular mesh with $m$ nodes;
Create time vector with $M$ time-stepping increments;
Assign constant parameter values to $K$ and $J_{L_1}$ used in Eqs. (4.11)–(4.15);
Call temperature-dependent parameter values for starting month;      // TempDep(month,1)
for $i \leftarrow 1$ to $m$ do
    Set initial conditions given in (4.20) for Eqs. (4.11)–(4.15);
end
Set applicable initial conditions as first column of each $\mathbf{U_n}$;
for $t \leftarrow 1$ to $M$ do
    if time increment a multiple of 30 then                           // mod(t,30)==0
        Update temp. dependent parameter values for new month;        // TempDep(month,t)
    end
    if $(t - t_E(\theta) - t_{L_1}(\theta) - t_{L_2}(\theta)) > 0$ then
        Perform spatial averaging for $L_2$ stage;                    // Algorithm 4.1
    end
    if time increment a multiple of frequency $f$ then                // mod(t,f)==0
        Allow additions to adult population $A$ at time $t$ ($1^{\text{st}}$ procedure for Eq. (4.6));
    end
    Determine coordinates for additions to adult population $A$ ($2^{\text{nd}}$ procedure for Eq. (4.6));
                                                                      // Algorithm 4.2
    for $i \leftarrow 1$ to $m$ do
        Determine nonlinear interactions for plant population $W$ using Eq. (4.11);
        if $(t - t_E(\theta)) > 0$ then calculate $R_{L_1}(i,t)$ using Eq. (4.7);
        else $R_{L_1}(i,t) = 0$;
        if $(t - t_E(\theta) - t_{L_1}(\theta)) > 0$ & $R_{L_1}(i, t - t_{L_1}(\theta)) > 0$ then calculate $R_{L_2}(i,t)$ using Eq. (4.8);
        else $R_{L_2}(i,t) = 0$;
        if $(t - t_E(\theta) - t_{L_1}(\theta) - t_{L_2}(\theta)) > 0$ then calculate $R_P(i,t)$ using Eq. (4.9);
        else $R_P(i,t) = 0$;
        if $(t - t_E(\theta)) > 0$ then determine nonlinear interactions for $L_1$ using Eq. (4.12);
        else nonlinear interactions for $L_1 = 0$;
        if $(t - t_E(\theta) - t_{L_1}(\theta)) > 0$ then determine nonlinear interactions for $L_2$ using Eq. (4.13);
        else nonlinear interactions for $L_2 = 0$;
        if $(t - t_E(\theta) - t_{L_1}(\theta) - t_{L_2}(\theta) - t_P(\theta)) > 0$ then determine nonlinear interactions for $A$ using
        Eq. (4.14);
        else nonlinear interactions for $A = 0$;
        if $(t - t_E(\theta) - t_{L_1}(\theta)) > 0$ then determine nonlinear interactions for $S_{L_1}$ using Eq. (4.15);
        else nonlinear interactions for $S_{L_1} = 0$;
    end
    Define nonlinear interaction terms for all $n$ PDEs at centerpoints of mesh triangles by
    interpolation using the built-in pdeintrp function;
    Solve all $n$ PDEs with the built-in parabolic function;
    Set zero as a lower bound for solutions of all $n$ PDEs;
    Append new solutions to each $\mathbf{U_n}$ for all $n$ PDEs;
end
```

The water hyacinth and weevil system incorporates variable temperature. Algorithm 4.4 gives more insight into the process being carried out when the `TempDep` function is called in lines 6 and 13 of the main algorithm. The temperature-dependent parameters used in system (4.11) – (4.15) are $r(\theta)$, $c_{L_2}(\theta)$, $q(\theta)$, $d_{L_2}(\theta)$, $t_E(\theta)$, $t_{L_1}(\theta)$, $t_{L_2}(\theta)$, $t_P(\theta)$, $\sigma_E(\theta)$, $\sigma_{L_1}(\theta)$, $\sigma_{L_2}(\theta)$, $\sigma_P(\theta)$, $\mu_{L_1}(\theta)$, $\mu_{L_2}(\theta)$ and $\mu_A(\theta)$. As described in Algorithm 4.4, the values of these parameters are updated at the beginning of each month when a new average temperature is set.

Algorithm 4.4: Temperature dependent parameters

Input : Starting month, time increments.
Output: Temperature-dependent parameter values, linear interactions and diffusion rates.

```
Set vector with monthly average temperatures, depending on starting month;
if first time increment then                                                   // $t$==1
    Set average temperature $\theta$ for first month;
    Calculate temp. dependent parameter values;
    Calculate temp. dependent linear interactions for Eqs. (4.11)–(4.15);
    Calculate temp. dependent diffusion coefficients for Eqs. (4.11)–(4.15);
else if time increment a multiple of 30 then                                   // mod($t$,$30$)==0
    Update average temperature $\theta$ for new month;
    Calculate temp. dependent parameter values;
    Calculate temp. dependent linear interactions for Eqs. (4.11)–(4.15);
    Calculate temp. dependent diffusion coefficients for Eqs. (4.11)–(4.15);
end
```

4.6 Model validation

Model validation may be described as the process of proving that a model yields results within a sufficient range of accuracy in accordance with the intended application of the model [33, 57]. A series of tests were performed to determine whether changes in certain parameter values yield the expected outcome. All simulations reported here were performed for an area of 10 m × 10 m, assumed to be entirely infested with water hyacinth to carrying capacity prior to BCA releases, unless otherwise stated.

The parameter θ has an effect on the growth rate of the plant, the weevil oviposition rate, damage rate, survival probabilities, mortality rates and development duration of the weevil stages, as well as the diffusion rate of the old larval stage. For values of θ close to 30°C, the plant will grow at a fast rate, accompanied by a high rate of ovipositing for adult weevils. The development time in each weevil life stage will be shorter than for values of θ deviating from 30°C, with high surviving probabilities and a high old larval daily diffusion rate, resulting in initial weevil infestation levels increasing faster. Since old larvae will cause maximum damage at this level of θ, plant populations are expected to decrease fast once old larvae enter the system. Due to density dependence, this will in time result in faster decreases in weevil populations, yielding greater oscillations of population densities.

As a result of more BCAs being present to cause damage, an increase in the parameter I is expected to result in a faster decrease in initial plant density in the short term. For high levels of I, density dependence in the young larval stage is expected to result in a faster decrease in weevil population densities compared to lower values of I. In time, decreases in the weevil populations will result in increases in the plant population densities again.

The parameters a and f have immediate effects on the weevil population densities, while parameter $c_{L_2}^{max}$ immediately affects the water hyacinth population density. An inverse relationship between a and the weevil population densities over time is expected due to the reduction in adult reproduction, while a direct relationship between the frequency f of BCA releases and the adult weevil population densities is expected. An inverse relationship between the maximum rate of damage caused by weevils, $c_{L_2}^{max}$, and the total water hyacinth population over time is expected. Any parameter influencing the weevil populations, indirectly influences the water hyacinth population and *vice versa*, due to the interaction between the two species.

Diffusion on a homogeneous domain with constant positive diffusion coefficients is expected to result in a gradual spread over time. Dispersal of the applicable population is expected to occur faster for higher values of d_A, $d_{L_2}(\theta)$ and d_W, respectively.

4.6.1 Model response to changes in θ

In order to test whether the model responds correctly in the short term and the long term to changes in temperature, simulations were performed with once-off BCA releases of 100 adults at time 0 at each of the four edges of the considered domain, with temperature held constant at 15°C, 20°C, 25°C, 30°C and 35°C over a period of three months and one year, respectively.

The short term model responses are given in Table 4.5, where it may been seen that the total plant density averaged over time, is lowest at the optimal temperature for weevil development (30°C) and the average weevil density reaches a maximum at this temperature, as expected. Average plant and weevil densities increase and decrease, respectively, at temperatures below or above the optimum temperature, as expected. It may be noted that the model output succeeds to accurately reflect the absence of larvae populations at a temperature of 15°C, since, in practice, weevil development is severely restricted at such low temperatures. At low temperatures, model responses correctly indicate that the weed will continue to flourish without any damage being caused by larvae. Model responses in the long term, documented in Table 4.6, indicate that the average total plant density will still reach a minimum at the optimal temperature for weevil development (30°C) over a longer period of time, but due to weevils being exposed to low plant densities for a longer period of time, density dependence is expected to result in sub-maximal weevil population densities at 30°C, as is reflected by model output. In Table 4.6 it may be noted that long term persistence of BCAs is only ensured at temperatures of 25°C and 30°C.

θ (°C)	Av. plant density (kg/100 m^2)	Av. young larval density (/100 m^2)	Av. old larval density (/100 m^2)	Av. adult density (/100 m^2)
15	7 000	0	0	212
20	6 988	410	46	218
25	6 666	1 016	350	316
30	**6 053**	**21 909**	**823**	**1 469**
35	6 959	215	70	55

TABLE 4.5: *Model response to varying temperatures over three months.*

θ (°C)	Av. plant density (kg/100 m^2)	Av. young larval density (/100 m^2)	Av. old larval density (/100 m^2)	Av. adult density (/100 m^2)
15	7 000	0	0	70
20	6 983	101	20	85
25	4 044	22 834	1 202	2 081
30	**3 241**	**18 252**	**940**	**1 357**
35	6 983	53	18	16

TABLE 4.6: *Model response to varying temperatures over one year.*

4.6.2 Model response to changes in I

In order to test whether the model responds correctly in the short term and the long term to changes in the number of adult weevils released, simulations were performed with once-off BCA releases of different magnitudes at time 0 at each of the four edges of the considered domain and with temperature held constant at 30°C over a period of three months and one year, respectively.

As expected, average short term plant densities decrease with increases in the number of adult weevils released at time 0 as a result of more weevils (old larvae) being present to cause damage and help to suppress weed population densities (see Figure 4.12).

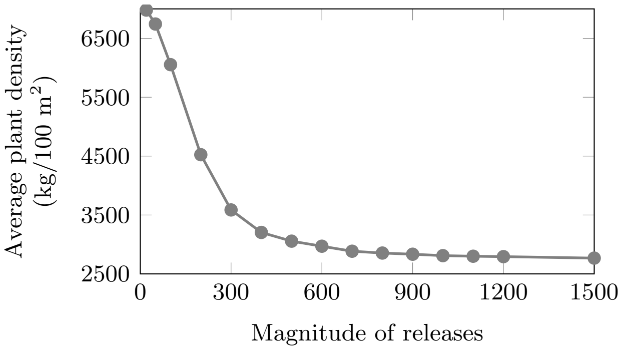


FIGURE 4.12: *Total plant population densities averaged over three months for varying magnitudes of once-off adult releases at each of the four edges of a 10 m × 10 m area infested with water hyacinth at time 0.*

Long term model responses to changes in the number of adult weevils released at time 0 are given in Table 4.7. Due to populations being exposed to density-dependent interactions for a longer period of time and averages being taken over a heterogeneous domain, the long term plant and weevil densities responses are more variable, as expected. The model correctly reflects the hydra effect where an increase in the number of BCAs released does not always result in lower average plant density in the long term due to a greater impact of density dependence on the larval stages when more BCAs are released, yielding less damage-causing old larvae to suppress weed densities. Lower old larvae population densities result in higher plant densities.

I	Av. plant density (kg/100 m^2)	Av. young larval density (/100 m^2)	Av. old larval density (/100 m^2)	Av. adult density (/100 m^2)
20	5 168	9 468	521	1 096
50	2 095	8 852	669	1 295
100	3 241	18 252	940	1 357
200	1 481	15 886	867	2 048
300	990	8 953	823	2 713
400	847	7 333	883	2 150
500	1 014	10 282	996	1 554
600	890	7 319	929	1 581
700	1 687	7 000	1 109	714
800	799	8 002	1 119	2 610
900	1 455	16 208	1 458	1 651
1 000	2 412	8 373	1 281	1 060
1 100	1 010	9 824	1 373	1 641
1 200	992	9 955	1 365	1 792
1 500	951	9 874	1 328	1 718
2 000	1 211	13 600	1 798	1 662

TABLE 4.7: *Model response to varying magnitudes of adult releases over one year.*

4.6.3 Model response to changes in a

In order to test whether the model responds correctly to changes in the Allee-effect threshold, simulations were performed with threshold values of 3, 4 and 5, respectively, with once-off BCA releases of 100 adult weevils at time 0 at each of the four edges of the considered domain and with temperature held constant at 30°C over a period of one year. As expected, model output indicates that the average total population densities for all the weevil life stages decrease with an increase in the Allee-effect threshold, due to a stricter limitation on weevil reproduction. Model output further indicates that these decreases in weevil population densities result in increases in the total plant population densities averaged over time, as expected.

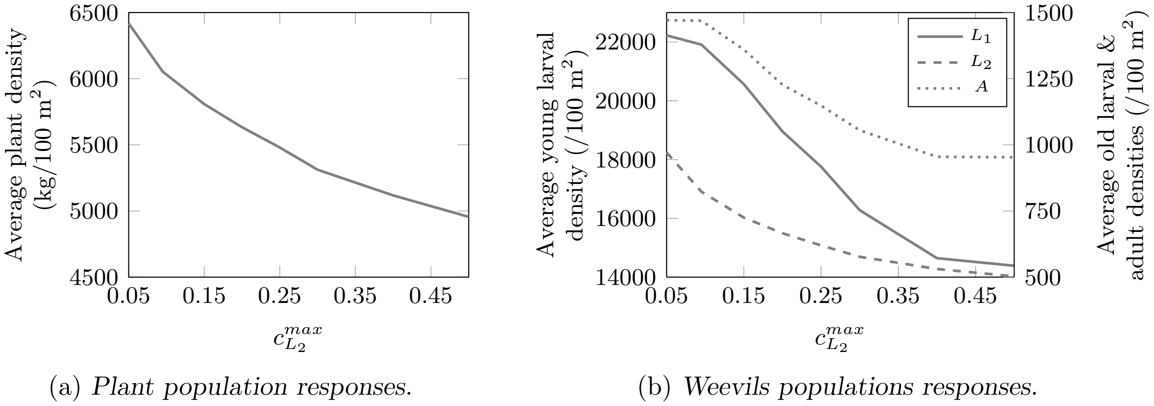
a	Av. plant density (kg/100 m^2)	Av. young larval density (/100 m^2)	Av. old larval density (/100 m^2)	Av. adult density (/100 m^2)
3	3 241	18 252	940	1 357
4	3 798	9 589	755	954
5	4 241	7 030	633	719

TABLE 4.8: *Model response to changes in the Allee-effect threshold, $a < 6$, over a period of one year. The parameter value used in the model is $a = 3$.*

4.6.4 Model response to changes in $c_{L_2}^{max}$

In order to test whether the model responds correctly in the short term and the long term to changes in the maximum rate of damage caused by old larvae, simulations were performed with varying damage rates, with once-off BCA releases of 100 adult weevils at time 0 at each of the four edges of the considered domain and with temperature held constant at 30°C over a period of three months and one year, respectively.

Figure 4.13 illustrates how, in the short term, an increase in the old larval damage rate results in a decrease in the total plant population densities averaged over time, as well as a decrease in total weevil population densities due to the density-dependent interaction between the plant and weevil species, as one would expect. The total weevil population densities decrease as host-plant densities are suppressed faster in the short term.



(a) *Plant population responses.* (b) *Weevils populations responses.*

FIGURE 4.13: *Model response to changes in the maximum rate of damage caused by older larvae over a period of three months. The parameter value used in the model is $c_{L_2}^{max} = 0.0951$.*

Long term model responses to changes in the maximum rate of damage caused by older larvae over a period of one year are given in Table 4.7. Due to populations being exposed to density dependent interactions for a longer period of time and averages being taken over a heterogeneous domain, the long term plant and weevil densities responses are more variable, as expected.

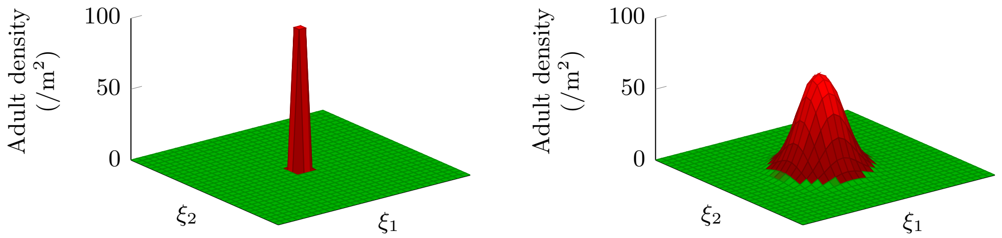
$c_{L_2}^{max}$	Av. plant density (kg/100 m^2)	Av. young larval density (/100 m^2)	Av. old larval density (/100 m^2)	Av. adult density (/100 m^2)
0.05	3 108	10 240	816	1 062
0.0951	3 241	18 252	940	1 357
0.15	2 396	10 214	653	938
0.20	2 535	6 271	393	684

TABLE 4.9: *Model response to changes in the maximum rate of damage caused by older larvae over a period of one year. The parameter value used in the model is* $c_{L_2}^{max} = 0.0951$.

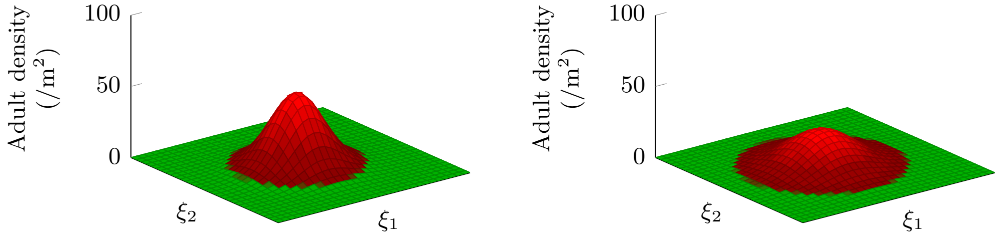
4.6.5 Model response to changes in d_A and $d_{L_2}(\theta)$

In order to test whether the implementation of the weevil dispersal process with constant diffusion coefficients responds correctly, simulations were performed with once-off BCA releases at time 0 at the centre of the considered domain, with varying diffusion coefficients and with temperature held constant at 30°C over a period of three months. Homogeneous initial water hyacinth population densities at carrying capacity K over the entire 30 m × 30 m domain were assumed.

As expected, gradual spreading of adult weevils occurred, with faster dispersal over time as the diffusion coefficient was increased (see Figure 4.14). Similar responses to changes in the old larval diffusion coefficient occurred, as expected for a population with a constant positive diffusion coefficient.



(a) *Initial adult population.* (b) *Final densities with* $d_A = 0.09$.



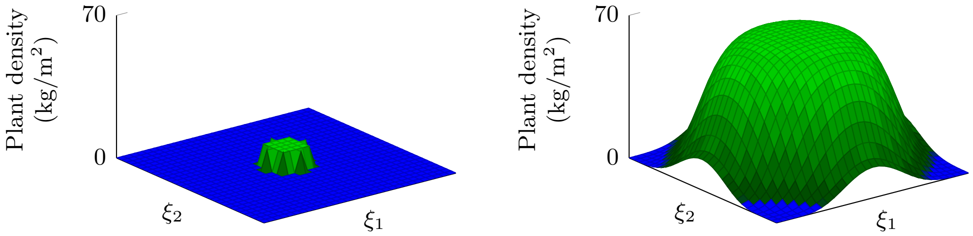
(c) *Final densities with* $d_A = 0.19$. (d) *Final densities with* $d_A = 0.29$.

FIGURE 4.14: *Adult weevil population densities for different diffusion coefficients over three months. The parameter used in the model is* $d_A = 0.09$.

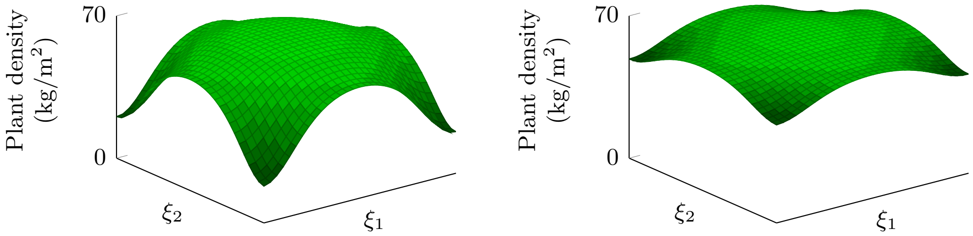
4.6.6 Model response to changes in d_W

In order to test whether the implementation of the water hyacinth dispersal process responds correctly, simulations were performed with varying diffusion coefficients, with temperature held constant at 30°C over a period of three months and without BCA releases. Initial water hyacinth population densities were concentrated at the centre of a 30 m × 30 m domain.

As expected, the plant gradually spread out over the domain, with faster dispersal over time as the diffusion coefficient was increased (see Figure 4.15). The differences between adjacent sites tended to zero as t increased, as expected for a model with positive diffusion coefficients. The model thus responds correctly to changes in the water hyacinth diffusion coefficient.



(a) *Initial plant population.* (b) *Final densities with* $d_W = 0.08$.



(c) *Final densities with* $d_W = 0.18$. (d) *Final densities with* $d_W = 0.28$.

FIGURE 4.15: *Plant population densities for different diffusion coefficients without BCA releases over three months. The parameter used in the model is* $d_W = 0.08$.

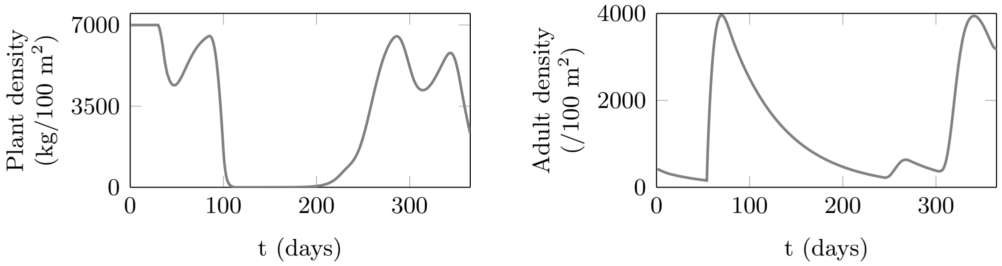
4.6.7 Model response to changes in f

In order to test whether the implementation of the frequent BCA release process responds correctly, simulations were performed with once-off, weekly, two-weekly and four-weekly releases, respectively, with a magnitude of 100 adult weevils per release at each of the four edges of the considered 10 m × 10 m domain and with temperature held constant at 30°C over a period of one year.

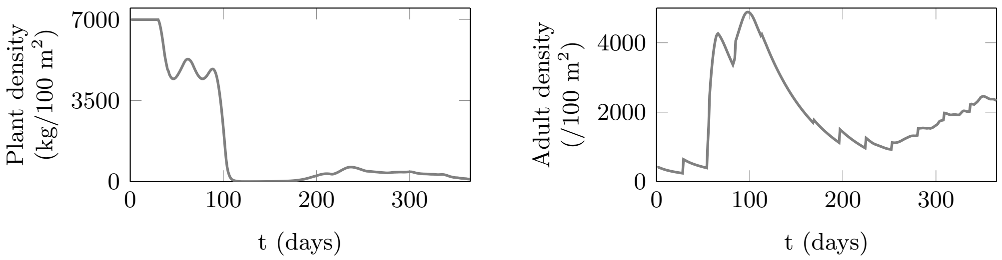
As expected, model responses indicate a decrease in the average plant population density over time when BCAs are released more often (see Table 4.10). In Figure 4.16, the plant and adult population densities, subject to once-off ($f = 0$), low frequency ($f = 28$) and high frequency ($f = 7$) releases over the period of one year, are shown. Water hyacinth populations are suppressed faster the more often adult weevils are released, as expected. The model implementation succeeds to accurately reflect the regrowth of the weed after a period of time, subsequent to being suppressed to very low densities over the entire domain. Frequent adult weevil releases are ceased once the weed is suppressed below a certain threshold and resumed when the weed grows back to sufficient densities for releases. As expected, higher frequencies of releases result in more effective weed suppressions after regrowth.

f (days)	Av. plant density (kg/100 m^2)
0	3 241
28	1 688
14	1 300
7	1 014

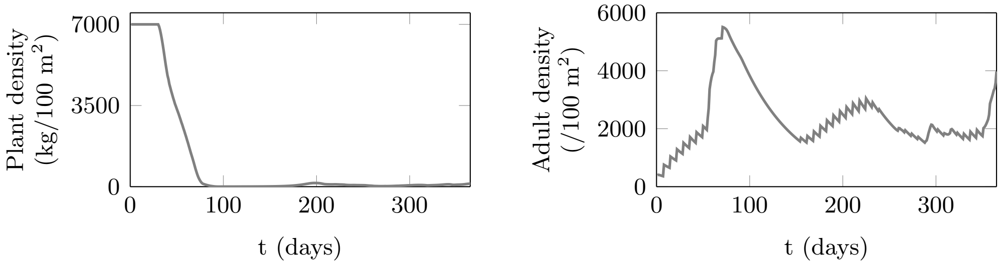
TABLE 4.10: *Model response to changes in the frequency of BCA releases, f, over a period of one year. The average plant density for a once-off release at time 0 ($f = 0$) is compared to average plant densities for four-weekly ($f = 28$), two-weekly ($f = 14$) and weekly ($f = 7$) releases.*



(a) *Plant densities with $f = 0$.* (b) *Adult densities with $f = 0$.*



(c) *Plant densities with $f = 28$.* (d) *Adult densities with $f = 28$.*



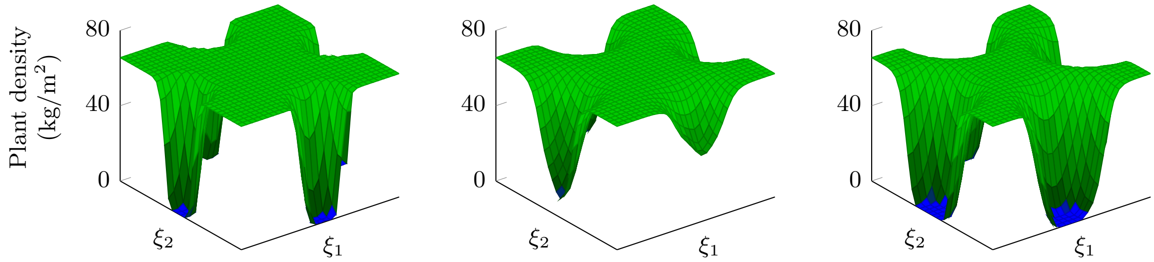
(e) *Plant densities with $f = 7$.* (f) *Adult densities with $f = 7$.*

FIGURE 4.16: *Plant and adult population densities for once-off ($f = 0$), low frequency ($f = 28$) and high frequency ($f = 7$) releases over a time period of one year.*

4.6.8 Model response to timing of BCA releases

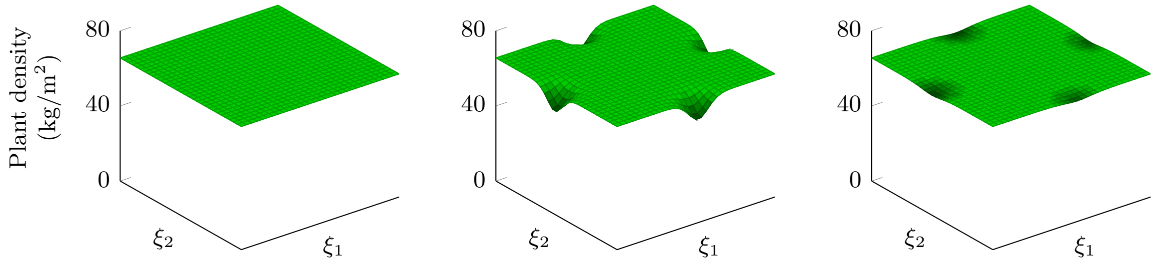
Simulations were performed to investigate the effect on water hyacinth populations in the Cape Town region when adult weevils are released once-off in summer (December, with an average high temperature of 25°C) or winter (June, with an average high temperature of 18°C), subject to monthly varying temperatures corresponding with historical weather data of the Cape

Town region [83]. Once-off releases of 1 000 BCAs at time $t = 0$ at each of the four edges of a 30 m × 30 m infested water body were simulated. Figures 4.17 and 4.18 illustrate the different spatial dynamics over two, four and six months for summer and winter releases, respectively, corresponding with the change in the total plant density over the entire domain, given in Figure 4.19. In Figure 4.19(a), it may be seen that the delay between subsequent damage-causing old larval generations gives the weed a chance to grow back (Figure 4.17(b)). Six months later, the BCAs that were released during summer are exposed to colder winter temperatures (Figure 4.17(c)), but favourable weather conditions during the first months after releases supported establishment and BCAs could still contribute towards the suppression of weed populations during subsequent colder seasons. Confirming what happens in practice, Figures 4.18 and 4.19(b) indicate that BCAs may not be able to establish under certain temperature thresholds due to slower development and higher mortality.



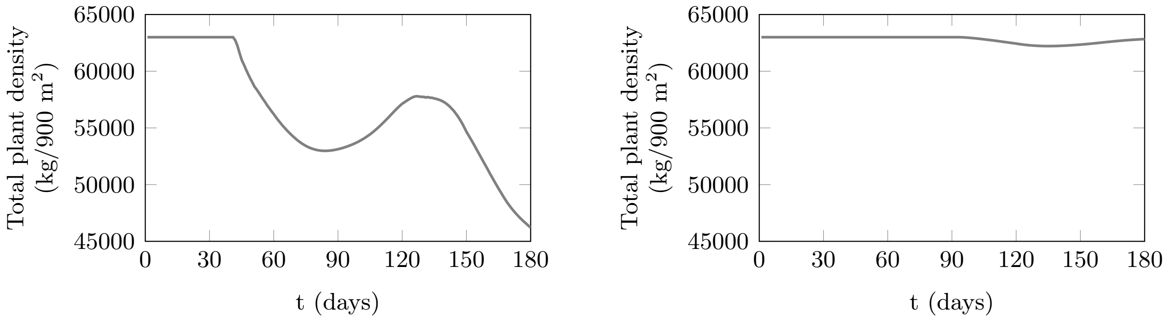
(a) *After two months.* (b) *After four months.* (c) *After six months.*

FIGURE 4.17: *Water hyacinth population dynamics after once-off BCA releases in December.*



(a) *After two months.* (b) *After four months.* (c) *After six months.*

FIGURE 4.18: *Water hyacinth population dynamics after once-off BCA releases in June.*



(a) *Summer release.* (b) *Winter release.*

FIGURE 4.19: *The change in the total plant density over a time period of six months after once-off releases of 1 000 BCAs at four edges in December (a) and June (b), respectively.*

4.6.9 Comparison with real-world data

At the time of this study, information regarding the detailed impact of real-life BCA releases in infested water hyacinth areas, especially the *N. eichhorniae* weevils as BCAs, has not been thoroughly recorded. Validating the model using real-world data was therefore quite challenging. The accuracy of the model presented in this study is evaluated by means of comparing the model output to the limited data available from the real-life BCA release scenario which took place at the Mkhadzi Spruit in the Kruger National Park in the Limpopo province of South Africa at the end of 2008 (geographical coordinates: 23°50'21"S 31°38'14"E).

The Mkhadzi Spruit forms part of the Engelhard Dam and is an example of a site where biological control of water hyacinth has been successful [13]. The Mkhadzi Spruit is classified as a medium nutrient and warm site, where BCAs are able to abound and cause significant damage to weeds. The demarcated region of interest is estimated to be an approximated surface area of 100 m × 50 m. The site was covered with water hyacinth prior to releases of a total of 20 000 water hyacinth BCAs, namely *Neochetina bruchi* Hustache (Coleoptera: Curculionidae) and *Eccritotarsus catarinensis* Carvalho (Heteroptera: Miridae), on 27 October 2008. Based on the available information, it is assumed that BCAs were released along one of the edges of the domain. After 72 days, openings in the water hyacinth mat confirmed the impact of the BCAs on the weed [13]. No information on whether the area was eventually completely cleared from water hyacinth or not, could be found.

A simulation of a once-off release of a total of 20 000 *N. eichhorniae* adult weevils distributed along one of the edges of a 100 m × 50 m domain (see Figure 4.20), with initial water hyacinth infestations at carrying capacity of the water body (70 kg/m^2), was performed over a time period of 72 days. Historical weather data for the year 2008 – 2009 for the Limpopo region was used to obtain the average monthly high temperatures of 27°C, 26°C, 26°C and 27°C for the months of October, November, December and January, respectively [83].

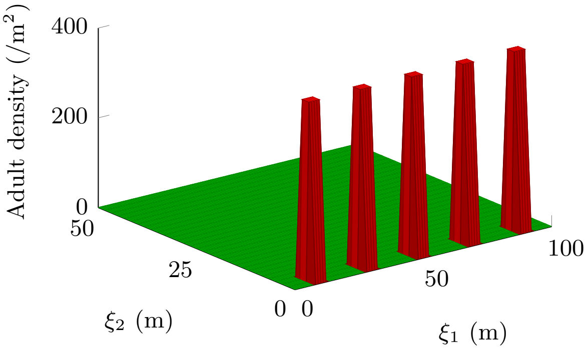


Figure 4.20: *Distribution of adult releases at time 0 for the simulation of the Mkhadzi Spruit release scenario.*

Since the exact surface area of the Mkhadzi Spruit on which the BCAs were released had to be estimated and different BCAs, which most probably possess different biological traits, were released, results are expected to differ somewhat. The BCAs may, for example, have different development rates, damage rates or movement behaviour from the *N. eichhorniae* weevils. Nevertheless, the simulation output reflects a realistic decrease in the total plant population densities over the considered period, as shown in Figure 4.21, as well as areas where the weed has been driven to extinction, as shown in Figure 4.22(c), reflecting the openings in the water hyacinth mat at the end of the 72-day investigation at the Mkhadzi Spruit. The model is therefore considered valid to describe the water hyacinth and weevil interactions in a temporally and spatially variable environment.

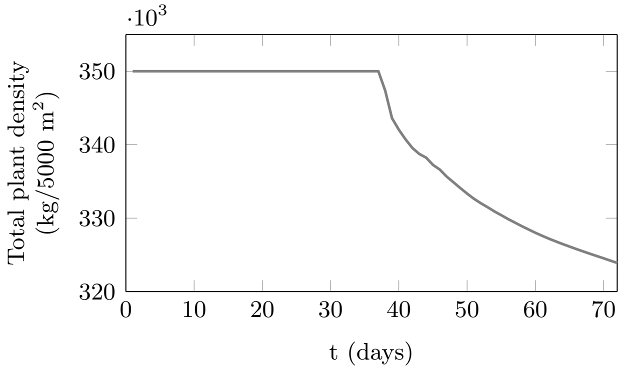
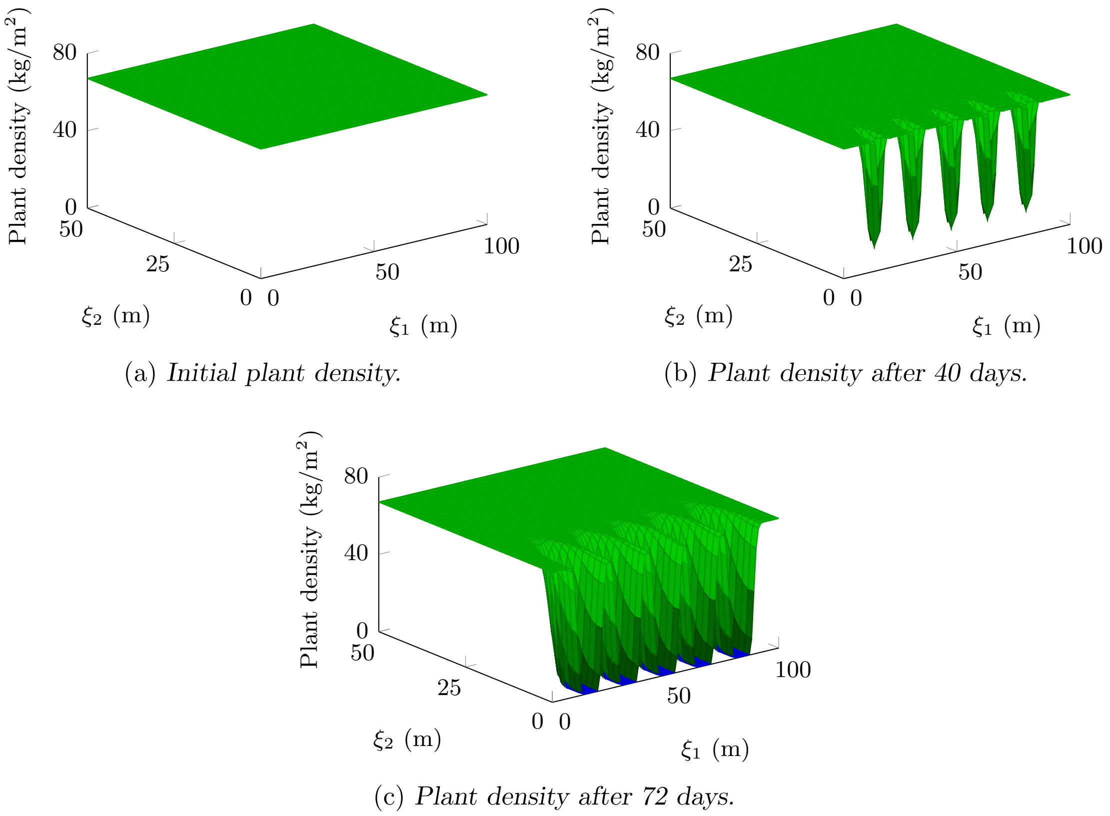


FIGURE 4.21: *Total plant population densities of the simulation over a period of 72 days.*

Simulation output of the water hyacinth density at time $t = 0$, $t = 40$ and $t = 72$ for the Mkhadzi Spruit scenario is given in Figure 4.22. Given the applicable temperatures, old larvae emerged 40 days after adult releases, starting to suppress plant density at their locations, as shown in Figure 4.22(b). Simulation results indicate that, after 72 days, the *N. eichhorniae* weevils succeeded to suppress plant density to extinction at areas surrounding the initial release sites, as shown in Figure 4.22(c).



(a) *Initial plant density.*

(b) *Plant density after 40 days.*

(c) *Plant density after 72 days.*

FIGURE 4.22: *Simulation of the suppression of water hyacinth population density at the Mkhadzi Spruit after a release of 20 000* N. eichhorniae *weevils distributed along one edge of the infested domain.*

4.7 Chapter summary

In this chapter, a reaction-diffusion model for a temporally and spatially variable environment, consisting of a system of coupled delay PDEs, has been developed to mathematically describe the spatio-temporal dynamics of water hyacinth populations and the interacting populations of the various life stages of the *N. eichhorniae* weevil as BCA on an isolated and bounded two-dimensional spatial domain. A number of simplifying model assumptions were discussed in §4.1, followed by the development and mathematical formulation of the reaction-diffusion model in §4.2. In §4.2.1, as a first step towards the modelling of the spatial dynamics of the water hyacinth and weevil system, diffusion terms were added to the applicable ordinary DDEs in the temporal model presented in previous studies, with the additions of an Allee-effect and a term allowing for frequent releases of adult weevils, a more detailed temperature dependence, as well as slight changes to the modelling of the through stage survival probabilities. Limitations of this modelling approach motivated the development of the final model formulated in §4.2.2, with a different approach towards the modelling of the recruitment and maturation terms for the weevil population and the derivation of a more accurate expression for the old larval maturation term, which includes spatial averaging. Subsequently, detailed descriptions of parameters incorporated into the model, namely the plant growth rate, durations of the weevil development stages, oviposition rate, damage rate, survival probabilities, mortality rates and temperature were provided in §4.3 together with the derivation of the respective diffusion coefficients. Model output parameters were discussed in §4.4 together with the derivation of a cost-benefit function which may be used to determine the most cost-effective release strategy for a specific scenario.

An elaborate description of the implementation of the model in MATLAB 9.0 has been given in §4.5 together with discussions on difficulties encountered during this process, regarding the appropriate system formulation, the incorporation of time lags, spatial averaging for a bounded two-dimensional spatial domain and frequent releases of BCAs.

Finally, numerous simulations were performed in order to validate the model output by means of testing various model responses and comparing the model output to real-world observations in §4.6. The model responded as expected to changes in θ, I, a, $c_{L_2}^{max}$, d_A, $d_{L_2}(\theta)$, d_W, f and the timing of BCA releases. Model simulation output realistically corresponded with field observations from a real-life BCA release scenario which took place at the Mkhadzi Spruit at the end of 2008. The spatially explicit model was therefore deemed valid to be used to provide guidance towards suitable BCA release strategies in a temporally and spatially variable environment.

CHAPTER 5

Results

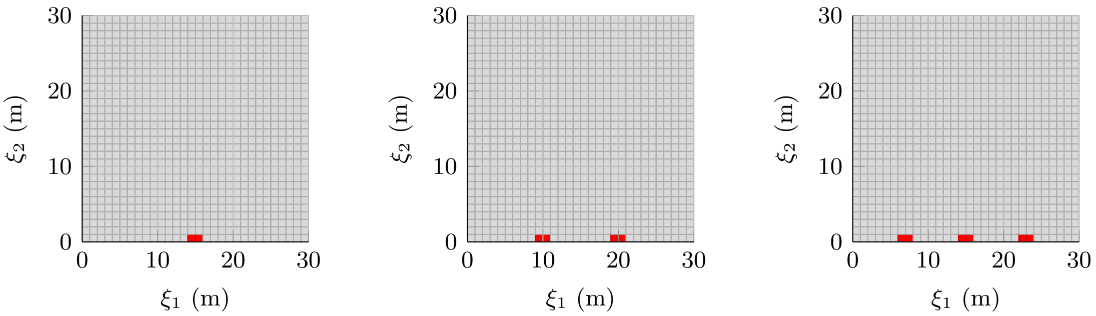
Contents

In this chapter, an investigation into the cost-effectiveness of different water hyacinth biological control release strategies is presented in §5.1 for both short term (§5.1.1) and long term (§5.1.2) scenarios, after which a sensitivity analysis is performed in §5.2 in order to ascertain how robust the model output is to changes in parameter values.

5.1 Numerical solutions

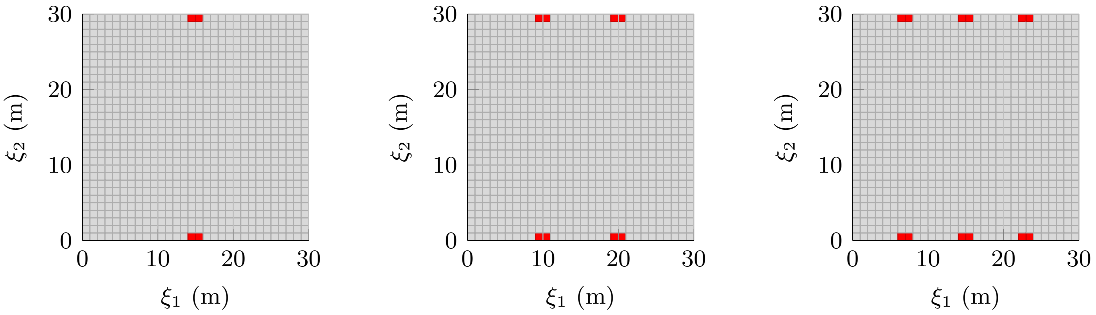
The cost-effective control of water hyacinth was analysed for different release strategies by means of simulation runs in Matlab. Release strategies for the short term (six months) and the long term (two years) were examined. The effect of commencing with biological control in different seasons of the year was investigated. For each starting season, the minimum number of BCAs required to reduce the total water hyacinth biomass (referred to as density) to 50% of the original plant population, in the short term, and 5% in the long term, for each release frequency and distribution, were obtained. Since the extent of damage caused by BCAs is not fully reflected when only the percentage surface area covered with weed is taken into account, the change in plant density was considered as the primary indication of the impact of BCAs on water hyacinth in this study. BCAs may cause much damage to the plant before open water patches appear. The total monetary value of water saved for each release strategy was reported. These values were used to determine the break-even cost per BCA, or the existence thereof, at which the cost of rearing and releasing BCAs in a mass rearing programme would be justified by the amount of water saved. Optimal release strategies for the short term and the long term were determined by comparing the break-even costs obtained at the optimal magnitudes of BCAs for the different release frequencies and distributions for each starting season. Short-term results were used to determine which long-term strategies should be investigated. All simulations were performed for a 30 m × 30 m isolated domain over a time period of either six months or two years, with an initial water hyacinth population density at carrying capacity of the water body (70 kg/m^2) over the entire domain. BCAs were assumed absent prior to releases for all simulations. The domain was assumed to be located in the Cape Town region, assuming parameter values as given in Chapter 4.

For all simulations, releases were assumed to occur at either one, two or all four edges of the domain, with possible release distributions of every 15 m (one release per 30 m), every 10 m (two releases per 30 m) or every 7.5 m (three releases per 30 m) along each of the considered edges. The nine release distribution options are illustrated in Figures 5.1 – 5.3. In real-world scenarios, the accessibility to edges of an infested domain may limit the options of possible release distributions. If, for example, a certain site is only accessible from one of its edges, the researchers will have to determine the best release strategy for one-edge releases. Because of the nature of weed infestations, biological control practitioners will consider long-term solutions in real-life release scenarios rather than short-term strategies. Short-term release strategies were merely investigated for analysis purposes.



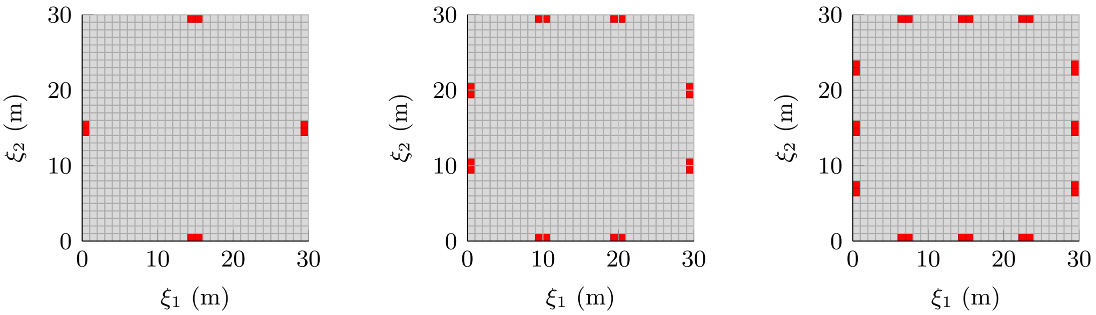
(a) *One edge, every 15 m.* (b) *One edge, every 10 m.* (c) *One edge, every 7.5 m.*

FIGURE 5.1: *Distribution options for releases occurring at one edge of the domain only.*



(a) *Two edges, every 15 m.* (b) *Two edges, every 10 m.* (c) *Two edges, every 7.5 m.*

FIGURE 5.2: *Distribution options for releases occurring at two edges of the domain.*



(a) *Four edges, every 15 m.* (b) *Four edges, every 10 m.* (c) *Four edges, every 7.5 m.*

FIGURE 5.3: *Distribution options for releases occurring at four edges of the domain.*

5.1.1 Short-term release strategies

The effect on the control of water hyacinth and the cost/benefit involved over a six-month time period for biological control commencing in summer or winter was investigated. For each starting season, the minimum number of BCAs required to reduce water hyacinth density to 50% of its original density within six months for each release frequency and distribution was obtained. At each release opportunity, which was determined by the release frequency, there was a maximum number of BCAs available to be released according to different distributions. Based on mass rearing data from the *Invasive Species Unit* in Cape Town [52, 60], a realistic maximum number of available BCAs of 48 000 per four-week time period was assumed to reflect possible resource constraints. Since *N. eichhorniae* adults live an average of only 58 days and lay most of their eggs during the early stages of their lives, it was assumed that all reared BCAs will be released within the four-week time period in order to maximise the efficiency of biological control. Since it is assumed that BCAs will not be kept at mass rearing facilities for longer than four weeks, release frequencies of less than every four weeks were not considered.

Summer

For the assumed parameter values, the total value of water loss through plant evapotranspiration would be R8 400 for the considered 30 m × 30 m water body covered with water hyacinth for the six-month time period from December (the first month of summer) to May, if no BCAs were released. The minimum number, I, of BCAs per release required to reduce water hyacinth population density to 50% within the six-month time period from December to May, for each frequency of once-off ($f = 0$), weekly ($f = 7$), two-weekly ($f = 14$) and four-weekly ($f = 28$) releases, and for each possible release distribution, is given in Tables 5.1 – 5.4, along with the monetary value of water saved due to the control of the weed for each biological control release strategy. In the case where, given a certain release strategy, the assumed maximum number of available BCAs was not sufficient to suppress water hyacinth population density to 50% of the original density within six months, the best suppression that could be obtained for that release strategy, subject to the constraints, is given.

It may be noted that for all release frequencies, none of the releases performed at only one edge of the domain, using the maximum number of available BCAs, were sufficient to suppress weed density to 50% in the short term (see Tables 5.1 – 5.4). For all frequencies, releases at at least two edges were required to achieve such suppression within six months (see Tables 5.1 – 5.4). However, in all cases where one-edge releases were more distributed along the edge, greater suppression was obtained, even if it did not reach 50% of the original weed density within the considered amount of time.

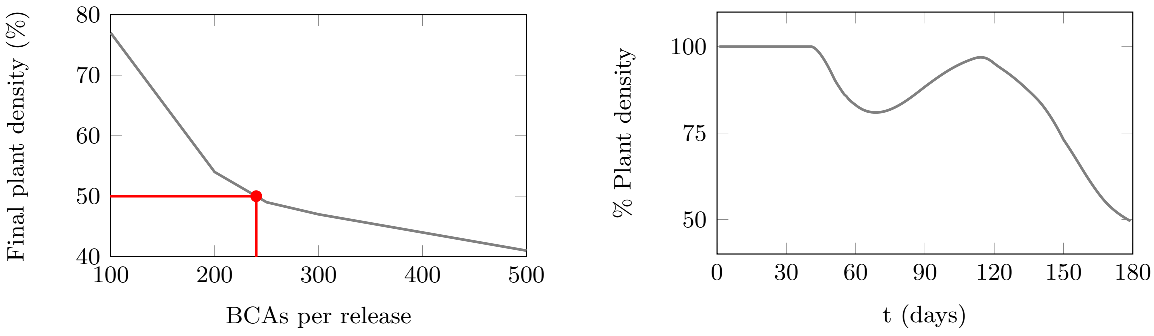
1. With once-off releases, it would not be possible to release more BCAs than the maximum number of BCAs that can be produced within one month. Provided the assumed resource constraints, a maximum of 48 000 BCAs would therefore be available for any once-off release strategy. In Table 5.1, it may be noted that where once-off releases were more distributed for two-edge and four-edge releases, less BCAs were required to achieve 50% control of the weed in the short term. From a water conservation point of view, for the assumed parameter values, a distribution of releases at two edges with releases every 7.5 m appeared to save the most water for once-off releases in summer, while succeeding to suppress the weed to 50% within six months (see Table 5.1). A distribution of releases at four edges with releases every 7.5 m, however, appeared to yield the most reachable

break-even cost per BCA for once-off releases in summer, requiring the smallest number of BCAs to successfully suppress the weed to 50% of its original density within six months.

Distribution	Min. I per release	Total released	Saved	Final plant density	Break-even cost/BCA
1 edge, every 15 m	48 000	48 000	R460	79%	R0,01
1 edge, every 10 m	24 000	48 000	R746	71%	R0,02
1 edge, every 7.5 m	16 000	48 000	R902	68%	R0,02
2 edges, every 15 m	24 000	48 000	R867	63%	R0,02
2 edges, every 10 m	11 600	46 400	R1 370	50%	R0,03
2 edges, every 7.5 m	4 800	28 800	R1 433	50%	R0,05
4 edges, every 15 m	7 500	30 000	R1 169	50%	R0,04
4 edges, every 10 m	890	7 120	R680	50%	R0,10
4 edges, every 7.5 m	240	2 880	R391	50%	R0,14

TABLE 5.1: *For once-off releases in summer, the minimum number, I, of BCAs per release required to reduce water hyacinth density to 50%, or as low as possible, and the value of water saved using that strategy, for each release distribution over the six-month time period from December to May.*

As illustration, Figure 5.4(a) shows how the minimum number, I, of BCAs per release required to reduce water hyacinth population density to 50% within the six-month time period from December to May for once-off releases at four edges of the domain with releases every 7.5 m was determined. The same procedure was followed to determine the minimum required number of BCAs for all other release frequencies and distributions. It may be noted that a much larger increase in the number of BCAs was required to achieve a lower weed suppression for the interval of 50% to 40% than for 60% to 50% in the short term, indicating that a suppression of 50% was a good short-term benchmark. For the minimum required number of BCAs per once-off release at four edges with releases every 7.5 m, determined in Figure 5.4(a), the change in the percentage plant density over the six-month time period from December to May is shown in Figure 5.4(b). After the first generation of BCAs, there was a delay before the second generation of damage-causing old larvae emerged, giving the weed a chance to grow back. Just before the 120-day mark, the second generation of old larvae emerged, continuing the suppression of weed density. After six months, the 240 BCAs that were released at each of the twelve locations at time $t = 0$ succeeded to decrease plant density from 100% to 50%.



(a)

(b)

FIGURE 5.4: *(a) The percentage plant density at six month after the release of different numbers of BCAs for once-off releases in the first month of summer at four edges of the domain with releases every 7.5 m. (b) The change in the percentage plant density over a period of six months after once-off releases of 240 BCAs each at four edges of the domain with releases every 7.5 m.*

2. For weekly releases, the maximum number of available BCAs per release opportunity was limited to 12 000 BCAs (48 000/4) per weekly release. In Table 5.2, it may be seen that, for certain release distributions, when only the benefit of saved water was considered, a break-even cost per BCA did not exist for weekly releases in summer, when attempting to suppress water hyacinth density to 50% within the six-month time period. For those strategies, no cost pertaining to BCA releases would be justified by the amount of water saved, resulting in an overall loss in the short term. Only the last four release distributions reported in Table 5.2 were able to suppress weed density to 50% of its original density within six months. Even with frequent releases, none of the releases performed at only one edge succeeded in suppressing the weed to 50% within the considered period of time. Weekly releases appeared to have a smaller effect on the weed in the short term compared to bulky once-off releases. This indicates that, in the short term, a large initial impact on the weed may be more effective than smaller continuous impacts from BCAs. Similar to once-off releases, a distribution of releases at two edges with releases every 7.5 m appeared to save the most water for weekly releases in summer, while succeeding to suppress the weed to 50% of its original density within six months. For the considered domain and the assumed parameter values, only release distributions at four edges appeared to be able to break even for weekly releases in summer, but the best break-even cost was lower than the best break-even cost for once-off releases, making it more difficult to attain.

Distribution	Min. I per release	Total released per opportunity	Grand total	Saved	Final plant density	Break-even cost/BCA
1 edge, every 15 m	12 000	12 000	312 000	R136	84%	None
1 edge, every 10 m	6 000	12 000	312 000	R348	73%	None
1 edge, every 7.5 m	4 000	12 000	312 000	R494	70%	None
2 edges, every 15 m	6 000	12 000	312 000	R400	67%	None
2 edges, every 10 m	3 000	12 000	312 000	R783	53%	None
2 edges, every 7.5 m	1 330	7 980	207 480	R993	50%	None
4 edges, every 15 m	1 350	5 400	140 400	R823	50%	R0,01
4 edges, every 10 m	235	1 880	48 880	R720	50%	R0,01
4 edges, every 7.5 m	150	1 800	46 800	R850	50%	R0,02

TABLE 5.2: *For weekly releases commencing in summer, the minimum number, I, of BCAs per release required to reduce plant density to 50%, or as low as possible, and the value of water saved using that strategy, for each release distribution over the six-month time period from December to May.*

3. For releases performed every second week, the available 48 000 BCAs at the beginning of each four-week cycle were split in half, yielding a maximum of 24 000 available BCAs every two weeks. The outcome of different release distributions of these 24 000 BCAs at each release opportunity is given in Table 5.3, where it may be seen that, for two-weekly releases also, none of the releases performed at only one edge of the domain succeeded in suppressing the weed to 50% of its original density within the six month period. Releases of BCAs at two edges, with releases at least every 10 m, or four edges, with any release distribution, were required to achieve such suppression within six months. For the assumed parameter values, similar to once-off and weekly releases commencing in summer, a distribution of releases at two edges with releases every 7.5 m appeared to save the most water for releases performed every second week, while succeeding to suppress the weed to 50% of its original density within six months. Again, for some release strategies, no cost pertaining to BCA releases would be justified by the amount of water saved in the short term. A distribution of releases at four edges with releases every 10 m or 7.5 m yielded the most reachable break-even cost per BCA for two-weekly releases in summer, requiring the smallest total number of BCAs to successfully suppress the weed to 50% within six months. The best

break-even cost for two-weekly releases was the same as for weekly releases, but still much lower than the best break-even cost for once-off releases, making it more difficult to achieve.

Distribution	Min. I per release	Total released per opportunity	Grand total	Saved	Final plant density	Break-even cost/BCA
1 edge, every 15 m	24 000	24 000	312 000	R367	76%	None
1 edge, every 10 m	12 000	24 000	312 000	R431	72%	None
1 edge, every 7.5 m	8 000	24 000	312 000	R632	70%	None
2 edges, every 15 m	12 000	24 000	312 000	R510	65%	None
2 edges, every 10 m	5 400	21 600	280 800	R980	50%	None
2 edges, every 7.5 m	1 650	9 900	128 700	R1 105	50%	R0,01
4 edges, every 15 m	2 150	8 600	111 800	R881	50%	R0,01
4 edges, every 10 m	400	3 200	41 600	R741	50%	R0,02
4 edges, every 7.5 m	200	2 400	31 200	R724	50%	R0,02

TABLE 5.3: *For two-weekly releases commencing in summer, the minimum number, I, of BCAs per release required to reduce plant density to 50%, or as low as possible, and the value of water saved using that strategy, for each release distribution over the six-month time period from December to May.*

4. For releases performed every fourth week, a maximum of 48 000 BCAs was available at the beginning of each four-week cycle. The outcome of different release distributions of these 48 000 BCAs at each release opportunity is given in Table 5.4. Releases performed at only one edge of the domain still did not succeed in suppressing the weed to 50% of its original density within the six month period, but did yield the best suppressions of the weed out of all the considered release frequencies in the short term. Similar to two-weekly releases, releases of BCAs at two edges, with releases at least every 10 m, or four edges, with any release distribution, were required to achieve 50% suppression within six months. For the assumed parameter values, similar to all considered release frequencies for summer, a distribution of releases at two edges with releases every 7.5 m appeared to save the most water for releases performed every fourth week, while succeeding to suppress the weed to 50% of its original density within six months. Again, for some release distributions, no cost pertaining to BCA releases would be justified by the amount of water saved in the short term. A distribution of releases at four edges with releases every 7.5 m yielded the best break-even cost per BCA for four-weekly releases in summer, requiring the smallest total number of BCAs to successfully suppress the weed to 50% of its original density within six months. The best break-even cost for four-weekly releases was slightly higher than for weekly and two-weekly releases, but still lower than the best break-even cost for once-off releases, making it more difficult to achieve.

   A comparison in terms of the change in the percentage plant density over six months for four-weekly releases of the minimum required number of BCAs between releases at two edges and four edges, respectively, both with releases every 7.5 m, may be seen in Figure 5.5. Both release distributions succeeded to achieve 50% control of the weed within six months, but because releases at two edges had a steady gradual decrease in plant density, with plant density being lower during the time period leading up to the six months mark, versus a sharp decrease at the end of the time period with releases at four edges, more water was saved for the release distribution at two edges with releases every 7.5 m. The better average suppression obtained with two-edge releases over the six month time period may be ascribed to the larger number of BCAs being released per opportunity. The release distribution at four edges with releases every 7.5 m, however, yielded a slightly better break-even cost per BCA as only a quarter of the BCAs were needed to achieve the same control after six months compared to the two-edge strategy.

Distribution	Min. I per release	Total released per opportunity	Grand total	Saved	Final plant density	Break-even cost/BCA
1 edge, every 15 m	48 000	48 000	336 000	R421	74%	None
1 edge, every 10 m	24 000	48 000	336 000	R522	68%	None
1 edge, every 7.5 m	16 000	48 000	336 000	R820	65%	None
2 edges, every 15 m	24000	48 000	336 000	R737	59%	None
2 edges, every 10 m	6 000	24 000	168 000	R1 024	50%	R0,01
2 edges, every 7.5 m	2 000	12 000	84 000	R1 094	50%	R0,01
4 edges, every 15 m	3 450	13 800	96 600	R920	50%	R0,01
4 edges, every 10 m	600	4 800	33 600	R693	50%	R0,02
4 edges, every 7.5 m	260	3 120	21 840	R567	50%	R0,03

TABLE 5.4: *For four-weekly releases commencing in summer, the minimum number, I, of BCAs per release required to reduce plant density to 50%, or as low as possible, and the value of water saved using that strategy, for each release distribution over the six-month time period from December to May.*

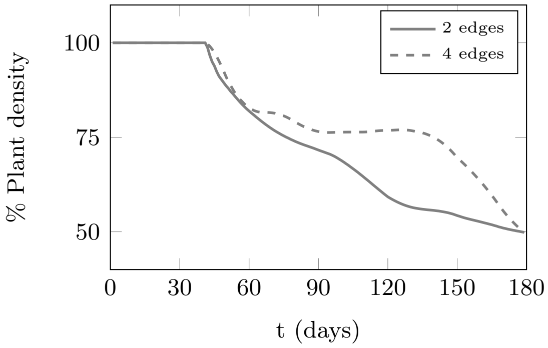


FIGURE 5.5: *The change in the percentage plant density over a period of six months after four-weekly releases of the minimum required number of BCAs for releases at two edges and four edges, respectively, both with releases every 7.5 m.*

Winter

For the assumed parameter values, the total value of water loss through plant evapotranspiration would be R6 335,40 for the considered 30 m × 30 m water body covered with water hyacinth for the six-month time period from June (the first month of winter) to November, if no BCAs were released. For releases commencing in winter, simulation results indicated that no release strategy for any release frequency or distribution, using the assumed maximum number of available BCAs, succeeded to suppress the weed density to 70% in the short term, let alone 50%. This may be explained by the fact that BCA development is much slower and mortality rates much higher when exposed to low temperatures, resulting in a delayed impact on the plant and less BCAs to cause damage to the weed. The best suppressions that could be obtained within the six-month time period from June to November, using the maximum number of available BCAs, for once-off ($f = 0$), weekly ($f = 7$), two weekly ($f = 14$) and four weekly ($f = 28$) releases, and for each possible release distribution, are given in Tables 5.5 – 5.8, along with the monetary value of water saved due to the control of the weed for each biological control release strategy. With once-off releases in winter, the lowest plant density was not always reached at the end of the six-month time period. In some cases, the oscillation reached a low point at the five-month mark due to the development cycle of the BCAs. For those cases, the lowest plant density percentage is given along with the final plant density percentage, where in all other cases, the weed density reached its lowest point for the considered period of time at the final time increment.

In Tables 5.5 – 5.8, it may be noted that, whether releases were performed at one, two or four edges of the domain, in all cases where releases were more distributed along the edges, greater suppression was obtained for all release frequencies. Furthermore, model output suggested that, for all winter release strategies, when only the benefit of water saved is considered, a break-even cost for BCAs did not exist for any release frequency when attempting to suppress plant density as low as possible within six months. Therefore, no cost pertaining to BCA releases in winter would be justified by the amount of water saved, resulting in a loss in the short term.

Distribution	I per release	Total released	Saved	Final plant density	Lowest plant density	Break-even cost/BCA
1 edge, every 15 m	48 000	48 000	R48	94%	94% (at 6 months)	None
1 edge, every 10 m	24 000	48 000	R77	92%	92% (at 5 months)	None
1 edge, every 7.5 m	16 000	48 000	R108	91%	89% (at 5 months)	None
2 edges, every 15 m	24 000	48 000	R82	92%	91% (at 5 months)	None
2 edges, every 10 m	12 000	48 000	R129	89%	86% (at 5 months)	None
2 edges, every 7.5 m	8 000	48 000	R168	86%	82% (at 5 months)	None
4 edges, every 15 m	12 000	48 000	R131	89%	85% (at 5 months)	None
4 edges, every 10 m	6 000	48 000	R169	85%	79% (at 5 months)	None
4 edges, every 7.5 m	4 000	48 000	R182	82%	76% (at 5 months)	None

TABLE 5.5: *For once-off ($f = 0$) releases in winter, the best suppressions that could be obtained, using the maximum number of available BCAs, and the value of water saved, for each release distribution over the six-month time period from June to November.*

Distribution	I per release	Total released per opportunity	Grand total	Saved	Final plant density	Break-even cost/BCA
1 edge, every 15 m	12 000	12 000	312 000	R4	99%	None
1 edge, every 10 m	6 000	12 000	312 000	R8	98%	None
1 edge, every 7.5 m	4 000	12 000	312 000	R10	98%	None
2 edges, every 15 m	6 000	12 000	312 000	R9	97%	None
2 edges, every 10 m	3 000	12 000	312 000	R17	96%	None
2 edges, every 7.5 m	2 000	12 000	312 000	R21	95%	None
4 edges, every 15 m	3 000	12 000	312 000	R19	95%	None
4 edges, every 10 m	1 500	12 000	312 000	R33	92%	None
4 edges, every 7.5 m	1 000	12 000	312 000	R39	92%	None

TABLE 5.6: *For weekly ($f = 7$) releases commencing in winter, the best suppressions that could be obtained, using the maximum number of available BCAs, and the value of water saved, for each release distribution over the six-month time period from June to November.*

Distribution	I per release	Total released per opportunity	Grand total	Saved	Final plant density	Break-even cost/BCA
1 edge, every 15 m	24 000	24 000	312 000	R5	99%	None
1 edge, every 10 m	12 000	24 000	312 000	R10	98%	None
1 edge, every 7.5 m	8 000	24 000	312 000	R13	98%	None
2 edges, every 15 m	12 000	24 000	312 000	R11	97%	None
2 edges, every 10 m	6 000	24 000	312 000	R21	96%	None
2 edges, every 7.5 m	4 000	24 000	312 000	R26	95%	None
4 edges, every 15 m	6 000	24 000	312 000	R23	94%	None
4 edges, every 10 m	3 000	24 000	312 000	R39	92%	None
4 edges, every 7.5 m	2 000	24 000	312 000	R46	92%	None

TABLE 5.7: *For two-weekly ($f = 14$) releases commencing in winter, the best suppressions that could be obtained, using the maximum number of available BCAs, and the value of water saved, for each release distribution over the six-month time period from June to November.*

Distribution	I per release	Total released per opportunity	Grand total	Saved	Final plant density	Break-even cost/BCA
1 edge, every 15 m	48 000	48 000	336 000	R7	98%	None
1 edge, every 10 m	24 000	48 000	336 000	R19	98%	None
1 edge, every 7.5 m	16 000	48 000	336 000	R23	97%	None
2 edges, every 15 m	24000	48 000	336 000	R18	97%	None
2 edges, every 10 m	12 000	48 000	336 000	R34	95%	None
2 edges, every 7.5 m	8 000	48 000	336 000	R41	95%	None
4 edges, every 15 m	12 000	48 000	336 000	R36	94%	None
4 edges, every 10 m	6 000	48 000	336 000	R56	91%	None
4 edges, every 7.5 m	4 000	48 000	336 000	R65	91%	None

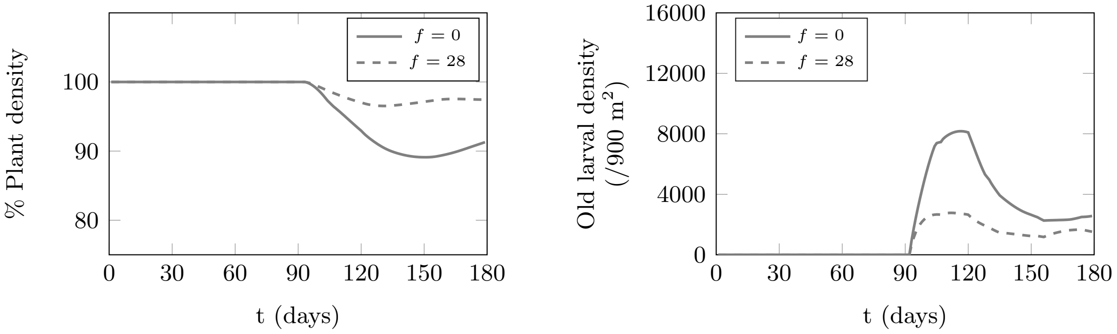
TABLE 5.8: *For four-weekly ($f = 28$) releases commencing in winter, the best suppressions that could be obtained, using the maximum number of available BCAs, and the value of water saved, for each release distribution over the six-month time period from June to November.*

In Figure 5.6, the change in the percentage plant density and old larval density over the six-month time period from June to November for once-off and four-weekly releases is compared for one-edge, two-edge and four-edge release distributions, respectively. Only the best distribution for each option is shown, which was releases every 7.5 m for one-edge, two-edge and four-edge releases for both the considered release frequencies. In Table 5.8 it may be noted that for four-weekly releases ($f = 28$), the total number of BCAs that were released at time $t = 0$ for once-off releases in winter, were released at the beginning of every four-week cycle. One would thus expect four-weekly releases to result in a greater suppression of weed densities than once-off releases, but due to a greater impact of density dependence on the larval stages when more BCAs were released, less damage-causing old larvae developed to suppress weed densities. Figure 5.6 shows that this is the case for one-edge, two-edge and four-edge release distributions. Lower old larvae population densities therefore resulted in higher plant densities for four-weekly releases, yielding a lower value of water saved than once-off releases in the short term. It is important to investigate the long-term effect of once-off winter releases since at the end of the considered six-month time period, water hyacinth densities were increasing again, while the plant densities subject to four-weekly releases started to form a downward slope (see Figure 5.6). More frequent releases may play an important role in the long term.

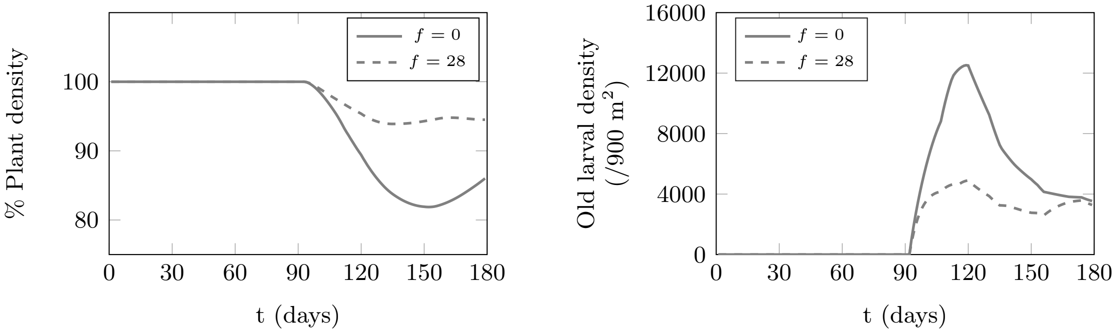
Optimal short-term release strategies

Since it was not possible to break-even with costs pertaining to the rearing and release of BCAs for winter releases in the short term, only the process of determining the best break-even cost per BCA for summer releases is discussed. The accessibility to the edges of an infested domain may limit the options of release distributions. Therefore, the most cost-effective short-term biological control release strategy for each case of having access to one, two or all four edges is discussed next, with a summary of the suggestions given in Table 5.9.

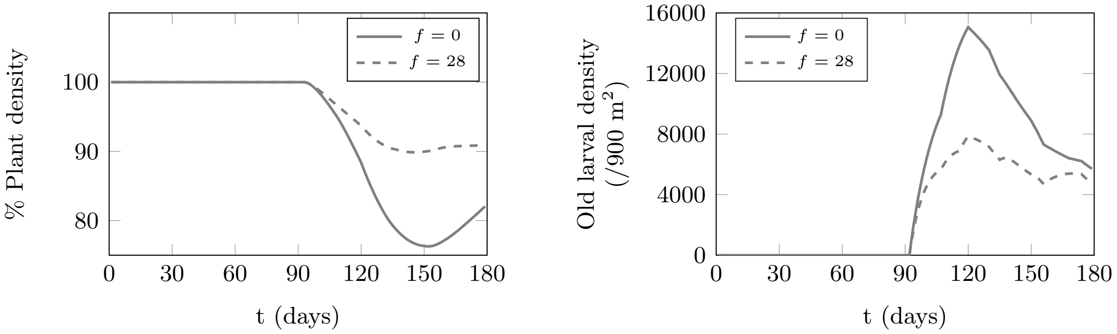
1. *One-edge releases.* For each release frequency of once-off, weekly, two-weekly and four-weekly releases at one edge of the domain, a distribution of releases every 7.5 m resulted in the lowest final plant density and yielded the highest value of water saved, even though one-edge release strategies did not succeed to suppress weed density to 50% in the short term. Since all one-edge release strategies for a specific release frequency used the same number of BCAs, the most cost-effective strategy for each frequency was the one that saved the most water during the six-month time period, even though it still resulted in an



(a) *One-edge releases.* (b) *One-edge releases.*



(c) *Two-edge releases.* (d) *Two-edge releases.*



(e) *Four-edge releases.* (f) *Four-edge releases.*

FIGURE 5.6: *Comparisons of the change in percentage plant density and old larval density over the six-month time period from June to November between once-off ($f = 0$) and four-weekly ($f = 28$) releases, for one-edge, two-edge and four-edge release distributions, respectively.*

overall loss. For short-term summer releases at only one edge of the domain, only once-off releases yielded possible break-even points for costs pertaining to BCA releases. All other frequencies for one-edge releases resulted in a definite loss and were less cost-effective. Provided field workers had access to only one edge of the considered infested domain, the optimal short-term summer release strategy was to release once-off with releases every 7.5 m along the edge, with 16 000 BCAs per point, suppressing water hyacinth density to 68% of its original density within the six-month time period.

2. *Two-edge releases.* In order to determine the optimal, most cost-effective short-term summer release strategy for the case where field workers had access to two edges of the considered infested domain, a comparison of the best break-even cost per BCA for each release

frequency for releases at two edges is shown in Figure 5.7. It may be seen that once-off releases outperformed other frequencies by yielding the highest break-even cost for two-edge releases. Provided field workers had access to two edges of the considered infested domain, they had the option of releasing at either one or two edges. Assuming the main priority was to suppress the weed to 50% of its original density within the given amount of time, the one-edge release option was disqualified. In this case, the optimal short-term summer release strategy was to release once off with releases every 7.5 m along both edges, with 4 800 BCAs per point, suppressing water hyacinth density to 50% of its original density within the six-month time period.

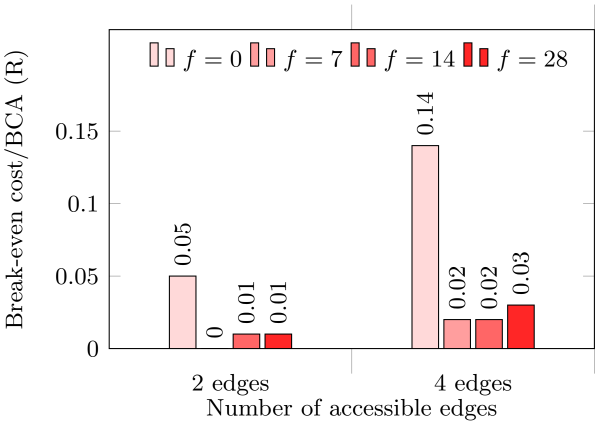


FIGURE 5.7: *Comparison of the best break-even cost per BCA for short-term summer releases at two or four edges for different release frequencies.*

3. *Four-edge releases.* In order to determine the optimal, most cost-effective short-term summer release strategy for the case where field workers had access to four edges of the considered infested domain, a comparison of the best break-even cost per BCA for each release frequency for releases at four edges is shown in Figure 5.7. It may be seen that once-off releases again outperformed other frequencies by yielding the highest break-even cost for four-edge releases. Provided field workers had access to all four edges of the considered infested domain and attempted to suppress water hyacinth density to 50% of its original density within the six-month time period, they had the option of releasing at either two or four edges. From Figure 5.7 it may be concluded that the optimal short-term summer release strategy in this case was to release once off with releases every 7.5 m along the four edges, with 240 BCAs per point, to successfully suppress water hyacinth density to 50% within the given amount of time.

In light of these investigations, the suggested most cost-effective short-term release strategies, consisting of a release frequency, distribution and magnitude, for summer and winter, is given in Table 5.9. It may not always be possible to wait for the appropriate season to commence with BCA releases and water loss costs will accumulate during the waiting period. Therefore, based on simulation results, release strategies for summer and winter were suggested for the considered scenario. When researchers identify a real-world problem where biological control needs to be applied to a water hyacinth infested area, the model may be used to determine the optimal time to commence with BCA releases, subject to the costs applicable to that specific scenario and the cost of delaying releases. The urgency of the matter may determine whether researchers will consider the short-term or long-term costs as a decision aid. Nevertheless, simulation results suggested that the optimal short-term strategy, yielding the most reachable break-even cost per BCA for the assumed parameter values applicable to the considered scenario, was to perform a once-off release of 240 BCAs per point at four edges with releases every 7.5 m (2 880 BCAs in total) in the first month of summer in order to suppress weed density to 50%. If the rearing and release of the BCAs could be conducted at a cost of R0,14 per BCA or lower, this release strategy might yield a profit in terms of the value of water saved. It should be noted that, in reality, the classical biological control approach, in which BCAs that survived quarantine are released directly in a new habitat, may also be used for once-off releases. This method yields a relatively small number of agents to be released, in comparison with large bulk releases made possible via mass rearing programmes. However, the analyses performed in this study assumed the availability of large numbers of BCAs via mass rearing, even for once-off releases, since the main focus of the study is to evaluate the efficiency and cost-effectiveness within local mass rearing programmes.

Season	Accessible edges	Optimal frequency	Optimal distribution	Optimal I per release	Grand total	Saved	Suppressed density	Break-even cost/BCA
Summer	1	once-off	every 7.5 m	16 000	48 000	R902	68%	R0,02
	2	once-off	every 7.5 m	4 800	28 800	R1433	50%	R0,05
	4	once-off	every 7.5 m	240	2 880	R391	50%	R0,14
Winter	1	once-off	every 7.5 m	16 000	48 000	R108	89%	None
	2	once-off	every 7.5 m	8 000	48 000	R168	82%	None
	4	once-off	every 7.5 m	4 000	48 000	R182	76%	None

TABLE 5.9: *The optimal short-term release strategies for releases commencing in summer or winter, respectively, as predicted by the model.*

5.1.2 Long-term release strategies

The effect on the control of water hyacinth and the cost-effectiveness of the involved release strategies over a two-year time period for biological control commencing in summer or winter was investigated. For each starting season, the minimum number of BCAs required to reduce water hyacinth density to 5% of its original biomass at some time increment over the two-year time period for one-edge, two-edge and four-edge release distributions, with once-off ($f = 0$), weekly ($f = 7$), two-weekly ($f = 14$) and four-weekly ($f = 28$) releases, respectively, was obtained. In real-world scenarios, water hyacinth plants exposed to long-term biological control often end up being small (10 – 20 cm tall) and unable to sink in the case of shallow water [81]. A plant density of 0% may therefore be considered unrealistic in some cases, making 5% a more reasonable benchmark for control. Furthermore, a plant cover of 5% of a water body's surface area has been recognised as an acceptable level of control where the ecological well-being of an area may be preserved [20]. Although the surface coverage and plant density are not the same, plant density is also used to measure the effectiveness of biological control [52], giving a good indication of the continuous impact of BCAs. Even though BCAs may succeed to suppress water hyacinth population density to very low levels or even extinction, the plant is infamous for regrowing at its exponential rate due to seeds remaining viable in water sediment or budding from remaining small plants [37, 69], making water hyacinth control/management an ongoing, long-term process. Since releases every 7.5 m along an edge proved to be most efficient and cost-effective for all short-term release strategies, for one-edge, two-edge and four-edge releases in both summer and winter, only this distribution was investigated for long-term release strategies. Similar to short-term releases, a resource constraint of a maximum of 48 000 BCAs per four-week time period was assumed. For the sake of practicality, only multiples of 100 BCAs per point of release were considered.

Summer

For the assumed parameter values, the total value of water loss through plant evapotranspiration would be R29 600 for the considered 30 m × 30 m water body covered with water hyacinth for the two-year time period starting in December (the first month of summer), if no BCAs were released.

In Table 5.10, the minimum number, I, of BCAs per release required to reduce water hyacinth population density to 5% of its original biomass at some time increment over the two-year time period, for one-edge, two-edge and four-edge release distributions, with releases every 7.5 m along an edge, for once-off, weekly, two-weekly and four-weekly releases, respectively, is given. In the case where the assumed maximum number of available BCAs was insufficient to suppress water hyacinth density to 5% within two years with a certain release strategy, the best (lowest) suppression that could be obtained for that strategy is given, along with the time at which the lowest suppression was obtained. The monetary value of water saved over the two-year time period due to the control of the weed for each biological control release strategy is also reported. This value, along with the grand total of BCAs released over the entire period, was used to determine the break-even cost per BCA for each strategy.

It may be noted that, for all release frequencies, none of the releases performed at only one edge of the domain succeeded to suppress the weed density to 5% at some time increment over the two-year time period. The same goes for once-off releases at any number of edges. More frequent releases at at least two edges were required to achieve sufficient suppression at some point within the two-year time period, starting in December.

Number of edges	Freq.	I per release	Total per opportunity	Grand total	Av. plant density	Lowest plant density	Saved	Break-even cost/BCA
1 edge	once	16 000	48 000	48 000	80%	66% (8 months)	R2 832	R0,06
1 edge	$f = 7$	4 000	12 000	1 236 000	54%	23% (24 months)	R9 151	R0,01
1 edge	$f = 14$	8 000	24 000	1 248 000	51%	22% (21 months)	R9 498	R0,01
1 edge	$f = 28$	16 000	48 000	1 248 000	51%	21% (24 months)	R9 638	R0,01
2 edges	once	8 000	48 000	48 000	64%	40% (8 months)	R4 916	R0,10
2 edges	$f = 7$	900	5 400	550 800	41%	5% (21 months)	R10 913	R0,02
2 edges	$f = 14$	1 500	9 000	468 000	41%	5% (21 months)	R10 462	R0,02
2 edges	$f = 28$	2 500	15 000	390 000	40%	5% (21 months)	R11 094	R0,03
4 edges	once	4 000	48 000	48 000	50%	18% (7 months)	R7 736	R0,16
4 edges	$f = 7$	300	3 600	362 800	32%	2% (21 months)	R12 137	R0,03
4 edges	$f = 14$	500	6 000	304 250	33%	4% (20 months)	R11 961	R0,04
4 edges	$f = 28$	800	9 600	245 070	35%	5% (21 months)	R10 978	R0,04

TABLE 5.10: *For releases commencing in summer, the minimum number of BCAs required to reduce plant density to 5%, or as low as possible, over the two-year time period, as well as the average plant density, the lowest plant density obtained, the value of water saved and the break-even cost per BCA for releases at one, two or four edges, with releases every 7.5 m along an edge, for once-off, weekly ($f = 7$), two-weekly ($f = 14$) and four-weekly ($f = 28$) releases, respectively.*

The long-term strategies for each release option – that is one-edge, two-edge and four-edge releases – commencing in the first month of summer, given in Table 5.10, are discussed below.

1. *One-edge releases.* Even though none of the one-edge release strategies succeeded to suppress weed density to 5% in the given amount of time, frequent releases had a significantly greater impact on the suppression of weed density in the long-term when compared to once-off releases. Simulation results indicated that frequent releases along one edge suppressed weed density to below 25% of the original density at some point within the two

years, while a once-off release reached a mere 66% at its best (see Table 5.10). In Figure 5.8, the change in the percentage plant density for once-off releases ($f = 0$) at one edge is compared to the change in the percentage plant density for four-weekly releases ($f = 28$) at one edge over the two-year time period, starting in summer. Even though there was not a major difference in the outcome of weekly, two-weekly and four-weekly releases, the latter proved to be the best frequency for one-edge releases by succeeding to suppress water hyacinth to the lowest density over the considered period of time, while yielding the highest value of water saved. Therefore, provided field workers had access to only one edge of the considered infested domain, the optimal long-term strategy for releases commencing in summer was to release 16 000 BCAs every 7.5 m along the edge every four weeks, suppressing water hyacinth density to 21% of the original density within the two-year time period, with a break-even cost of R0,01 per BCA.

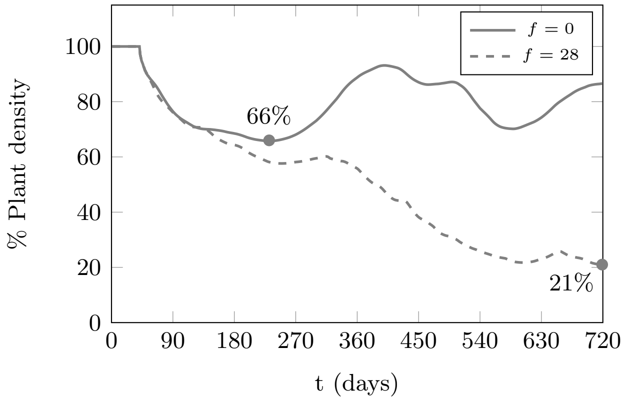


FIGURE 5.8: *The change in the percentage plant density over a period of two years, starting in December, for once-off ($f = 0$) and four-weekly ($f = 28$) releases of the minimum required number of BCAs at one edge of the domain, both with releases every 7.5 m along the edge.*

2. *Two-edge releases.* For once-off releases at two edges, the maximum number of available BCAs was required to suppress plant density as low as possible over the considered period of time, even though the bench mark of 5% was not reached. Multiple releases of weekly, two-weekly or four-weekly releases were required to achieve the desired control at some time increment over the two-year time period, highlighting the value of frequent releases. Once-off releases yielded a more reachable break-even cost per BCA since less BCAs were used, even though the total value of water saved was significantly lower than for frequent releases. However, since once-off releases yielded insufficient control in the long term, this release option was regarded as inadequate.

   Weekly, two-weekly and four-weekly releases at two edges for a two-year time period yielded results in close proximity to each other in terms of the value of water saved, the average plant density and the break-even cost per BCA (see Table 5.10 and Figure 5.9). Since four-weekly releases used the smallest total number of BCAs, yielded a slightly lower average plant density than weekly and two-weekly releases, a slightly higher value of water saved, as well as a slightly higher break-even cost per BCA, the optimal suggested long-term strategy for two-edge releases commencing in summer was to release 2 500 BCAs every 7.5 m along the edges every four weeks, suppressing water hyacinth density to 5% of the original density within the two-year time period, with a break-even cost of R0,03 per BCA.

   Additional simulation runs over a time period of five years were performed in order to determine whether the optimal strategy according to the two-year simulation results remained dominant over an extended period of time. From Table 5.11 it may be seen that

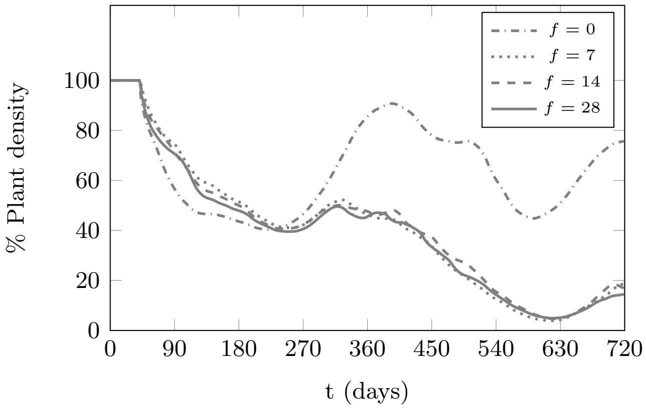


Figure 5.9: *The change in the percentage plant density over a period of two years, starting in December, for once-off ($f = 0$), weekly ($f = 7$), two-weekly ($f = 14$) and four-weekly ($f = 28$) releases of the minimum required number of BCAs at two edges of the domain, with releases every 7.5 m along the considered edges.*

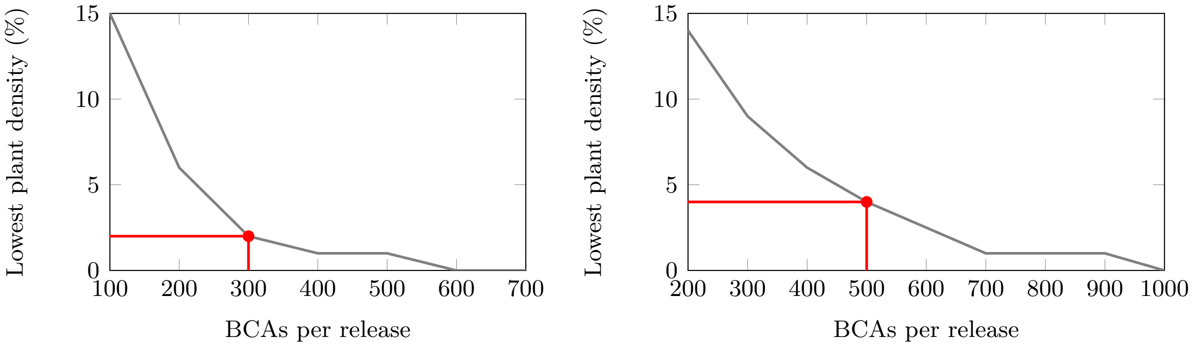
once-off releases at two edges remained insufficient to suppress water hyacinth populations to the desired density over the extended period of time. Again, results for frequent releases were relatively closely related. Two-weekly releases yielded the lowest average plant density over the extended period of time, accompanied by the highest total value of water saved. However, since four-weekly releases required 172 500 BCAs less than two-weekly releases over the extended period of time, this strategy resulted in the same break-even cost per BCA as two-weekly releases, even though the value of water saved was slightly lower. Four-weekly releases had the additional benefit of yielding lower travel expenses since field-workers only had to travel to the considered site every fourth week to perform releases instead of every second week, adding to the cost-effectiveness of four-weekly releases. These considerations confirm that four-weekly releases may be suggested as the optimal, most cost-effective long-term strategy for two-edge releases commencing in summer.

Number of edges	Freq.	I per release	Total per opportunity	Grand total	Av. plant density	Lowest plant density	Saved	Break-even cost/BCA
2 edges	once	8 000	48 000	48 000	52%	12% (45 months)	R16 905	R0,35
2 edges	$f = 7$	900	5 400	1 325 700	25%	1% (30 months)	R36 518	R0,03
2 edges	$f = 14$	1 500	9 000	1 125 000	22%	1% (55 months)	R39 809	R0,04
2 edges	$f = 28$	2 500	15 000	952 500	24%	1% (31 months)	R37 695	R0,04

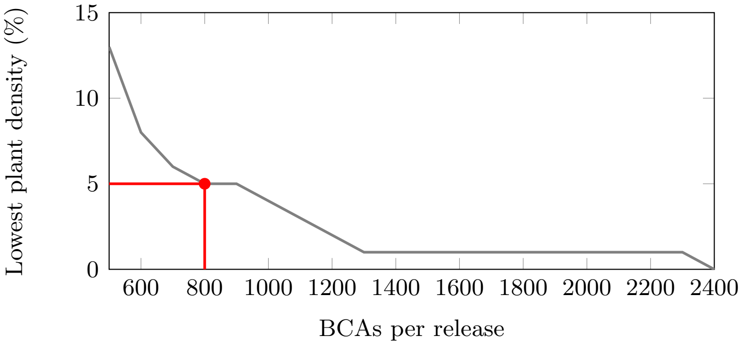
Table 5.11: *Model output for five-year simulations of releases at two edges, with releases every 7.5 m along an edge, for once-off, weekly ($f = 7$), two-weekly ($f = 14$) and four-weekly ($f = 28$) releases, commencing in summer.*

3. *Four-edge releases.* For once-off releases at four edges, similar to one-edge and two-edge releases, the maximum number of available BCAs was required to suppress plant density as low as possible over the considered period of time, even though the benchmark of 5% was not reached. Repetitions of weekly, two-weekly or four-weekly releases were required to achieve the desired control. Figure 5.10 shows how the minimum number of BCAs per point of release required to reduce plant density to 5% at some time increment within the two-year time period (starting in December) was determined for weekly, two-weekly and four-weekly releases, respectively, at four edges of the domain, with releases every 7.5 m. Since only multiples of 100 BCAs per release were considered, the lowest plant density obtained may be slightly lower than 5% when the previous multiple yielded an insufficient

suppression, but the subsequent multiple resulted in a minimum plant density of less than 5%.



(a) *Weekly releases.* (b) *Two-weekly releases.*



(c) *Four-weekly releases.*

FIGURE 5.10: *Determining the minimum required number of BCAs for weekly, two-weekly and four-weekly releases at four edges of the domain with releases every 7.5 m, by evaluating the lowest percentage plant density obtained at some time increment over the two-year time period for different numbers of BCAs per release, for releases commencing in the first month of summer.*

In Table 5.10 it may be seen that weekly releases yielded a slightly lower average plant density in comparison with two-weekly and four-weekly releases and thus resulted in the highest total value of water saved over the considered period of time, but also a worse break-even cost per BCA since more BCAs were used. Four-weekly releases, on the other hand, required a smaller total number of BCAs, yielding a break-even cost per BCA equivalent to two-weekly releases.

Since two-year simulation results did not indicate a clearly dominant strategy in all considered categories between weekly, two-weekly and four-weekly releases, additional simulation runs over a time period of five years were performed for these strategies in order to determine if the one outperformed the other in an extended amount of time. In Figure 5.11, the change in the percentage plant density over a period of five years, starting in December, for weekly ($f = 7$), two-weekly ($f = 14$) and four-weekly ($f = 28$) releases of the minimum required number of BCAs at four edges of the domain, with releases every 7.5 m along the considered edges, is given. Oscillations formed as BCA generations passed through the system. It may be seen that the three considered four-edge release strategies followed a similar pattern in the extended amount of time, alternating between better weed suppressions at different times, with more significant differences in plant density after the three-year mark (1 080 days).

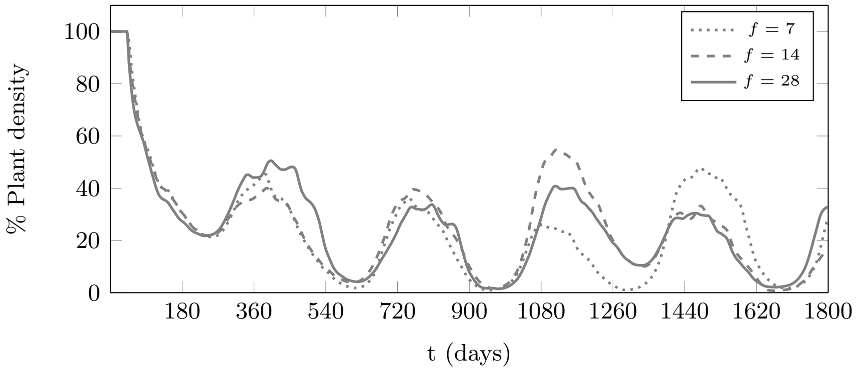


FIGURE 5.11: *The change in the percentage plant density over a period of five years, starting in December, for weekly ($f = 7$), two-weekly ($f = 14$) and four-weekly ($f = 28$) releases of the minimum required number of BCAs at four edges of the domain, with releases every 7.5 m along the edges.*

From Table 5.12 it may be seen that weekly, two-weekly and four-weekly releases at four edges still yielded results in close proximity to each other in terms of the value of water saved and the average plant density over the extended period of time. Four-weekly releases, however, outperformed the other considered four-edge release strategies in terms of the break-even cost per BCA in the extended amount of time. The four-weekly release strategy required about 280 000 BCAs less than weekly releases and about 150 000 BCAs less than two-weekly releases, while achieving very similar control over the five-year time period, yielding the best break-even cost per BCA. In light of these results, provided field workers had access to four edges of the considered infested domain, the optimal, most cost-effective long-term strategy for releases commencing in summer was to release 800 BCAs every 7.5 m along the edges every four weeks, sufficiently suppressing water hyacinth populations to the desired density within the two-year time period.

Number of edges	Freq.	I per release	Total per opportunity	Grand total	Av. plant density	Lowest plant density	Saved	Break-even cost/BCA
4 edges	$f = 7$	300	3 600	895 900	24%	1% (32 months)	R36 332	R0,04
4 edges	$f = 14$	500	6 000	759 830	26%	1% (56 months)	R34 039	R0,04
4 edges	$f = 28$	800	9 600	608 270	26%	1% (32 months)	R34 336	R0,06

TABLE 5.12: *Model output for five-year simulations of releases at four edges, with releases every 7.5 m along an edge, for weekly ($f = 7$), two-weekly ($f = 14$) and four-weekly ($f = 28$) releases, commencing in summer.*

Winter

For the assumed parameter values, the total value of water loss through plant evapotranspiration would be R29 600 for the considered 30 m × 30 m water body covered with water hyacinth for the two-year time period starting in June (the first month of winter), if no BCAs were released. This is equivalent to the value of water loss for the two-year time period starting in December, since both will be exposed to the same temperatures (seasons) for the same amount of time, just in a different order.

In Table 5.13, the minimum number, I, of BCAs per release required to reduce water hyacinth population density to 5% of its original biomass at some time increment over the two-year time period, for one-edge, two-edge and four-edge release distributions, with releases every 7.5 m along an edge, for once-off, weekly, two-weekly and four-weekly releases commencing in winter, is given. In the case where the assumed maximum number of available BCAs was insufficient to suppress water hyacinth density to 5% within two years with a certain release strategy, the best (lowest) suppression that could be obtained for that strategy is given. For releases commencing in winter, the lowest plant density was reached at the end of the two-year time period for all release distributions and frequencies. The monetary value of water saved over the two-year time period due to the control of the weed for each biological control release strategy is also reported. This value, along with the grand total of BCAs released over the entire period, was used to determine the break-even cost per BCA, or the lack thereof, for each strategy.

It may be noted that, similar to long-term releases commencing in summer, none of the releases performed at only one edge of the domain succeeded to suppress the weed density to 5% at some time increment over the two-year time period. The same goes for once-off releases at any number of edges. More frequent releases at at least two edges were required to achieve sufficient suppression at some point within the two-year time period, starting in June. However, simulation results indicated that the total value of water saved in the long term as a result of biological control commencing in winter was, for all strategies, considerably lower than for releases commencing in summer.

Number of edges	Freq.	I per release	Total per opportunity	Grand total	Av. plant density	Lowest plant density	Saved	Break-even cost/BCA
1 edge	once	16 000	48 000	48 000	84%	69%	R2 114	R0,04
1 edge	$f = 7$	4 000	12 000	1 236 000	77%	36%	R3 979	None
1 edge	$f = 14$	8 000	24 000	1 248 000	77%	34%	R4 207	None
1 edge	$f = 28$	16 000	48 000	1 248 000	76%	32%	R4 224	None
2 edges	once	8 000	48 000	48 000	80%	56%	R2 183	R0,05
2 edges	$f = 7$	2 000	12 000	1 236 000	65%	7%	R5 391	None
2 edges	$f = 14$	3 800	22 800	1 185 600	65%	5%	R5 485	None
2 edges	$f = 28$	6 900	41 400	1 076 400	64%	5%	R5 876	R0,01
4 edges	once	4 000	48 000	48 000	70%	31%	R3 445	R0,07
4 edges	$f = 7$	800	9 600	942 930	58%	4%	R6 864	R0,01
4 edges	$f = 14$	1 400	16 800	840 930	59%	5%	R6 465	R0,01
4 edges	$f = 28$	1 900	22 800	586 470	60%	5%	R6 052	R0,01

TABLE 5.13: *For releases commencing in winter, the minimum number of BCAs required to reduce plant density to 5%, or as low as possible, over the two-year time period, as well as the average plant density, the lowest plant density obtained, the value of water saved and the break-even cost per BCA for releases at one, two or four edges, with releases every 7.5 m along an edge, for once-off, weekly ($f = 7$), two-weekly ($f = 14$) and four-weekly ($f = 28$) releases, respectively.*

The long-term strategies for each release option – that is one-edge, two-edge and four-edge releases – commencing in the first month of winter, given in Table 5.13, are discussed below.

1. *One-edge releases.* Once again, none of the one-edge release strategies succeeded to suppress weed density to 5% in the given amount of time and the best suppressions reached for releases commencing in winter were worse (higher) than for releases commencing in summer, for all one-edge strategies. Similar to summer commencements, frequent releases commencing in winter also had a significantly greater impact on the suppression of weed density in the long-term in comparison with once-off releases. Four-weekly releases were the one-edge strategy with the greatest impact on the weed, yielding a suppression of 32% of the original density, accompanied by the highest value of water saved for one-edge releases commencing in winter. However, long-term simulation results indicated that, when commencing in winter, there was no break-even cost per BCA for frequent releases at

one edge over the two-year time period. Consequently, the most cost-effective long-term strategy for one-edge releases commencing in winter was to release 16 000 BCAs once-off every 7.5 m along the edge, suppressing weed density to 69% of the original density over the two-year time period, with a break-even cost of R0,04 per BCA.

In Figure 5.12, the change in the percentage plant density for once-off releases ($f = 0$) at one edge is compared to the change in the percentage plant density for four-weekly releases ($f = 28$) at one edge over the two-year time period, starting in winter. The red line indicates where the short-term investigations stopped (see Figure 5.6(a)). From Figure 5.12 it may be noted that, for winter commencement of biological control, four-weekly releases only started to outperform once-off releases after a year, resulting in significantly greater weed suppressions than once-off releases in the long term. Therefore it is important to not only consider short-term effects. Once-off releases were still more cost-effective due to the relatively small amount of water saved for releases commencing in winter, which was not able to justify the cost pertaining to the large number of BCAs used with frequent releases in the long term.

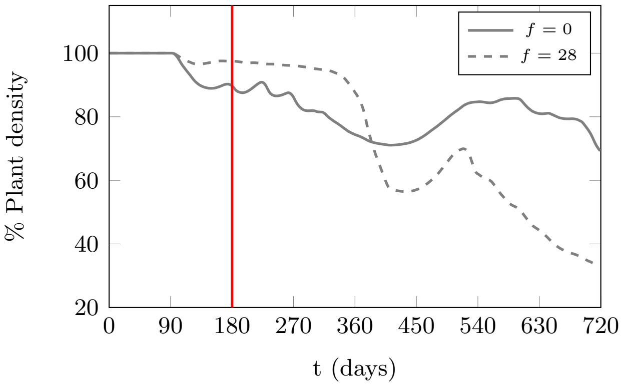


FIGURE 5.12: *The change in the percentage plant density over a period of two years, starting in June, for once-off ($f = 0$) and four-weekly ($f = 28$) releases of the minimum required number of BCAs at one edge of the domain, both with releases every 7.5 m along the edge.*

2. *Two-edge releases.* For two-edge releases commencing in winter, only once-off and four-weekly releases yielded feasible break-even costs, where the former dis not succeed to suppress water hyacinth density to the desired level within the two-year time period. Two-weekly and four-weekly releases were the only two-edge release strategies succeeding to suppress weed density to the desired level of control within the considered period of time. Furthermore, four-weekly releases outranked other two-edge release strategies by using the smallest total number of BCAs, while obtaining the lowest average plant density and the highest value of water saved over the considered period of time (see Table 5.13).

   For the minimum required number of BCAs per four-weekly release at two edges, with releases every 7.5 m, the change in the percentage plant density and the total old larval density over the two-year time period, starting in June, is shown in Figure 5.13. It may be noted that, as the simulation approached the colder winter temperatures a year later (just before the 360-day mark), the total old larval population started to increase significantly. Due to large numbers of young larvae emerging and thriving at higher temperatures, density dependence strongly limited the number of individuals maturing to the old larval stage. As the decrease in temperature limited the number of emerging young larvae, the resistance from density dependence was lifted and more old larvae developed to suppress weed density. This highlights the undeniably significant effect of density dependence that should be taken into account when suggesting effective biological control release strategies.

As plant density became low, *i.e.* BCA food resources became scarce, the total old larval population density decreased, giving the weed time to redeem itself. Provided field workers had access to two edges of the considered infested domain and wanted to start releases in winter, the optimal long-term strategy was to release 6 900 BCAs every 7.5 m along the two edges every four weeks, obtaining a final plant density of 5% at the end of the two-year time period, with a break-even cost of R0,01 per BCA (see Table 5.13).

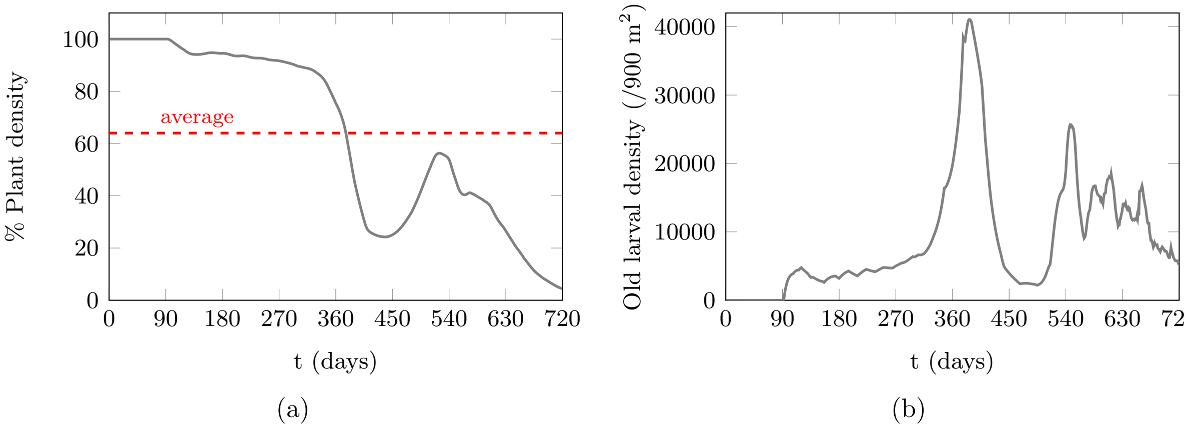


FIGURE 5.13: *The change in the percentage plant density (a) and the total old larval density (b) over a period of two years for four-weekly releases of the minimum required number of BCAs per point of release (6 900) for releases at two edges of the domain, with releases every 7.5 m, commencing in winter.*

Additional simulation runs over a time period of five years were performed in order to determine whether the optimal strategy according to the two-year simulation results remained dominant over an extended period of time. From Table 5.14 it may be seen that once-off releases at two edges remained insufficient to suppress water hyacinth populations to the desired density over the extended period of time, with an average plant density of more than double the average plant density obtained with frequent releases. Again, results for frequent releases were in close proximity to each other in terms of the value of water saved and the average plant density over the extended period of time. Four-weekly releases, however, outperformed the other considered two-edge frequent release strategies in terms of the break-even cost per BCA in the extended amount of time. These results confirm that four-weekly releases may be suggested as the optimal, most cost-effective long-term strategy for two-edge releases commencing in winter.

Number of edges	Freq.	I per release	Total per opportunity	Grand total	Av. plant density	Lowest plant density	Saved	Break-even cost/BCA
2 edges	once	8 000	48 000	48 000	61%	8%	R13 152	R0,27
2 edges	$f = 7$	2 000	12 000	2 680 000	29%	0%	R37 551	R0,01
2 edges	$f = 14$	3 800	22 800	2 574 500	29%	0%	R37 693	R0,01
2 edges	$f = 28$	6 900	41 400	2 401 200	30%	0%	R36 222	R0,02

TABLE 5.14: *Model output for five-year simulations of releases at two edges, with releases every 7.5 m along an edge, for once-off, weekly ($f = 7$), two-weekly ($f = 14$) and four-weekly ($f = 28$) releases, commencing in winter.*

3. *Four-edge releases.* For four-edge releases commencing in winter, all considered strategies yielded feasible break-even costs, but only frequent releases of weekly, two-weekly and four-weekly releases succeeded to suppress weed density to the desired level of control within the

two-year time period. From Table 5.13 it may be seen that weekly and two-weekly releases yielded a slightly lower average plant density in comparison with four-weekly releases and thus resulted in a higher total value of water saved over the considered period of time, but four-weekly releases used a smaller total number of BCAs, yielding a break-even cost per BCA equivalent to weekly and two-weekly releases. Since two-year simulation results did not indicate a clearly dominant strategy between weekly, two-weekly and four-weekly releases, additional simulation runs over a time period of five years were performed for these three strategies in order to determine if the one outperformed the other in an extended amount of time (see Table 5.15).

In Figure 5.14, the change in the percentage plant density over a period of five years, starting in June, for weekly ($f = 7$), two-weekly ($f = 14$) and four-weekly ($f = 28$) releases of the minimum required number of BCAs at four edges of the domain, with releases every 7.5 m along the considered edges, is given. It may be noted that the considered four-edge release strategies followed a similar pattern in the extended amount of time, until just before the three and a half year mark (1 260 days), where plant density subject to different frequencies of BCA releases started to differ significantly.

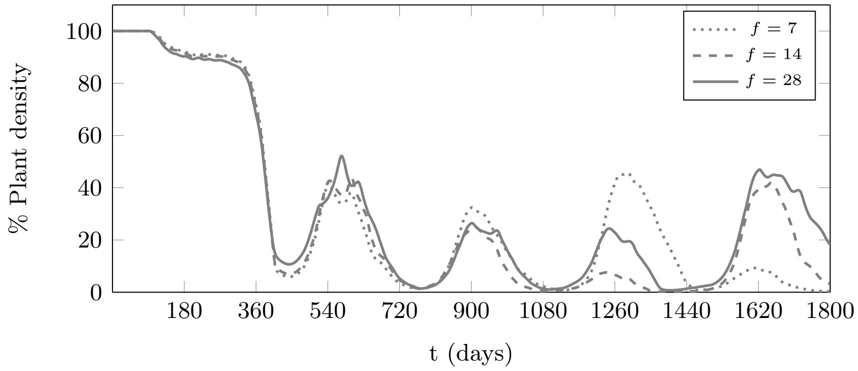


FIGURE 5.14: *The change in the percentage plant density over a period of five years, starting in June, for weekly ($f = 7$), two-weekly ($f = 14$) and four-weekly ($f = 28$) releases of the minimum required number of BCAs at four edges of the domain, with releases every 7.5 m along the considered edges.*

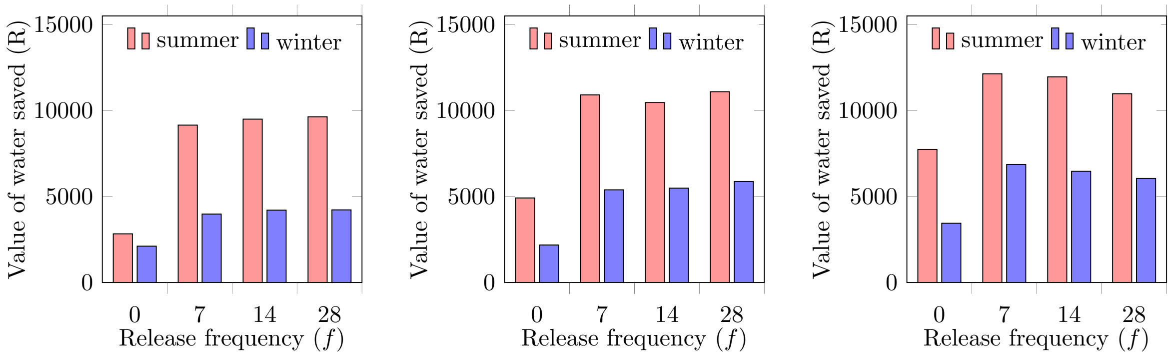
From Table 5.15 it may be seen that the weekly release strategy ($f = 7$) was dominated by the two-weekly release strategy ($f = 14$) over the five-year time period, since two-weekly releases yielded a slightly lower average plant density, a higher total value of water saved, while using a lower total number of BCAs in comparison with weekly releases. Even though two-weekly releases also yielded a lower average plant density in comparison with four-weekly releases ($f = 28$) and thus resulted in the higher total value of water saved over the extended period of time, four-weekly releases again used a smaller total number of BCAs, with a break-even cost equivalent to the two-weekly release strategy, still not resulting in a clearly dominant strategy between two-weekly and four-weekly releases over the extended period of time. Since there was not a major difference between the outcome of two-weekly and four-weekly releases and the value of water saved with two-weekly releases was only about R3 500 greater than with four-weekly releases over a period of five years, the strategy with less frequent releases was preferred in order to minimise travel expenses pertaining to each release opportunity. In addition to the benefit of lower travel expenses, four-weekly releases also used about 560 000 BCAs less than two-weekly releases to achieve quite similar control over the five-year time period. Therefore, provided field workers had access to four edges of the considered infested domain and wanted to start releases in winter, the optimal, most cost-effective long-term strategy was to release 1 900 BCAs every 7.5 m along the four edges every four weeks.

Number of edges	Freq.	I per release	Total per opportunity	Grand total	Av. plant density	Lowest plant density	Saved	Break-even cost/BCA
4 edges	$f = 7$	800	9 600	2 198 500	30%	0% (60 months)	R35 439	R0,02
4 edges	$f = 14$	1 400	16 800	1 970 500	29%	0% (46 months)	R35 893	R0,02
4 edges	$f = 28$	1 900	22 800	1 407 900	33%	1% (47 months)	R32 350	R0,02

TABLE 5.15: *Model output for five-year simulations of releases at four edges, with releases every 7.5 m along an edge, for weekly ($f = 7$), two-weekly ($f = 14$) and four-weekly ($f = 28$) releases, commencing in winter.*

Optimal long-term release strategies

The long-term release strategies commencing in summer were compared to the long-term release strategies commencing in winter, with the total value of water saved, the minimum required number of BCAs and the break-even cost per BCAs for different release strategies as the bases of comparison. In Figure 5.15, it may be seen that, for all considered biological control strategies, simulation results indicated that releases commencing in summer saved significantly more water than releases commencing in winter over a two-year time period. On average, for one-edge and two-edge releases, the ratio of the value of water saved for releases commencing in summer to the value of water saved for releases commencing in winter was 2:1 and for four-edge releases, the ratio was 1.9:1.

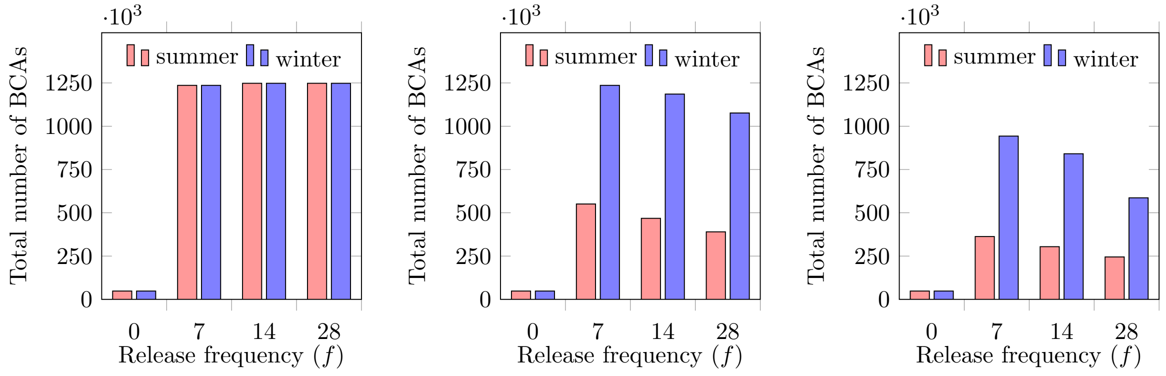


(a) *One-edge releases.* (b) *Two-edge releases.* (c) *Four-edge releases.*

FIGURE 5.15: *Comparison of the total value of water saved between long-term summer and winter release strategies at one, two or four edges for different release frequencies over a time period of two years.*

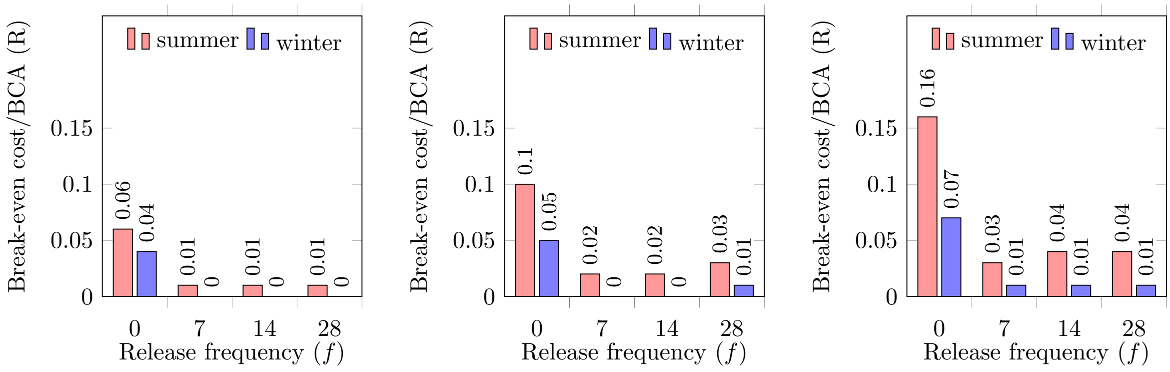
Furthermore, in Figure 5.16, it may be seen that, in addition to the benefit of yielding significantly higher values of water saved, releases commencing in summer also required less BCAs than winter commencements to obtain the desired weed suppression, or as close to it as possible, for all considered long-term release strategies, with the exception of one-edge releases, where both summer and winter release strategies required the maximum available number of BCAs.

In concurrence with conclusions drawn from Figures 5.15 and 5.16, Figure 5.17 indicates that the break-even cost per BCA for releases commencing in summer was more reachable than for winter commencements, for all considered long-term release strategies. For the considered scenario and the assumed parameter values, simulation results therefore indicated that releases commencing in summer were always more cost-effective than releases commencing in winter, over a two-year period of time. These conclusions emphasise the importance of the timing of releases, when determining cost-effective biological control release strategies.



(a) *One-edge releases.* (b) *Two-edge releases.* (c) *Four-edge releases.*

FIGURE 5.16: *Comparison of the total required number of BCAs between long-term summer and winter release strategies at one, two or four edges for different release frequencies over a time period of two years.*

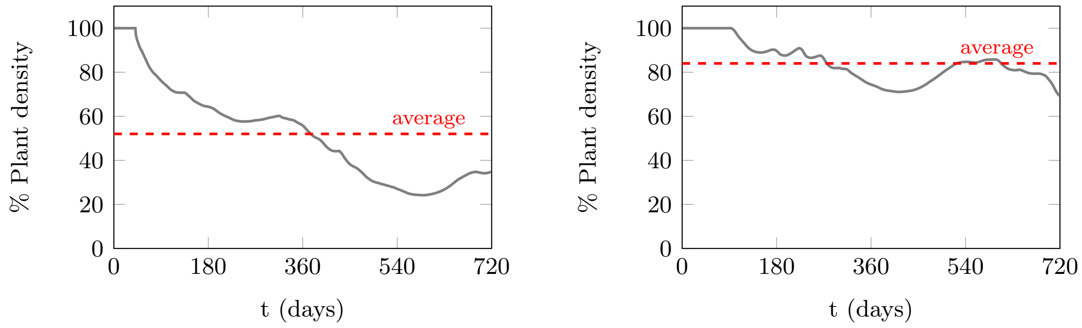


(a) *One-edge releases.* (b) *Two-edge releases.* (c) *Four-edge releases.*

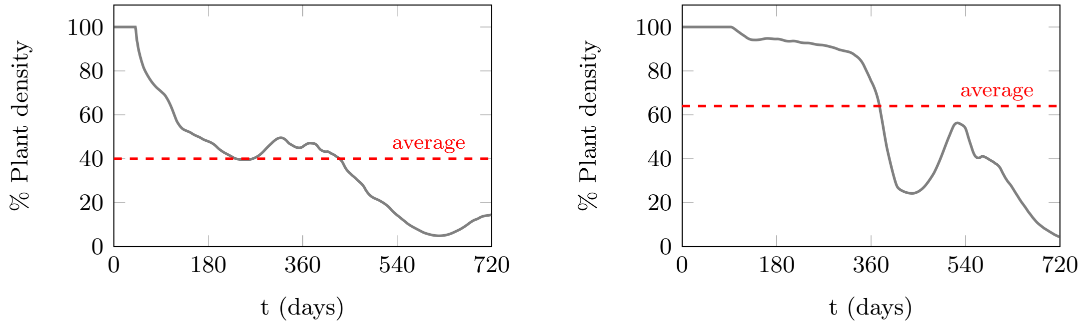
FIGURE 5.17: *Comparison of the break-even cost per BCA between long-term summer and winter release strategies at one, two or four edges for different release frequencies over a time period of two years.*

Earlier in §5.1.2, it was determined that out of all the considered long-term summer release strategies, only frequent releases (weekly, two-weekly or four-weekly releases) at two or four edges succeeded to suppress water hyacinth populations to the desired density at some point in time within the considered two-year period, while for long-term winter release strategies, only two-weekly or four-weekly releases at two edges or weekly, two-weekly or four-weekly releases at four edges proved to be adequate. These results accentuated the beneficial impact of releasing at more than one edge of an infested domain, with releases being more distributed. The model showed that the closer the distribution of BCAs got to a uniform distribution over the infested domain, the better the control of water hyacinth was. Additionally, the value of frequent releases over an extended period of time compared to a once-off release was also highlighted. While short-term results indicated that once-off releases were optimal for all considered scenarios, long-term results clearly pointed out that once-off releases were inadequate to achieve the desire weed suppression over a longer period of time.

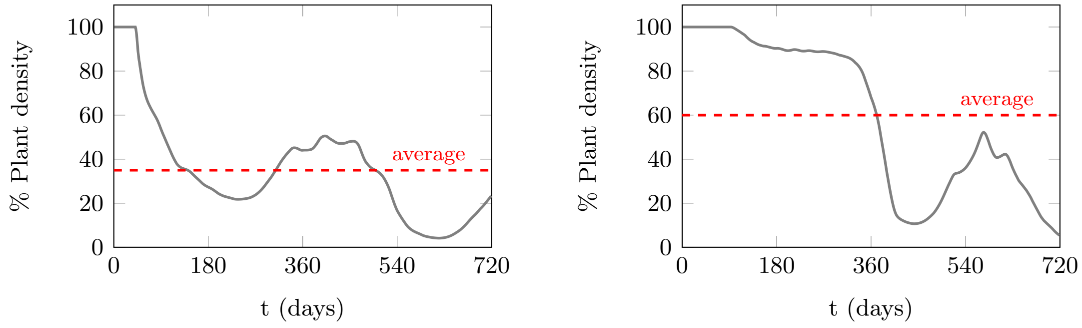
In Figure 5.18, the change in the percentage plant density over a period of two years, for the optimal, most cost-effective long-term one-edge, two-edge and four-edge release strategies, for releases commencing in summer and winter, respectively, is given. All the suggested optimal strategies consisted of four-weekly releases, except for the one-edge winter release strategy, where a once-off release was suggested to be most cost-effective, since, for the considered scenario and assumed parameter values, a break-even cost per BCA did not exist for frequent release strategies in that case. Weekly, two-weekly and four-weekly release frequencies proved to yield results in a close proximity to each other in the long term for all the considered release distributions. The fact that four-weekly releases in some cases slightly outperformed weekly and two-weekly releases regarding the average plant suppression obtained, while using lower total numbers of BCAs, but greater numbers per point of release, indicated that a bigger impact from BCAs once every four weeks tended to be more effective than smaller impacts every week or second week in these cases. In other cases, where results did not indicate a clearly dominant strategy, four-weekly releases were preferred simply on the basis of saving on travelling expenses due to releases being performed less often.



(a) *Optimal one-edge strategy (summer).* (b) *Optimal one-edge strategy (winter).*



(c) *Optimal two-edge strategy (summer).* (d) *Optimal two-edge strategy (winter).*



(e) *Optimal four-edge strategy (summer).* (f) *Optimal four-edge strategy (winter).*

FIGURE 5.18: *The change in the percentage plant density over a period of two years, for the optimal one-edge, two-edge and four-edge release strategies, for releases commencing in summer and winter, respectively.*

Once again, in Figure 5.18, it may be noted that, even though the considered two-edge and four-edge release strategies reached the desired level of suppression at some point in time over the two years for both summer and winter strategies, the average plant densities for releases commencing in summer were lower than for winter strategies for all considered cases. This may be partly ascribed to the extended initial delay before damage-causing larvae emerged as a result of low winter temperatures. Furthermore, once young larvae emerged, density dependence had a greater effect on winter release strategies than on summer strategies because more BCAs were required for releases commencing in winter to obtain the desired level of control, resulting in a stronger limitation on the number of individuals maturing to the damage-causing old larval stage. Once more, the undeniably significant effect of density dependence in the BCA populations was pointed out – an important factor that should be taken into account when suggesting effective biological control release strategies.

In conclusion, simulation results suggested that, for the considered scenario, the overall optimal, most cost-effective long-term release strategy was to commence with four-weekly releases at four edges in summer, with 800 BCAs per point of release, every 7.5 m along the edges, while sufficiently suppressing water hyacinth populations to the desired density within a time period of two years.

5.2 Sensitivity analysis

As with the construction of any mathematical model, parameter values and assumptions are subject to change and error since simplifying assumptions are made in order to describe a part of a real-world process [53]. The procedure of investigating the impacts that these potential changes and errors may have on the conclusions drawn from the model, is known as a *sensitivity analysis* [53]. For simulation models used for decision support, sensitivity analyses may aid in making recommendations more credible, understandable, compelling or persuasive or in prioritising the acquisition of information [53].

Some of the input parameter values used in the model were assumed or derived based on laboratory experiments or experiments performed in different parts of the world under different conditions. This data may differ from data in actual field behaviour in South Africa. For some other parameter values, *i.e.* the Allee-effect threshold, a, no experimental values were available at the time of the study and certain values and relationships had to be assumed.

In order to test whether the model output is reliable, single input parameters were varied either side of their standard values by percentages reflecting their realistic possible ranges, while keeping all other parameters constant. The percentage change in the input parameter was then compared to a percentage change in an output parameter in order to ascertain how robust the output is in the face of different parameter values. If the model output is robust (insensitive to changes in parameter values), confidence in the implementation or recommendation of certain strategies is increased, while if it is not robust, sensitivity analysis may be used to assess the risk involved in implementing a suggested strategy. For the purposes of decision aid, this basic approach is considered adequate [53].

5.2.1 Sensitivity of the average plant population density

Sensitivity analyses of the average plant density over the entire domain were performed. Single input parameters were varied for simulations of a once-off release of 100 BCAs at time $t = 0$ at the midpoint of one edge of a 30 m × 30 m domain, with the daily temperature and dew point temperature held constant over a considered period of time.

Short-term analysis

The sensitivity of the model output was firstly analysed over a time period of six months, with the daily temperature held constant at 30°C and the dew point temperature held constant at 14.5°C. In Figure 5.19, it may be seen that the average plant density over the entire domain is most sensitive to changes in the carrying capacity of water, K, in the short term. The Allee-effect threshold, a, was varied by 33,33% and 66,66% on either side of the standard value, which is $a = 3$, to reflect the realistic possible range of $a = 1$ to $a = 5$. Even these significant variations yielded a change in the average plant density of less than 2% on either side of the original average plant density over a time period of six months. In the short term, the average plant density over the entire domain is more sensitive to a decrease in the Allee-effect threshold than an increase. The values of parameters σ_E^{max} and σ_P^{max} were increased by a maximum of 5%, since a larger increase would yield unrealistic survival probabilities of greater than 1. For all other input parameters, variations of up to 20% on either side of their standard values resulted in a change in the average plant density of less than 1% over a time period of six months.

Long-term analysis at a high constant daily temperature

Subsequently, the sensitivity of the average plant density over the entire domain was analysed over a time period of two years, with the daily temperature held constant at 30°C and the dew point temperature held constant at 14.5°C. From Figure 5.20 it may be seen that, for the assumed temperatures, the sensitivity of the average plant density is more capricious in the long term than in the short term and does not yield monotone decreasing or increasing functions as with the short-term sensitivity analysis. Perturbations in input parameters may result in altered oscillations in the plant and weevil population cycles, even for different perturbations in the same input parameter, yielding more variable averages of the plant density when averaged over a longer period of time.

In the long term, with the daily temperature held constant at 30°C and the dew point temperature at 14.5°C, the average plant density appears to be most sensitive to changes in the input parameters K, a, $\alpha_{L_1}^{max}$ and μ_A, with at least one of the considered variations in each of these respective parameters resulting in a change in the average plant density of more than 10% (see Figure 5.20). Perturbations in the other input parameter values yield changes of less than 10%. The average plant density is more sensitive to a decrease in the maximum daily development rate of the young larval stage, $\alpha_{L_1}^{max}$, than an increase. A decrease in the daily development rate of the young larval stage leads to an increase in the development duration of the young larval stage, delaying the emergence of damage-causing old larvae, explaining the increase in the average plant density. Furthermore, the average plant density is more sensitive to an increase in the adult weevil mortality rate, μ_A, than a decrease. In the case that the model overestimates the adult weevil mortality rate, the average plant density will not be influenced that much. In order to minimise the average plant density over the long term, the model predicts that BCAs should be released during the time of the year when the climate is optimal for the development of young larvae and the survival of adult weevils. It may particularly be noted that, at this high temperature, the average plant density appears to be relatively insensitive to a change in the number of BCAs released, I. In the case that the model over– or underestimates the optimal number of BCAs to be released, the average plant density will not be affected that much (less than 4% over a time period of two years).

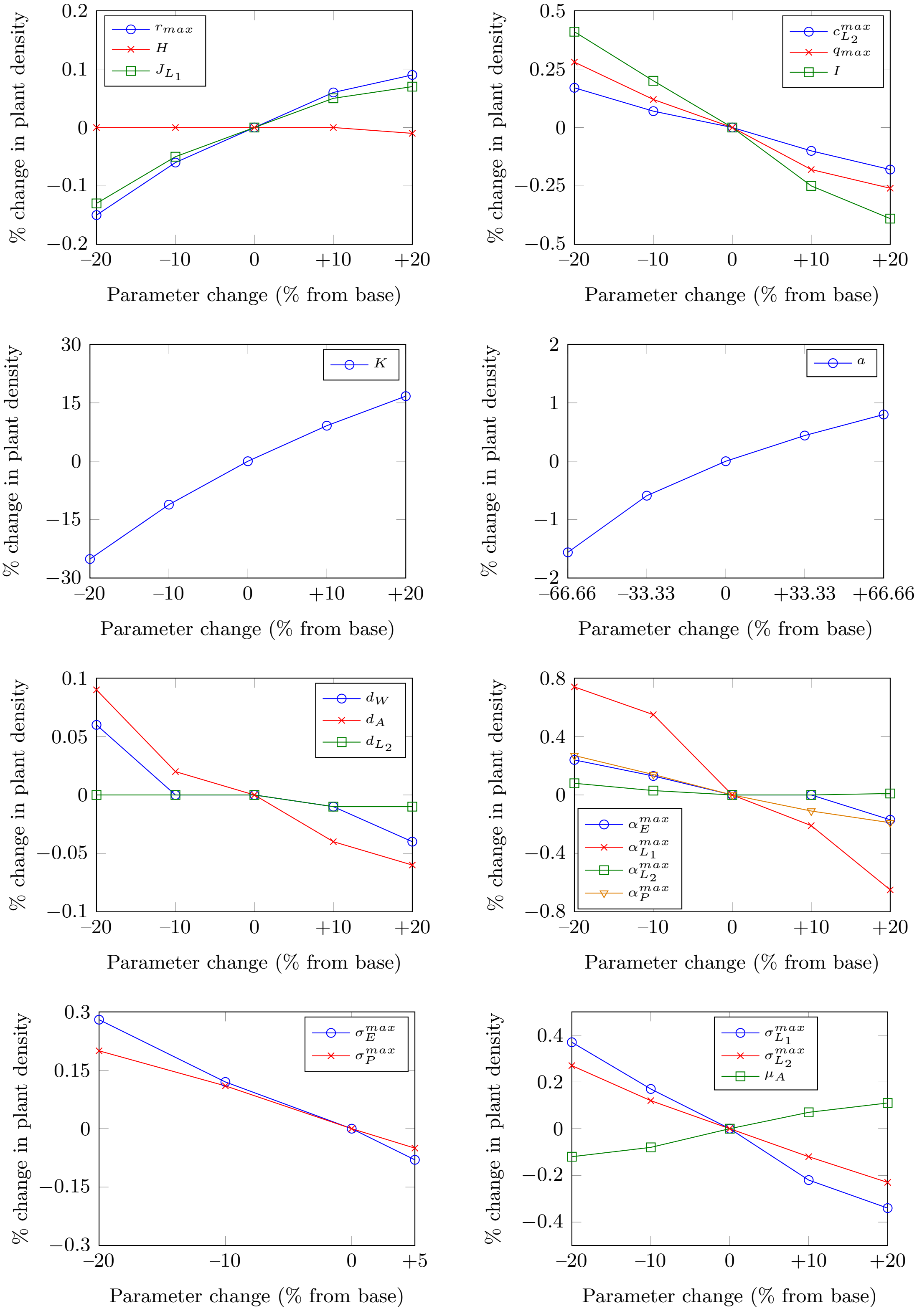


FIGURE 5.19: *Short-term sensitivity analysis of the average plant density, with respect to percentage changes in various parameters, with daily temperature held constant at 30° C and dew point temperature held constant at 14.5° C over a time period of six months.*

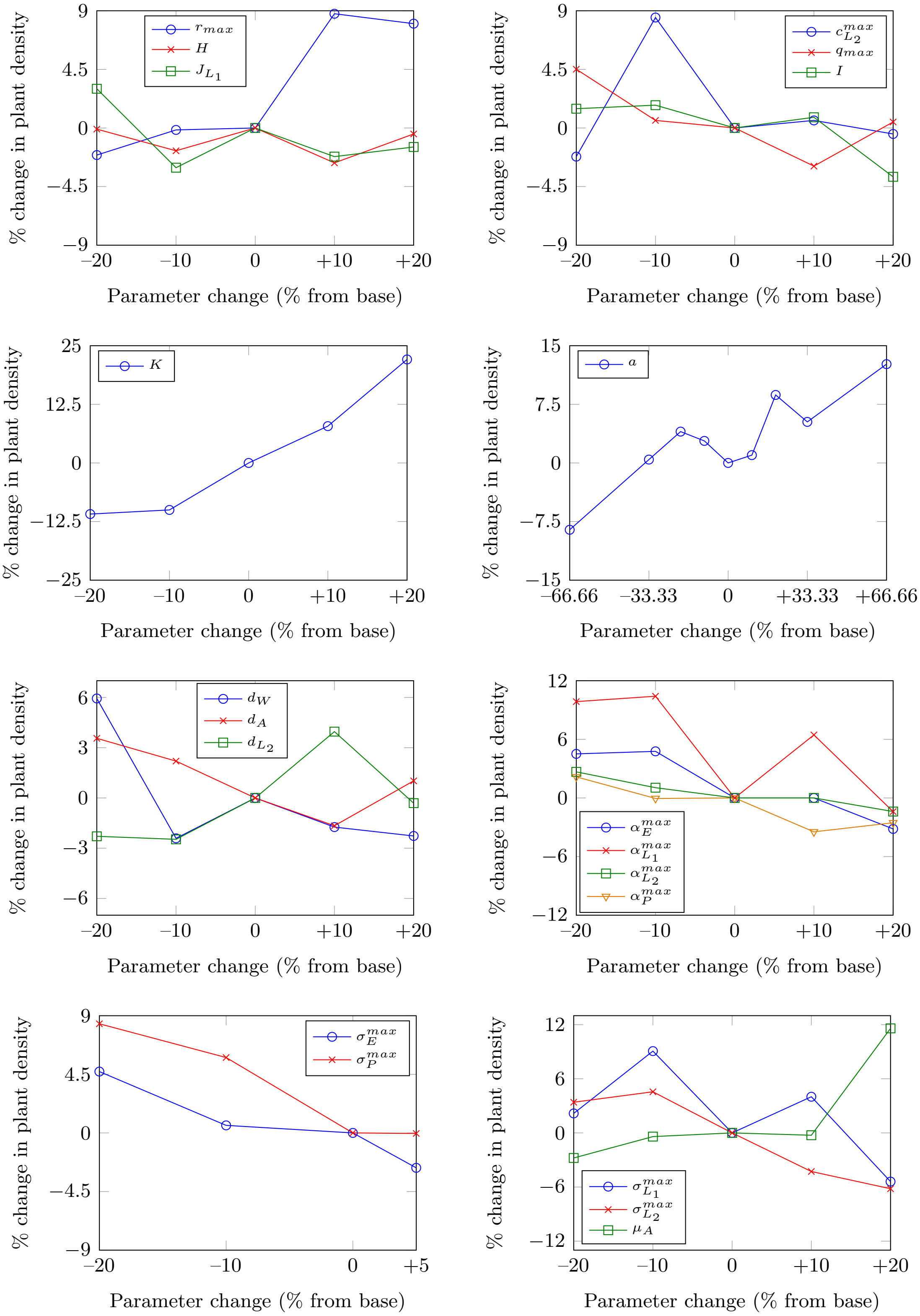


FIGURE 5.20: *Long-term sensitivity analysis of the average plant density, with respect to percentage changes in various parameters, with daily temperature held constant at 30° C and dew point temperature held constant at 14.5° C over a time period of two years.*

Long-term analysis at a lower constant daily temperature

The sensitivity of the average plant density over the entire domain was further analysed over a time period of two years, with the daily temperature held constant at 25°C and the dew point temperature held constant at 13°C. From Figure 5.21 it may be seen that the long-term sensitivity of the average plant density is generally more stable at the lower temperature than at the higher one. At this lower temperature, the average plant density is mostly less sensitive to changes in parameter values, with the exceptions of an extreme increase (+20%) in the value of parameter J_{L_1} or an extreme decrease (–20%) in the values of parameters $c_{L_2}^{max}$, K, a, $\sigma_{L_1}^{max}$ and $\sigma_{L_2}^{max}$, where the average plant density is somewhat more sensitive at the lower temperature than at the higher one over a time period of two years. At a constant daily temperature of 25°C and a dew point temperature of 13°C, the average plant density appears to be most sensitive to changes in the input parameters K and a, with at least one of the considered variations in each of these respective parameters resulting in a change in the average plant density of more than 10% over a time period of two years, while perturbations in the other input parameter values yield changes of less than 10% (see Figure 5.21). The average plant density is more sensitive when decreasing the values of K and a than when these parameter values are increased.

Again it may be noted that, even at this lower temperature, the average plant density appears to be relatively insensitive to a change in the number of BCAs released, I. In the case that the model over– or underestimates the optimal number of BCAs to be released, the average plant density will not be affected that much (less than 4% over a time period of two years), increasing the confidence in recommended release strategies. At this temperature, the average plant density seems to be slightly more sensitive when the number of BCAs released is decreased than when it is increased. In order to minimise the average plant density in the case where BCAs possibly struggle to adapt in a new habitat or a disaster hits and a lot of them die (larger adult mortality, μ_A, which consequently decreases I), it is recommended to release a slightly larger number of BCAs than the optimal number.

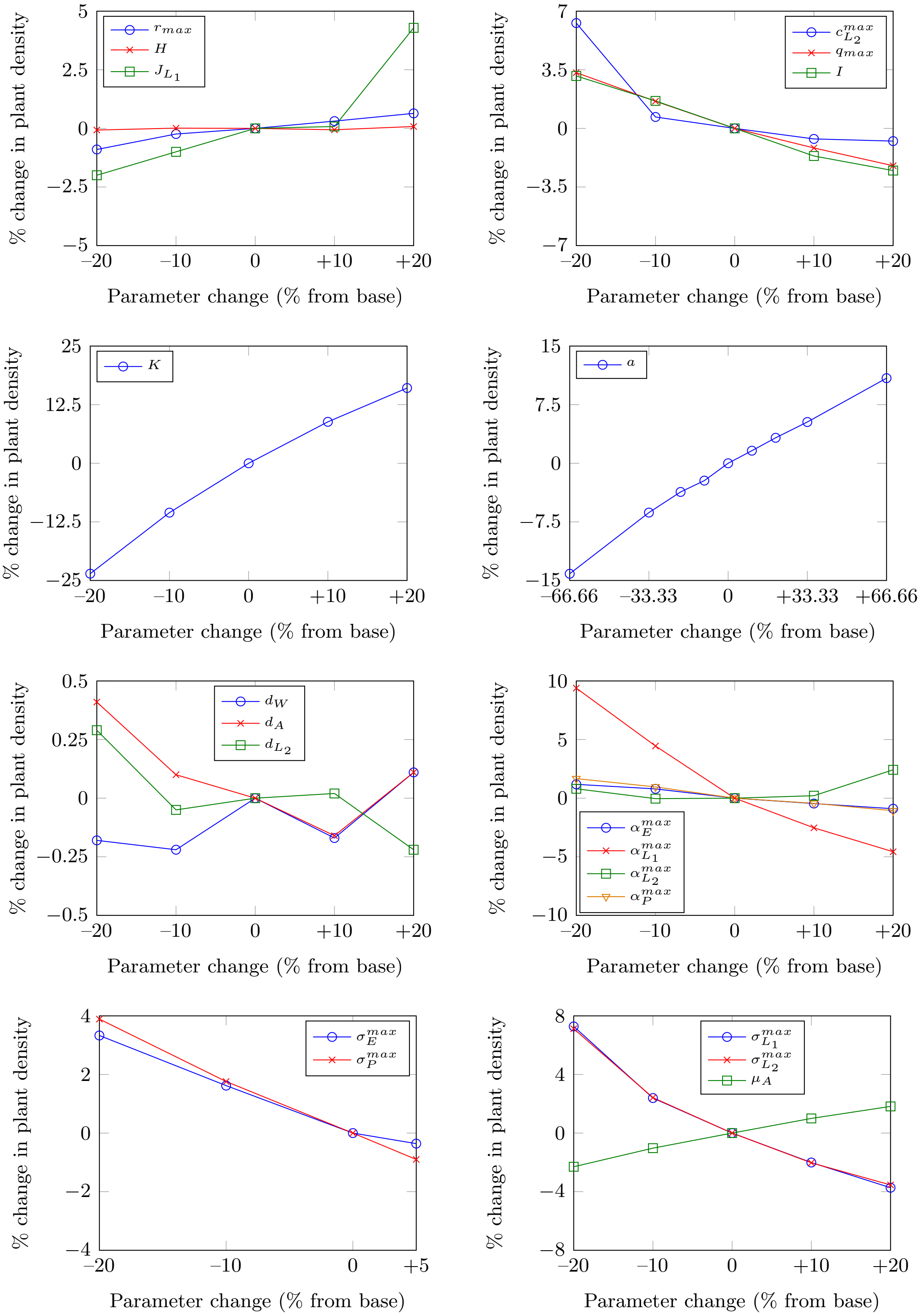


FIGURE 5.21: *Long-term sensitivity analysis of the average plant density, with respect to percentage changes in various parameters, with daily temperature held constant at 25°C and dew point temperature held constant at 13°C over a time period of two years.*

5.2.2 Sensitivity of the benefit of biological control release strategies

Sensitivity analyses of the total value of water saved were performed. Single input parameters were varied for a simulation of a once-off release of 100 BCAs at time $t = 0$ at the midpoint of one edge of a 30 m × 30 m domain, with the daily temperature and dew point temperature held constant over a considered period of time.

Short-term analysis

Firstly, the sensitivity of the total value of water saved was analysed over a time period of six months, with the daily temperature held constant at 30°C and the dew point temperature held constant at 14.5°C. In Figure 5.22, it may be seen that the total value of water saved is most sensitive to changes in the parameters I, a, $\alpha_{L_1}^{max}$, $\sigma_{L_1}^{max}$, c_{wa} and e_n, with at least one of the considered variations in each of these respective parameters resulting in a change in the total value of water saved of more than 15% in the short term. Furthermore, the total value of water saved is relatively sensitive to changes in the parameters $c_{L_2}^{max}$, q_{max}, α_P^{max}, σ_E^{max} and $\sigma_{L_2}^{max}$, with at least one of the considered variations in each of these respective parameters resulting in a change in the total value of water saved of between 10% and 15% in the short term, but relatively insensitive to changes in the rest of the input parameters. As expected, analyses indicate that there exists an inverse relationship between the sensitivity of the average plant density and the sensitivity of the value of water saved in the short term. When a perturbation in a certain parameter value results in a lower average plant density, the value of water saved is higher for that same perturbation in the short term.

Long-term analysis at a high constant daily temperature

Subsequently, the sensitivity of the total value of water saved was analysed over a time period of two years, with the daily temperature held constant at 30°C and the dew point temperature held constant at 14.5°C. From Figure 5.23 it may be seen that, for the assumed temperatures, the total value of water saved is most sensitive to changes in the input parameters $\sigma_{L_2}^{max}$, c_{wa} and e_n, with at least one of the considered variations in each of these respective parameters resulting in a change in the total value of water saved of more than 20% in the long term. At a constant daily temperature of 30°C and a dew point temperature of 14.5°C, the value of water saved appears to be more sensitive when decreasing the value of water, c_{wa}, and the value of the evaporation rate of open water, e_n, than when these parameter values are increased, and when $\sigma_{L_2}^{max}$ is increased than when it is decreased. Therefore, in the case that the values of c_{wa} and e_n are underestimated, the total value of water saved will not be affected as much as an overestimation. Additionally, the total value of water saved is relatively sensitive to changes in the parameters J_{L_1}, K, I, a, d_W, d_A, $\alpha_{L_1}^{max}$, $\alpha_{L_2}^{max}$, α_P^{max}, $\sigma_{L_1}^{max}$ and μ_A, with at least one of the considered variations in each of these respective parameters resulting in a change in the total value of water saved of between 10% and 15% in the long term, and relatively insensitive to the rest of the input parameter values. It may be noted that the sensitivity of the total value of water saved as a result of perturbations in c_{wa} and e_n in the long term is equivalent to the sensitivity of the total value of water saved as a result of similar perturbations in the short term.

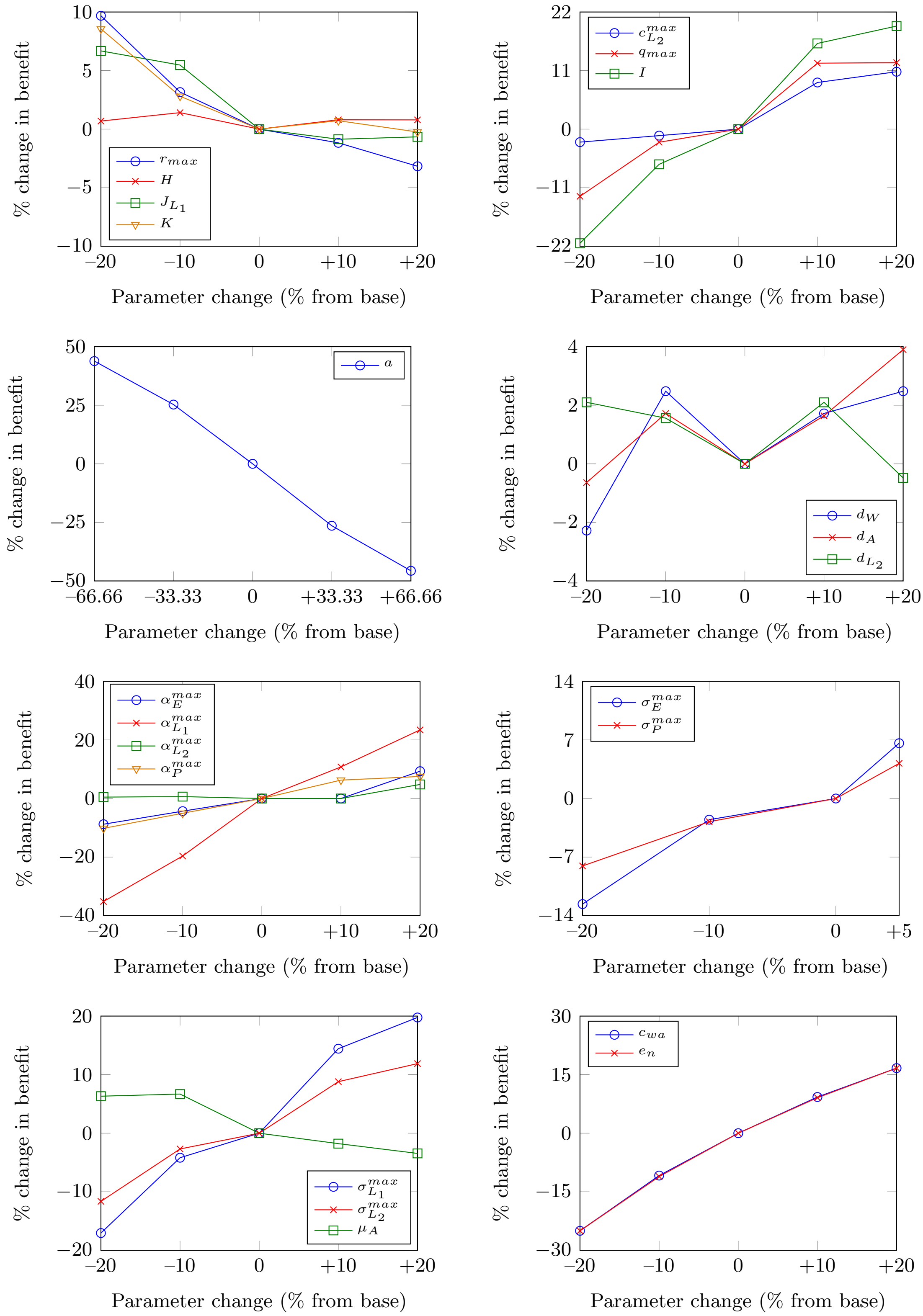


FIGURE 5.22: *Short-term sensitivity analysis of the total value of water saved, with respect to percentage changes in various parameters, with daily temperature held constant at 30° C and dew point temperature held constant at 14.5° C over a time period of six months.*

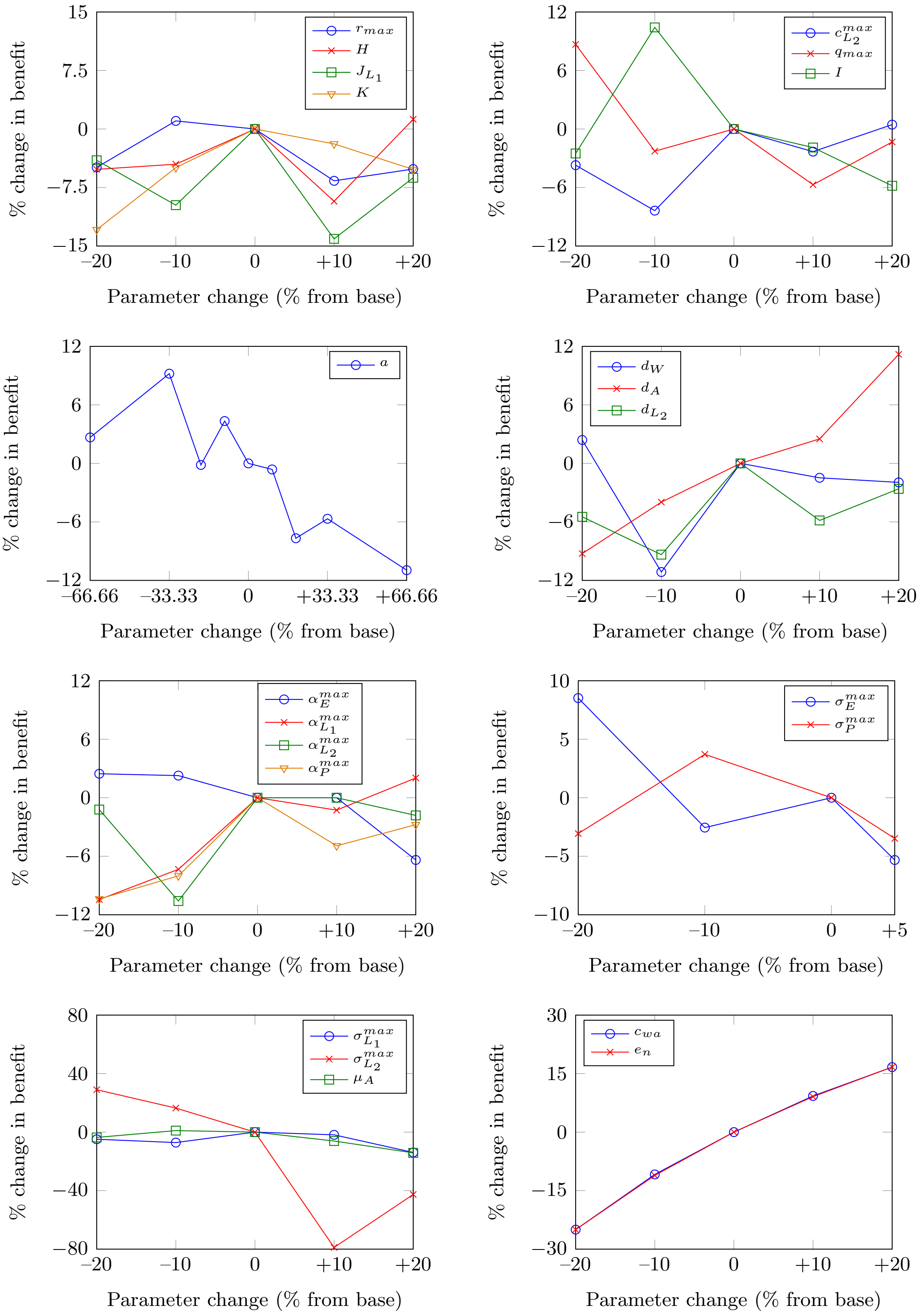


FIGURE 5.23: *Long-term sensitivity analysis of the total value of water saved, with respect to percentage changes in various parameters, with daily temperature held constant at 30° C and dew point temperature held constant at 14.5° C over a time period of two years.*

Long-term analysis at a lower constant daily temperature

The sensitivity of the total value of water saved was further analysed over a time period of two years, with the daily temperature held constant at 25°C and the dew point temperature held constant at 13°C. From Figure 5.24 it may be seen that, similar to the analysis of the average plant density, the sensitivity of the value of water saved is also generally more stable at the lower temperature than at the higher one. At this lower temperature, the value of water saved is mostly more sensitive to changes in parameter values, with the exceptions of changes in the values of parameters H, d_A and d_{L_2}, or increases in $\sigma_{L_2}^{max}$, where the value of water saved is somewhat less sensitive at the lower temperature than at the higher one, over a time period of two years, or for perturbations in c_{wa} and e_n, where the sensitivity of the value of water saved at the lower temperature remains equivalent to the sensitivity of the value of water saved as a result of similar perturbations at the higher temperature. For the assumed lower temperatures, the value of water saved is especially sensitive to extreme increases (+20% or more) in the values of parameters J_{L_1} and a, or extreme decreases (–20%) in the values of parameters $c_{L_2}^{max}$, $\alpha_{L_1}^{max}$, $\sigma_{L_1}^{max}$ and $\sigma_{L_2}^{max}$ over a time period of two years. For all parameters, except for K, the value of water saved is significantly more sensitive than the average plant density at this lower temperature, over a time period of two years.

At a constant daily temperature of 25°C and a dew point temperature of 13°C, the total value of water saved appears to be most sensitive to changes in the input parameters J_{L_1}, $c_{L_2}^{max}$, q_{max}, I, a, $\alpha_{L_1}^{max}$, $\alpha_{L_2}^{max}$, σ_{E}^{max}, $\sigma_{L_1}^{max}$, $\sigma_{L_2}^{max}$, σ_{P}^{max}, c_{wa} and e_n, with at least one of the considered variations in each of these respective input parameters resulting in a change in the total value of water saved of more than 20% over a time period of two years, while perturbations in the other input parameter values yield changes of less than 20% (see Figure 5.24). At a constant daily temperature of 30°C, the value of water saved was most sensitive to changes in only three parameter values, namely $\sigma_{L_2}^{max}$, c_{wa} and e_n. These analyses indicate that temperature plays a vital role in the sensitivity of the total value of water saved.

It may be noted that, at this lower temperature, the total value of water saved seems to be slightly more sensitive when I, the number of BCAs released, is decreased than when it is increased. In order to maximise the total value of water saved in the case where BCAs possibly struggle to adapt in a new habitat or a disaster hits and a lot of them die (larger adult mortality, μ_A, which consequently decreases I), it may again be recommended to release a slightly larger number of BCAs than the optimal number. Furthermore, to obtain maximum benefit, it is recommended to release BCAs during the time of the year when temperatures are as close as possible to optimum (30°C) in order to maximise the old larval damage rate, $c_{L_2}^{max}$, the oviposition rate, q_{max}, larval development rates, $\alpha_{L_1}^{max}$ and $\alpha_{L_2}^{max}$, as well as survival rates, σ_{E}^{max}, $\sigma_{L_1}^{max}$, $\sigma_{L_2}^{max}$ and σ_{P}^{max}, since suboptimal temperatures may significantly affect these parameter values, resulting in drastic decreases in the benefit obtained through biological control, in terms of water saving.

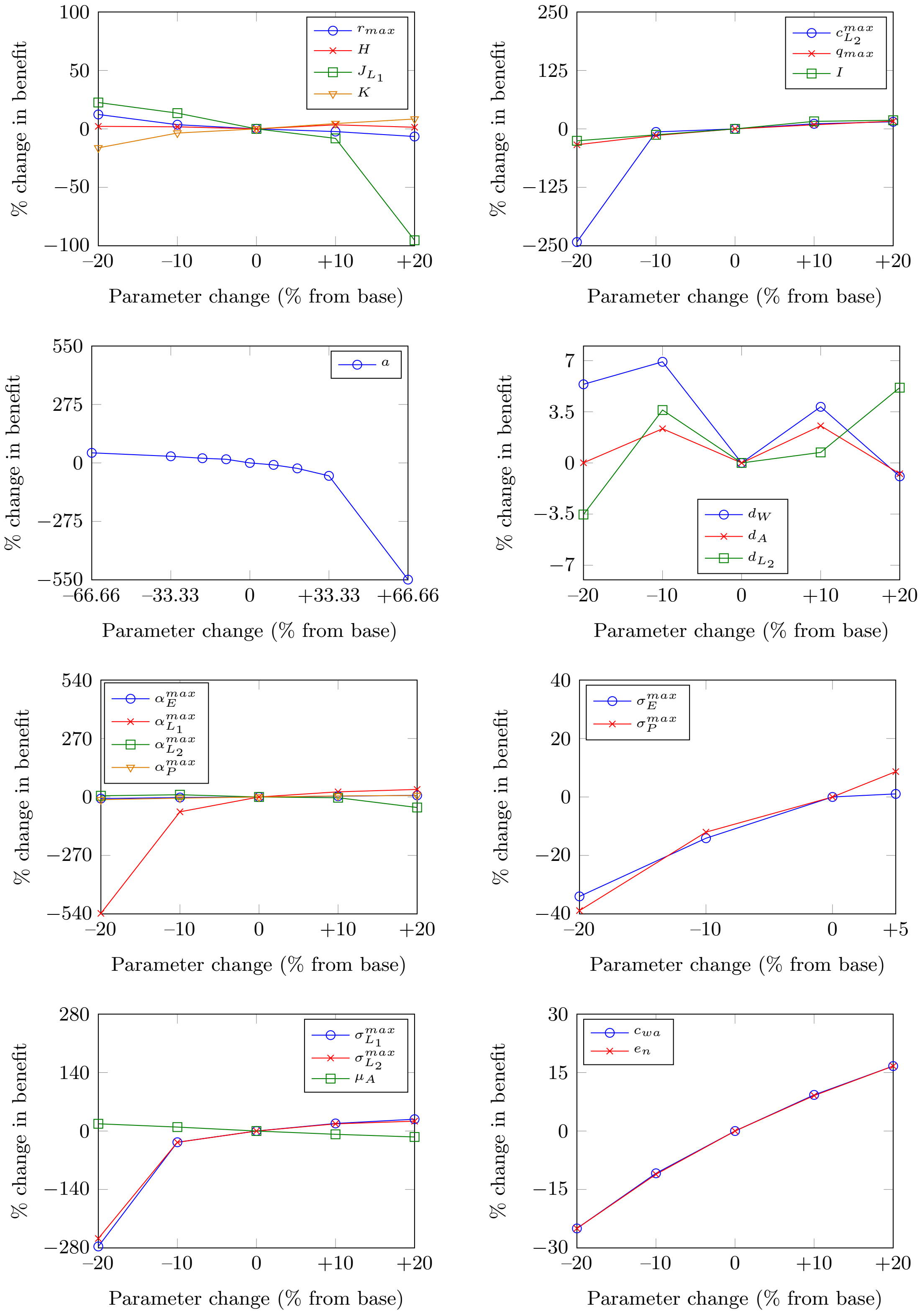


FIGURE 5.24: *Long-term sensitivity analysis of the total value of water saved, with respect to percentage changes in various parameters, with daily temperature held constant at 25° C and dew point temperature held constant at 13° C over a time period of two years.*

5.3 Chapter summary

In §5.1, the cost-effectiveness of different water hyacinth biological control release strategies for both short-term (six months) and long-term (two years) scenarios were investigated by means of numerical simulation. From short-term analyses in §5.1.1, it was concluded that, for a 30 m × 30 m domain located in the Cape Town region, once-off releases were more cost-effective than frequent releases over a time period of six months and that summer releases were, for all considered release strategies, more efficient and cost-effective than winter releases. Summer releases at at least two edges were required to obtain the desired level of weed suppression in the short term. Cases where releases were more distributed along an edge yielded greater suppression of weed density and therefore proved to be more cost-effective. Simulation results suggested that the optimal short-term strategy, yielding the most reachable break-even cost per BCA for the assumed parameter values, was to perform a once-off release at four edges with releases every 7.5 m along the edges in the first month of summer, with 240 BCAs per point of release, in order to suppress weed density to the desired level of control within six months. This number of BCAs correlates with the smaller numbers of BCAs released in real-life scenarios when mass rearing is not available.

Long-term analyses in §5.1.2 indicated that releases commencing in summer yielded significantly higher benefits (in terms of water saving) over a two-year time period, while requiring lower total numbers of BCAs to obtain the desired weed suppression in comparison with releases commencing in winter. Additionally, it was concluded that only frequent releases (weekly, two-weekly or four-weekly releases) at two or four edges succeeded to obtain the desired weed suppression within the considered two-year period, accentuating the benefit of releasing at more than one edge of an infested domain, as well as the value of frequent releases compared to a once-off release in the long term. Frequent releases yielded results in a close proximity to each other in the long term. In some cases, however, four-weekly releases slightly outperformed weekly and two-weekly releases by obtaining better weed suppression, suggesting that releases of larger numbers of BCAs once every four weeks tended to be more effective than releases of smaller numbers more regularly. In other cases, where results did not indicate a clearly dominant strategy, four-weekly releases were preferred simply on the basis of saving on travelling expenses due to releases being performed less often. When large numbers of BCAs were released at the same position, a strong limitation on the number of individuals maturing to the damage-causing old larval stage due to density dependence reduced the success of water hyacinth control. These results emphasised the importance of taking density dependence into account when suggesting effective biological control release strategies, confirming that it will be more effective to distribute BCA releases along edges, striving towards a uniform distribution of BCAs over the entire domain, rather than releasing at a singular point.

From sensitivity analyses in §5.2.1, it was concluded that the average plant density appeared to be relatively insensitive to changes in the number of BCAs released, increasing the confidence in recommended release strategies. Similar to results obtained from sensitivity analyses performed by Van Schalkwyk and Potgieter [74] on a mean-field model, the model output was slightly more sensitive when the number of BCAs released was decreased than when it was increased. In order to minimise the average plant density in the case where BCAs may struggle to adapt in a new habitat or a disaster hits and a lot of them die, it was recommended to release a slightly larger number of BCAs than the optimal number, as well as to release during the time of the year when the climate is optimal for the development of young larvae and the survival of adult weevils. Further analyses in §5.2.2 revealed that the total value of water saved is more sensitive at a lower constant temperature (25°C) than a higher one (30°C). In order to obtain maximum benefit, it was recommended to release BCAs during the time of the year when temperatures are as close as possible to optimum (30°C) in order to maximise the old larval damage rate, the oviposition rate, larval development rates, as well as weevil survival rates, concurring with suggestions from Van Schalkwyk and Potgieter [74]. Suboptimal temperatures may significantly affect these parameter values, resulting in drastic decreases in the benefit obtained through biological control, in terms of water saving.

CHAPTER 6

Real-world application

Contents

In this chapter, the model is applied to a real-world release site in order to illustrate how the model may be utilised to provide guidance towards the optimal magnitude, frequency, timing and distribution of BCA releases, which may minimise costs while maximising the benefit for a specific site.

6.1 Background and description of release site

The model developed in §4.2 was applied to the Kuilsriver site (33°57'17"S 18°39'47"E), where a real-life BCA release programme commenced in March 2015 when the site was completely invaded by water hyacinth. The Kuilsriver site is situated in a suburb of Cape Town. The original BCA release programme for this site has not been very successful. After one and a half years of BCA releases, consisting of mostly *M. scutellaris* (about 380 000 from March 2015 to May 2016), but also a few *N. bruchi* weevils (about 2 600), the site was still completely covered with water hyacinth, with little evidence of the impact of BCAs. Releases mostly occurred weekly or two-weekly on Fridays over the considered period of time, with the exception of three incidents where releases were interrupted for about two months on end, due to other sites getting priority over the Kuilsriver site or workers being away on holiday [52]. The unsuccessful control of water hyacinth at this site may be ascribed to the cold, unfavourable Cape Town weather conditions under which species may not be able to become abundant and control the weed, inadequate BCAs or flawed release procedures.

During the first week of August 2016, the entire water hyacinth infestation along with the BCAs at the Kuilsriver site were washed away by flood waters, leaving the site cleared of mature weeds. This is a classic example of how the success of biological control may often be limited by unpredictable circumstances which cannot be prevented or controlled [31, 32]. The weed is expected to grow back once seeds that remained in the water sediment start to germinate. BCAs will have to be re-established at the site. Model simulations may aid in improving the cost-effective control of water hyacinth, especially in the colder Cape Town area where BCAs often struggle to establish, by providing suggestions towards more effective release strategies

Simulations of different release strategies for *N. eichhorniae* weevils at the Kuilsriver site over a period of two years were performed in order to determine the best cost-effective water hyacinth biological control release strategy for this site. Parameter values as given in Chapter 4 were assumed for all simulations. The demarcated area where biological control was being performed by the *Invasive Species Unit* in Cape Town [52, 60], is about 60 m × 30 m. For the purpose of this investigation, initial water hyacinth population density was assumed to be at carrying capacity of the water body (70 kg/m2) over the entire domain and BCAs were assumed absent prior to release for all simulations. Field workers had access to only one edge of the considered infested domain and were therefore limited to performing releases at this one edge only. Access to other edges was hampered by water, as well as reeds and other plants growing in the wetlands, creating obstruction (see Figure 6.1). In light of these physical constraints, one-edge release strategies were first investigated in order to be able to suggest suitable release strategies, which take the limitations pertaining to the specific site into account. Thereafter, the potential benefit of clearing another edge to enable releases at two edges of the infested domain, was explored. In §5.1, it was concluded that biological control commencing in summer will always be more efficient and cost-effective in comparison with releases commencing in winter over a time period of two years. Therefore, all simulations of releases at the Kuilsriver site were performed for releases commencing in December, the first month of summer. Based on mass rearing data from the *Invasive Species Unit* in Cape Town [52, 60], a realistic maximum number of available BCAs of 48 000 per four-week time period was assumed to reflect possible resource constraints. For the sake of practicality, only multiples of 100 BCAs per point of release were considered.

FIGURE 6.1: *Water hyacinth blankets the Kuilsriver site in Cape Town, June 2015.*

6.2 Cost of biological control at the *Invasive Species Unit* in Cape Town

The *Invasive Species Unit* in Cape Town had several once-off start-up expenses when the mass rearing facility was established in 2014. The initial costs pertaining specifically to the rearing of water hyacinth BCAs are given in Table 6.1. At the time of this study, water hyacinth BCAs were reared in four portable pools. Clicker counters are used to count the number of BCAs when they are harvested for in-field releases. Pill holders and small pipes are also used during the harvesting process.

Item	Quantity	Cost per item	Total cost[1]
Portable pools	4	R1 295,48	R5 181,92
Clicker counters	4	R859,28	R3 437,10
Pill holders			R7,95
Pipes			R36,00
Total			R9 958,45

TABLE 6.1: *Start-up costs for mass rearing facility at Invasive Species Unit in Cape Town in 2014.*

In Table 6.2, the fixed running costs per four-week cycle pertaining to the mass rearing of water hyacinth BCAs at the *Invasive Species Unit* in Cape Town is given. Apart from the salaries of the five staff members working 20 days per four-week cycle on mass rearing related tasks, the running costs pertaining to mass rearing at the facility are marginal, since they mainly make use of recycled material and retrieve new water hyacinth plants from the field when old ones become unhealthy. Fertiliser is changed once in three months, yielding a cost of R195,65 per four-week cycle. Harvested BCAs are transported in small recycled plastic containers on paper towels. In addition to the fixed running costs per four-week cycle, there is a variable expense for travelling between the mass rearing facility and the release site. Every time releases are performed, field workers travel a total of 74 km by car to and from the Kuilsriver site, at R4,10/km in 2016 Rand values. Travelling expenses thus amount to R303,40 per release opportunity. Since the mass rearing facility is already established at the *Invasive Species Unit* in Cape Town, the initial start-up expenses of the facility will not be taken into account when the cost of a release strategy is determined. Only the running costs will be considered.

Item	Quantity	Cost per item	Total cost[2]
Salaries	5	R2 704,60	R13 523,00
Fertiliser			R195,65
Paper towels			R10,00
Total			R13 728,65

TABLE 6.2: *Fixed running costs per four-week cycle for mass rearing facility at Invasive Species Unit in Cape Town.*

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[1] Costs are given in 2014 Rand values, since it was once-off expenses which occurred in 2014.

[2] Costs are given in 2016 Rand values.

6.3 Numerical results pertaining to one-edge release strategies for the Kuilsriver site

For the assumed parameter values, the total value of water loss through plant evapotranspiration will be R58 436 for the considered 60 m × 30 m water body at the Kuilsriver site covered with water hyacinth for a time period of two years, if no control method is being applied. The number, I, of *N. eichhorniae* weevils per point of release which yields the best suppression of water hyacinth population density over a time period of two years, commencing in December, for once-off, weekly ($f = 7$), two-weekly ($f = 14$), and four-weekly ($f = 28$) releases, respectively, at one of the long edges of the domain, was determined.

In Table 6.3, this number, I, of BCAs per point of release is given for releases every 7.5 m along the edge (seven releases per edge - see Figure 6.2), together with the total number of BCAs used, the average plant density, the lowest plant density obtained, the total value of water saved, the total cost and cost/benefit, CB, for each considered release frequency. The lowest plant density over the entire domain was reached between 20 and 21 months for the considered release strategies. Firstly, it may be noted that frequent releases are significantly more effective to suppress plant density in comparison with once-off releases over a time period of two years. Secondly, it may be seen that four-weekly releases at one edge yield better weed suppression than weekly and two-weekly releases, suggesting that, for this site, it is more effective to release all the available number of BCAs during a single release opportunity every four weeks, with a larger magnitude per point of release, rather than to divide the BCAs between more regular releases with smaller magnitudes per point of release. As a result of greater plant suppression, four-weekly releases also yield the highest total value of water saved between all the other considered release strategies. Finally, four-weekly releases additionally result in the lowest total cost amongst the considered frequent release strategies, by requiring only 26 expeditions to and from the release site, while weekly and two-weekly releases require 103 and 52 trips, respectively, amounting to significantly greater travelling expenses over the two-year time period. With the highest value of water saved and the lowest total cost amongst the frequent release strategies, four-weekly releases is considered the most cost-effective strategy, with the best CB-value between the considered frequent release strategies. In contrast to previous control strategies for this site, which consisted of weekly or two-weekly releases, this suggestion of less frequent releases may aid in improving the efficient and cost-effective control of water hyacinth at the Kuilsriver site.

When only considering the benefit of water saving due to the biological control of water hyacinth for the Kuilsriver site, once-off releases appear to be more cost-effective than frequent releases, even though the former is remarkably less efficient in suppressing water hyacinth populations. On the surface, the high costs pertaining to biological control appear to outweigh the benefits. However, in the bigger picture, it should be noted that additional advantages of the effective control of water hyacinth, applicable to the Kuilsriver site, include the conservation of biodiversity and reduction in health risks [42]. Water hyacinth has an incredible mechanism to outgrow any native species occurring in the system, resulting in a decline in biodiversity [37, 69, 76]. Health risks arise with the plants providing breeding grounds for mosquitoes and other disease carriers, as well as reducing water quality, affecting nearby communities [31, 38, 69]. The sooner the weed populations are suppressed, the greater the benefit. These benefits are difficult to quantify, but should not be ignored. Furthermore, job creation through engaging otherwise unemployed people in control programmes may in fact be considered as a socio-economic benefit of biological control [42]. Where it is assumed that once-off releases only require employment of workers for one month, frequent release strategies involve long-term employment, yielding a significantly greater socio-economic benefit in comparison with once-off release strategies. Salaries account for 90%, 94% and 96,2% of the total cost of weekly, two-weekly and four-weekly releases, respectively, for the considered one-edge release strategy (see Tables 6.2 – 6.3). Consequently, 90%, 94% and 96,2% of the costs pertaining to the respective frequent release strategies, may in fact be seen as investments in the socio-economic development of the country, making biological control an even more appealing solution to the problem of water hyacinth. When these factors are taken into consideration, four-weekly releases, which yield a significantly higher socio-economic benefit together with the more effective control of water hyacinth over the considered two-year time period, may be recommended above once-off releases for one-edge releases at the Kuilsriver site. In the end, the focus may shift from breaking even with costs, to determining the investment society is willing to make for the sake of the environment, biodiversity, health and quality of life.

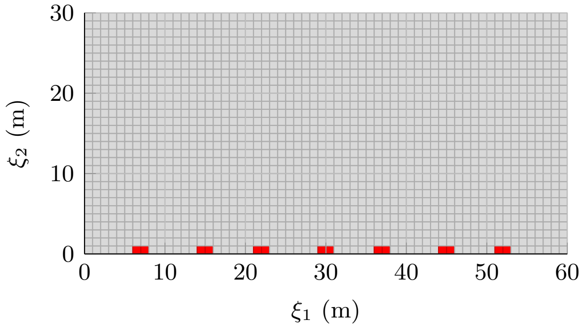
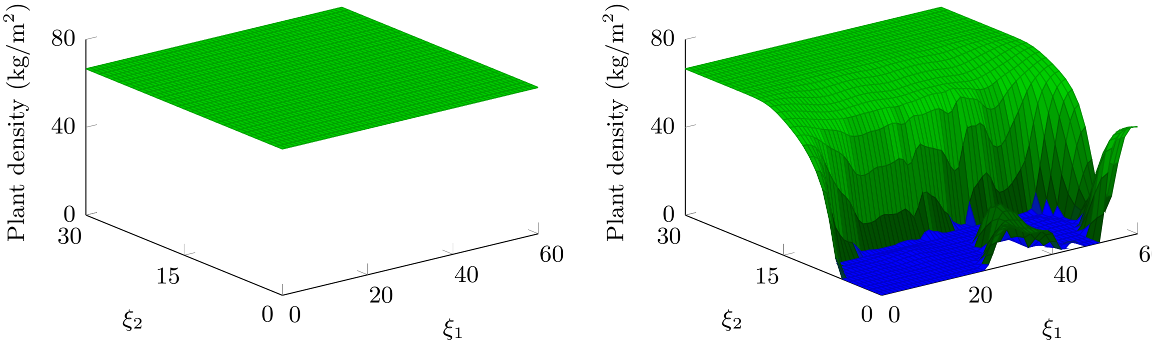


FIGURE 6.2: *One-edge releases every 7.5 m at the Kuilsriver site.*

Freq.	I per release	Total per opportunity	Grand total	Average plant density	Lowest plant density	Saved	Total cost	CB
once	6 800	47 600	47 600	76%	63%	R7 295	R14 032,05	-R6 737,50
$f = 7$	1 700	11 900	1 225 700	61%	38%	R14 562	R360 737,80	-R346 175,80
$f = 14$	3 400	23 800	1 237 600	60%	37%	R15 320	R345 264,40	-R329 944,40
$f = 28$	6 800	47 600	1 237 600	57%	34%	R16 082	R337 376,00	-R321 294,00

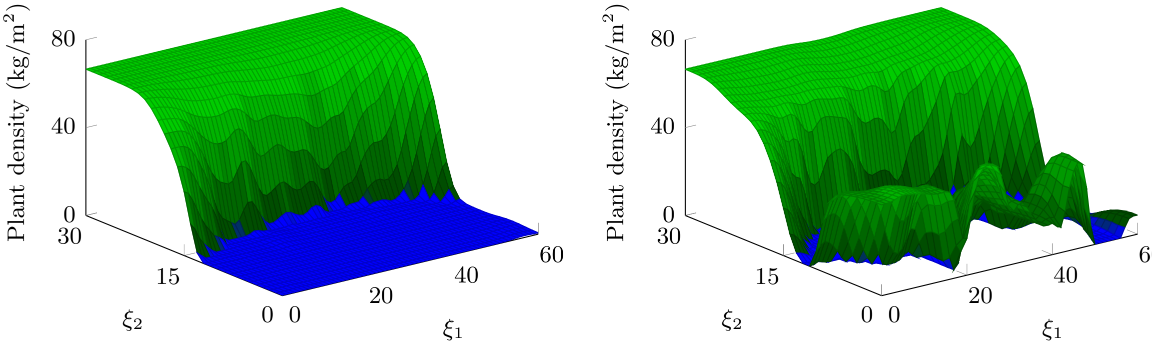
TABLE 6.3: *For releases every 7.5 m along one edge of the infested Kuilsriver site, the number of BCAs yielding the best suppression, the average plant density, the lowest plant density obtained, as well as the total value of water saved, the total cost and cost/benefit (CB) for once-off, weekly ($f = 7$), two-weekly ($f = 14$) and four-weekly ($f = 28$) release strategies over a time period of two years, commencing in December, as determined from the simulation.*

Model output of the initial water hyacinth density, as well as the plant density after one year, one and a half years and two years for the Kuilsriver simulation of four-weekly releases of 6 800 BCAs every 7.5 m along one of the long edges of the domain, is given in Figure 6.3. The best weed suppression was obtained just after the one and a half year mark (see Figure 6.3(c)), where the total water hyacinth population density for the entire domain reached 34% of the original plant density. Once open water appears at the edges where BCAs were initially released, field workers will have to move through the water to reach the water hyacinth plants where releases need to be performed. When the plants are no longer accessible from the edges of the land, small boats or other flotation devices may be used to reach the plants in order to be able to continue with frequent releases along the edge of the water hyacinth mat. As BCAs generations pass, plants grow back, yielding a final plant density, as shown in Figure 6.3(d), at the end of the considered two-year time period. This indicates that biological control is a long-term process and will have to be continued after two years at the Kuilsriver site.



(a) *Initial plant density.*

(b) *After one year.*



(c) *After one and a half years.*

(d) *After two years.*

Figure 6.3: *Water hyacinth population dynamics for four-weekly releases of 6 800 BCAs every 7.5 m along one edge of the Kuilsriver site over a time period of two years, commencing in December.*

In Table 6.4, the number, I, of BCAs per point of release is given for releases every 15 m along the long edge (three releases per edge – see Figure 6.4), together with the total number of BCAs used, the average plant density, the lowest plant density obtained, the total value of water saved, the total cost and cost/benefit, CB, for each considered release frequency. The lowest total plant density over the entire domain was reached at some point in time between 19 and 21 months for the considered release strategies. The total cost per release strategy remains the same as with one-edge releases every 7.5 m along the edge, since only the distribution per release opportunity differs, while the running expenses remain unchanged. With the available number of BCAs now being equally distributed between only three points of release instead of seven, more BCAs may be released per point. In accordance with conclusions drawn from results in §5.1, model output indicates that strategies where releases are more distributed along an edge will yield better average weed suppressions and higher total values of water saved in comparison with strategies where releases are less spread out, even though the latter may use greater magnitudes of BCAs per point of release. Consequently, releases every 15 m yield lower CB-values than releases every 7.5 m for all considered one-edge release strategies. Releases every 7.5 m along the edge will thus be preferred to releases every 15 m for all considered one-edge release frequencies for this domain, yielding more efficient and cost-effective results.

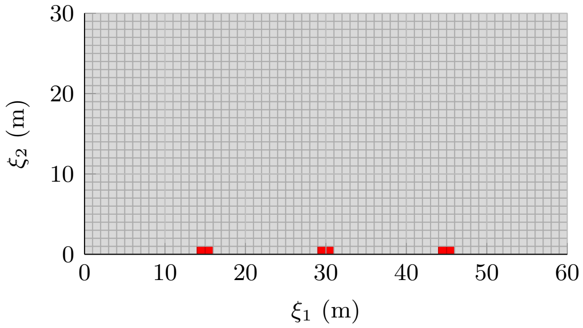


FIGURE 6.4: *One-edge releases every 15 m at the Kuilsriver site.*

Freq.	I per release	Total per opportunity	Grand total	Average plant density	Lowest plant density	Saved	Total cost	CB
once	16 000	48 000	48 000	84%	73%	R4 161	R14 032,05	-R9 871,05
$f = 7$	4 000	12 000	1 236 000	64%	37%	R12 955	R360 737,80	-R347 782,80
$f = 14$	8 000	24 000	1 248 000	64%	39%	R13 101	R345 264,40	-R332 163,40
$f = 28$	14 500	43 500	1 131 000	62%	37%	R13 953	R337 376,00	-R323 423,00

TABLE 6.4: *For releases every 15 m along one edge of the infested Kuilsriver site, the number of BCAs yielding the best suppression, the average plant density, the lowest plant density obtained, as well as the total value of water saved, the total cost and cost/benefit (CB) for once-off, weekly ($f = 7$), two-weekly ($f = 14$) and four-weekly ($f = 28$) release strategies over a time period of two years, commencing in December, as determined from the simulation.*

It is interesting to note that four-weekly releases every 15 m along the edge is the only one-edge release strategy where the maximum number of available BCAs (16 000 per point of release) does not yield the best weed suppression and highest total value of water saved for the domain under consideration. When the average plant density obtained by different release magnitudes does not indicate a clearly optimal strategy, the value of water saved is used as an indication to determine the optimal magnitude (see Figure 6.5). The hydra effect is evident here. When more than 14 500 BCAs per point are being released every four weeks, density dependence in the weevil life stages has a great impact on the number of individuals that survive through the young larval stage to the damage-causing old larval stage, resulting in a smaller overall impact on water hyacinth and therefore a lower value of water saved. The BCA density per area plays a vital role in the effectiveness of the release strategy.

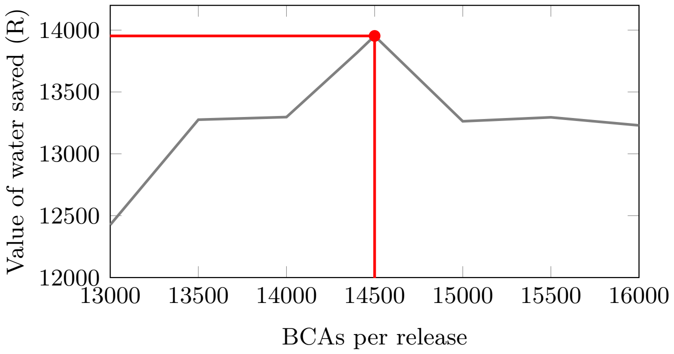


FIGURE 6.5: *Determining the number of BCAs per point of release which yields the highest value of water saved over a time period of two years, commencing in December, for four-weekly one-edge releases every 15 m along the edge at the Kuilsriver site.*

6.4 Numerical results pertaining to two-edge release strategies for the Kuilsriver site

Two-edge release strategies were investigated to determine the potential benefit of getting access to another edge of the infested area in order to improve the cost-effectiveness of biological control at the Kuilsriver site. The number, I, of *N. eichhorniae* weevils per point of release which yields the best suppression of water hyacinth population density over a time period of two years, commencing in December, for once-off, weekly ($f = 7$), two-weekly ($f = 14$), and four-weekly ($f = 28$) releases, respectively, at the two long edges of the domain, was determined. In Table 6.5, the number, I, of BCAs per point of release is given for releases every 7.5 m along the edges (seven releases per edge, fourteen in total - see Figure 6.6), together with the total number of BCAs used, the average plant density, the lowest plant density obtained, the total value of water saved, the total cost and cost/benefit, CB, for each considered release frequency. The lowest total plant density over the entire domain was reached at some point in time between 19 and 20 months for the considered two-edge release strategies. The total cost per release strategy remains the same as with one-edge releases, since only the distribution per release opportunity differs, while the running expenses remain unchanged. With the available number of BCAs now being equally distributed between fourteen points of release instead of three or seven, smaller magnitudes of BCAs are released per point than with one-edge releases. Four-weekly releases still outperform other frequent release strategies at two edges by yielding a better weed suppression and higher total value of water saved in comparison with weekly and two-weekly releases.

Similar to one-edge releases, if only the benefit of water saving due to the biological control of water hyacinth is considered, once-off releases at two edges appear to be more cost-effective than frequent releases at two edges, even though the former is remarkably less efficient in suppressing water hyacinth populations. However, the effective control of water hyacinth offers additional advantages which include the conservation of biodiversity and reduction in health risks. Furthermore, the job creation through long-term, labour-intensive control programmes may again be seen as a socio-economic benefit, with frequent releases yielding a significantly greater socio-economic benefit through employment in comparison with once-off release strategies. When these factors are taken into consideration, four-weekly releases may be recommended above once-off releases for two-edge releases at the Kuilsriver site.

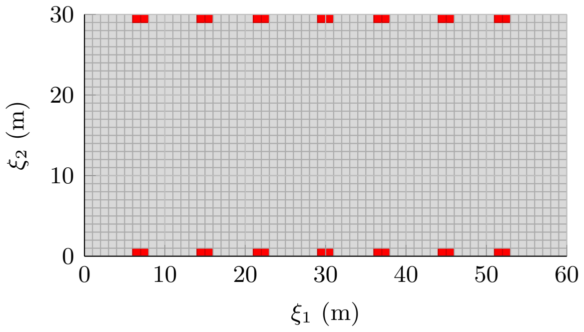


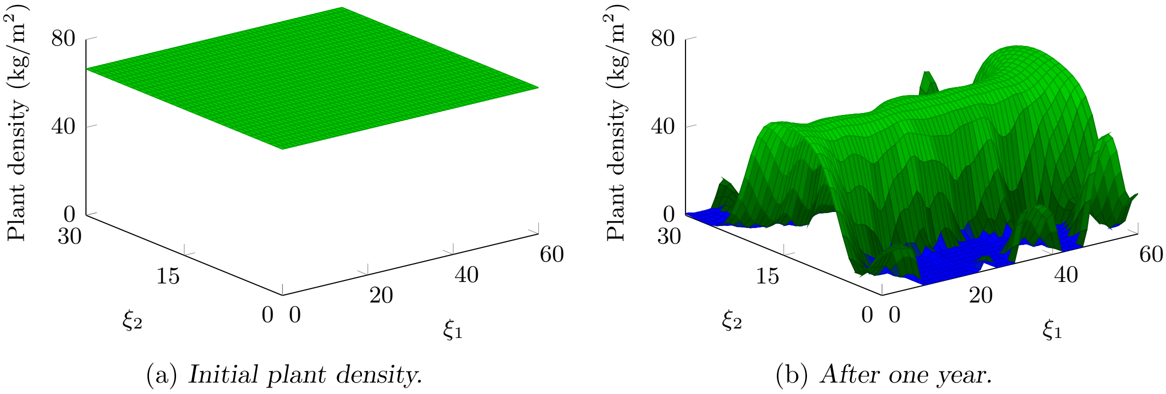
FIGURE 6.6: *Two-edge releases every 7.5 m at the Kuilsriver site.*

In Figure 6.7, model output of the initial water hyacinth density, as well as the plant density after one year, one and a half years and two years for the Kuilsriver simulation of four-weekly releases of 3 400 BCAs every 7.5 m along the two long edges of the domain, is given. The best weed suppression for this two-edge release strategy was obtained just after the one and a half year mark (see Figure 6.7(c)), where the total water hyacinth population density for the entire

Freq.	I per release	Total per opportunity	Grand total	Average plant density	Lowest plant density	Saved	Total cost	CB
once	3 400	47 600	47 600	61%	39%	R10 938	R14 032,05	-R3 094,05
$f = 7$	800	11 200	1 111 200	35%	2%	R25 012	R360 737,80	-R335 725,80
$f = 14$	1 700	23 800	1 167 000	34%	1%	R25 940	R345 264,40	-R319 324,40
$f = 28$	3 400	47 600	1 183 200	30%	1%	R27 618	R337 376,00	-R309 758,00

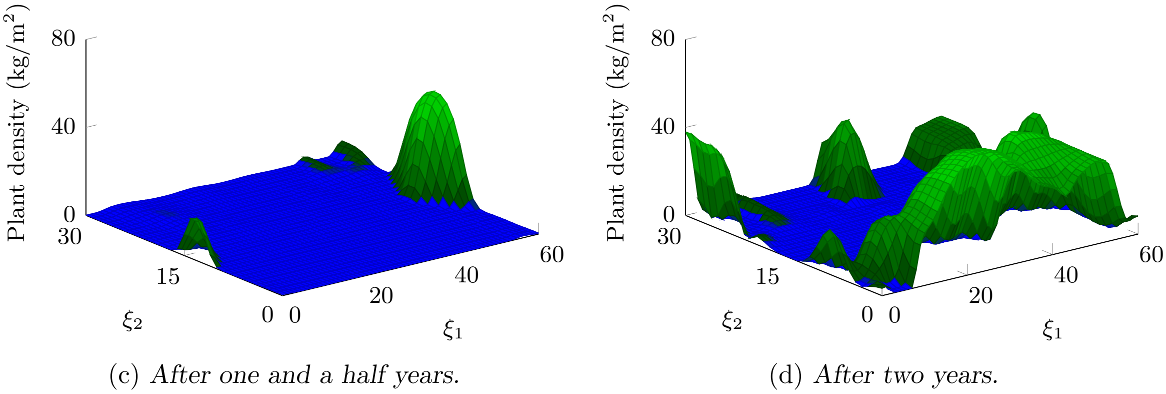
TABLE 6.5: *For releases every 7.5 m along the two long edges of the infested Kuilsriver site, the number of BCAs yielding the best suppression, the average plant density, the lowest plant density obtained, as well as the total value of water saved, the total cost and cost/benefit (CB) for once-off, weekly ($f = 7$), two-weekly ($f = 14$) and four-weekly ($f = 28$) release strategies over a time period of two years, commencing in December, as determined from the simulation.*

domain reached 1% of the original plant density. Similar to one-edge releases, plants grow back as BCAs generations pass, yielding a final plant density, as shown in Figure 6.7(d), at the end of the considered two-year time period. Simulation results indicate that even if releases are performed at two edges, biological control will have to be continued for more than two years in order to maintain water hyacinth control at the Kuilsriver site.



(a) *Initial plant density.*

(b) *After one year.*



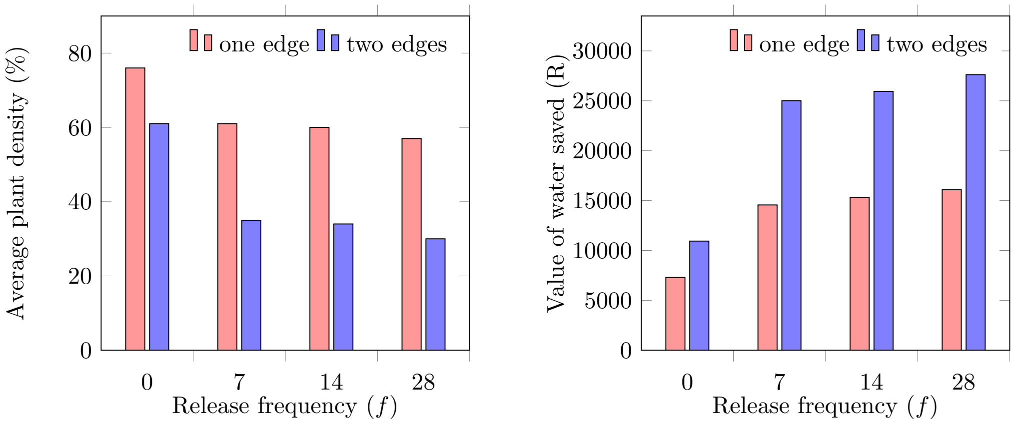
(c) *After one and a half years.*

(d) *After two years.*

FIGURE 6.7: *Water hyacinth population dynamics for four-weekly releases of 3 400 BCAs every 7.5 m along the two long edges of the Kuilsriver site over a time period of two years, commencing in December.*

6.5 Comparison between one-edge and two-edge release strategies

Two-edge releases yield significantly better water hyacinth suppressions in comparison with one-edge releases, with the same number of available BCAs per four-week cycle over a time period of two years (see Figure 6.8(a)). Even though two-edge releases use smaller magnitudes of BCAs per point of release, the impact of attacking the weed from two sides instead of waiting for the BCAs to spread to the other side in their own time, is significant. Furthermore, for once-off releases, releases at two edges yield a value of water saved of 1.5 times the value obtained with releases at one edge, while frequent releases at two edges yield a value of water saved of 1.7 times the value obtained with releases at one edge (see Figure 6.8(b)). Since the costs pertaining to one-edge and two-edge release strategies remain the same, while the benefits increase significantly for two-edge releases, it is clear that the latter will be considerably more cost-effective in comparison with one-edge releases over a time period of two years. It will therefore be worth it for biological control practitioners from the *Invasive Species Unit* in Cape Town to investigate the option of getting access to the other long edge at the Kuilsriver site, while maintaining biodiversity on the banks, in order to enable releases at two edges.



(a) *Average plant density.* (b) *Value of water saved.*

FIGURE 6.8: *Comparison of the average plant density obtained (a) and the total value of water saved (b) between one-edge and two-edge releases every 7.5 m along the considered edges, for different release frequencies over a time period of two years.*

6.6 Recommendations

For the current model assumptions, simulation results indicate that *N. eichhorniae* weevils may be able to sufficiently develop and establish at the Kuilsriver site, under the assumed weather conditions for Cape Town. BCAs may suppress water hyacinth populations to a minimum of 34% of the original total plant density at some point in time over a period of two years, commencing in December, with one-edge releases every four weeks with releases every 7.5 m along the edge, or to a minimum of 1% of the original total plant density at some point in time over a period of two years, with two-edge releases every four weeks with releases every 7.5 m along the edges. Two-edge releases will be more cost-effective in comparison with one-edge releases and once-off releases will be more cost-effective in comparison with frequent releases, when only the benefit of water saving is considered and if there is not a desired level of control that needs to be obtained within a time period of two years. Since salaries account for by far the largest part of the expenses pertaining to the rearing and releasing of BCAs at the *Invasive Species Unit* in Cape Town, the programme managers are encouraged to review the efficiency of their current employment situation, re-evaluating the necessary and sufficient number of employees and hours allocated to the programme.

In the bigger picture, further benefits of the effective control of water hyacinth, including the conservation of biodiversity, reduction in health risks and increase in quality of life for nearby communities, should be considered. This may shift the focus from aiming to break even with costs, to regarding the expenses as an investment for the sake of the environment and society.

6.7 Chapter summary

In this chapter, the model was applied to a real-world release site in order to illustrate how the model may be utilised to provide guidance towards suitable BCA release strategies, which will minimise costs and maximise the benefit for a specific site. A description of the site was provided in §6.1, followed by a review of the costs involved with the rearing and releasing of BCAs by the *Invasive Species Unit* in Cape Town in §6.2.

Simulation results in §6.3 indicated that, for the assumed parameter values, four-weekly releases commencing in summer, with releases of 6 800 BCAs every 7.5 m along the edge, will be the most efficient one-edge release strategy for the Kuilsriver site. In contrast to previous control strategies for this site, which consisted of weekly or two-weekly releases, this suggestion of less frequent releases may aid in improving the efficient and cost-effective control of water hyacinth at the Kuilsriver site. However, when only the benefit of water saving due to the biological control of water hyacinth is considered, once-off releases appeared to be more cost-effective than frequent releases, even though once-off releases were remarkably less efficient in suppressing plant populations. It was emphasised that further benefits of biological control, including the conservation of biodiversity and reduction in health risks, should also be considered to be able to perform a more encompassing cost-benefit analysis.

Numerical results for two-edge release strategies in §6.4 were compared to one-edge release strategies in §6.5, where it was found that two-edge releases yielded significantly better water hyacinth suppressions in comparison with one-edge releases, with the same number of available BCAs per four-week cycle over a time period of two years. Furthermore, releases at two edges yielded a value of water saved of up to 1.7 times the value obtained with releases at one edge, predicting that two-edge release strategies will be considerably more cost-effective in comparison with the current one-edge releases at the Kuilsriver site, suggesting that it will be worth it for biological control practitioners to investigate the option of getting access to another edge at the Kuilsriver site, while maintaining biodiversity. The chapter closed with practical recommendations towards how the *Invasive Species Unit* in Cape Town may improve the efficient and cost-effective control of water hyacinth at the Kuilsriver site in §6.6.

CHAPTER 7

Conclusion

Contents

This chapter consists of a brief summary of the work presented in this study, as well as an overview of the main contributions of the study with respect to the mathematical modelling of biological control strategies for water hyacinth. The chapter concludes with suggestions for possible future work to further this research.

7.1 Thesis summary

In the introduction of this study, the serious problems posed by water hyacinth were shortly discussed, followed by a brief history of the control of water hyacinth globally and in South Africa. After the national importance of water management and the economic and social benefits that could be drawn from biological control programmes were emphasised, the current challenges experienced in the sound and cost-effective management of the weed in South Africa were provided. The scope of and objectives pursued in this study also form part of the introductory chapter.

In Chapter 2, the necessary biological background of the water hyacinth, *Eichhornia crassipes*, and the *Neochetina eichhorniae* weevil, consisting of the life cycles of the plant and its enemies, as well as the way they influence each other, was provided. This provided the necessary biological foundation in order to model the interaction of the two species and to understand the assumptions made during the construction of the model in subsequent chapters (in fulfillment of Thesis Objective I).

The mathematical background with respect to the modelling of water hyacinth population growth and interaction models of water hyacinth and the *N. eichhorniae* weevil, together with the limitations of current modelling approaches, was discussed in Chapter 3 (in fulfillment of Thesis Objective II(a)). Previous temporal mean-field models proved to be unrealistic in the context of assuming that BCAs are uniformly distributed throughout an area. A spatially explicit model was therefore required to model the distribution of water hyacinth and the weevils in a heterogeneous environment. A discussion on reaction-diffusion theory, which is the main modelling approach adopted in this study, and its application in ecology, was given (in fulfillment of Thesis Objective II(b)).

In Chapter 4, a reaction-diffusion model for a temporally variable and spatially heterogeneous environment, consisting of a system of coupled delay PDEs, was developed to mathematically describe the spatio-temporal dynamics of water hyacinth populations and the interacting populations of the various life stages of the *N. eichhorniae* weevil as BCA on an isolated and bounded two-dimensional spatial domain. In order to translate the biological background provided in Chapter 2 to a mathematical model that represents the population dynamics of the plant and weevil species, a number of simplifying assumptions was discussed in §4.1, followed by the development and mathematical formulation of the reaction-diffusion model in §4.2. As a first attempt to model the spatial dynamics of the water hyacinth and weevil system, diffusion terms were added to the applicable ordinary DDEs in the temporal model presented in previous studies, with the additions of an Allee-effect and a term allowing for frequent releases of adult weevils, a more detailed temperature dependence, as well as slight changes to the modelling of the through stage survival probabilities (in partial fulfillment of Thesis Objective III(a)). Limitations of this modelling approach motivated the development of the final model formulated in §4.2.2, with a different approach towards the modelling of the recruitment and maturation terms for the weevil population and the derivation of a more accurate expression for the old larval maturation term, which includes spatial averaging (in final fulfillment of Thesis Objective III(a)). Subsequently, detailed discussions and derivations of the model input and output parameters were provided in §4.3 and §4.4, respectively (in fulfillment of Thesis Objective III(b)), including the derivation of a cost-benefit function which may be used to determine the most cost-effective release strategy for a specific scenario (in partial fulfillment of Thesis Objective IV). An elaborate description of the implementation of the model in MATLAB 9.0, together with difficulties encountered during this process, was given in §4.5. Finally, numerous simulations were performed in order to validate the model output by means of testing various model responses and comparing the model output to real-world data in §4.6 (in fulfillment of Thesis Objective III(c)). The model responded as expected to changes in θ, I, a, $c_{L_2}^{max}$, d_A, $d_{L_2}(\theta)$, d_W, f and the timing of BCA releases. Furthermore, model simulation output reflected a realistic decrease in the total plant population densities over the considered period, corresponding to field observations from the real-life BCA release scenario which took place at the Mkhadzi Spruit at the end of 2008. The spatially explicit model was therefore considered valid to be used to provide guidance towards the optimal magnitude, frequency, timing and distribution of BCA releases in a temporally and spatially variable environment.

Chapter 5 contains investigations into the cost-effectiveness of different water hyacinth biological control release strategies for both short-term (six months) and long-term (two years) scenarios by means of numerical simulation, as provided in §5.1 (in fulfillment of Thesis Objective IV(a)). In §5.1.1, it was concluded that, for a 30 m × 30 m domain located in the Cape Town region, once-off releases were more cost-effective than frequent releases in the short term and that summer releases were, for all considered release strategies, more efficient and cost-effective than winter releases in the short term. Summer releases at at least two edges were required to obtain the desired level of weed suppression in the short term. Cases where releases were more distributed along an edge yielded greater suppression of weed density and therefore proved to be more cost-effective. Simulation results suggested that the optimal short-term strategy, yielding the most reachable break-even cost per BCA for the assumed parameter values, was to perform a once-off release at four edges with releases every 7.5 m along the edges in the first month of summer in order to suppress weed density to the desired level of control within six months (in partial fulfillment of Thesis Objective IV(b)). Long-term analyses in §5.1.2 indicated that releases commencing in summer yielded significantly higher benefits (in terms of water saving) over a two-year time period, while requiring lower total numbers of BCAs to obtain the desired weed suppression in comparison with releases commencing in winter. Additionally, it was concluded that only frequent releases (weekly, two-weekly or four-weekly releases) at two or four edges succeeded to obtain sufficient weed suppression within the considered two-year period, accentuating the benefit of releasing at more than one edge of an infested domain, as well as the value of frequent releases compared to a once-off release in the long term. Frequent releases yielded results in a close proximity to each other in the long term. In some cases, however, four-weekly releases slightly outperformed weekly and two-weekly releases by obtaining better weed suppression, indicating that releases of larger numbers of BCAs once every four weeks tended to be more effective than releases of smaller numbers more regularly. In other cases, where results did not indicate a clearly dominant strategy, four-weekly releases were preferred simply on the basis of saving on travelling expenses due to releases being performed less often. When large numbers of BCAs were released at the same position, a strong limitation on the number of individuals maturing to the damage-causing old larval stage due to density dependence reduced the success of water hyacinth control. These results emphasised the importance of taking density dependence into account when suggesting effective biological control release strategies, confirming that it will be more effective to distribute BCA releases along edges, rather than releasing at a singular point (in final fulfillment of Thesis Objective IV(b)).

Sensitivity analyses in §5.2 revealed that the total value of water saved is generally significantly more sensitive to changes in parameter values in comparison with the sensitivity of the average plant density for similar perturbations in input parameters, especially at a lower constant temperature (25°C). In §5.2.1, it was concluded that the average plant density appeared to be relatively insensitive to changes in the number of BCAs released, I, increasing the confidence in recommended release strategies. Similar to results obtained from sensitivity analyses performed by Van Schalkwyk and Potgieter [74] on a mean-field model, the model output was slightly more sensitive when the number of BCAs released was decreased than when it was increased. In order to minimise the average plant density in the case where BCAs may struggle to adapt in a new habitat or a disaster hits and a lot of them die (larger adult mortality, which consequently decreases I), it was recommended to release a slightly larger number of BCAs than the optimal number, as well as to release during the time of the year when the climate is optimal for the development of young larvae and the survival of adult weevils. Further analyses in §5.2.2 revealed that the total value of water saved is more sensitive at a lower constant temperature (25°C) than a higher one (30°C). In order to obtain maximum benefit, it was recommended to release BCAs during the time of the year when temperatures are as close as possible to optimum (30°C) in order to maximise the old larval damage rate, the oviposition rate, larval development rates, as well as survival rates, concurring with suggestions from Van Schalkwyk and Potgieter [74]. Suboptimal temperatures may significantly affect these parameter values, resulting in drastic decreases in the benefit obtained through biological control, in terms of water saving.

In Chapter 6, the model was applied to a real-world release site in order to illustrate how the model may be utilised to provide guidance towards suitable BCA release strategies, which will minimise costs and maximise the benefit for a specific site (in fulfillment of Thesis Objective V). The results of simulations performed on this domain were given in §6.3 – §6.5, with resulting recommendations in §6.6.

7.2 Main contributions

The main contributions of this study within the context of research on the biological control of water hyacinth in South Africa are discussed in this section.

1. *The development of a spatio-temporal model describing the water hyacinth and* N. eichhorniae *weevil interactions.*

   A reaction-diffusion model was applied to water hyacinth and *N. eichhorniae* weevil population growth, dispersal and interaction in a temporally variable and spatially heterogeneous environment. Although previous studies have started to examine the influence of temperature on the population dynamics of the two species and the control of the weed under constant conditions, the introduction of spatial dynamics is a new contribution. For the first time in research of biological control of water hyacinth, different BCA release strategies were compared by means of mathematical modelling to provide guidance towards how the weevils can be optimally utilised as BCAs in a spatially heterogeneous environment in South Africa.

2. *The construction of a complex spatially explicit stage-structured time-delay plant-herbivore model.*

   A complex two-species spatial model, with spatial terms for both species, incorporating stage structure, time delays, an Allee-effect, variable temperature and external additions to one of the species was developed. An encompassing expression for the time-delayed maturation term for the old larval stage, where there is diffusion and time delay simultaneously, was derived for the model in a bounded, two-dimensional spatial domain with homogeneous Neumann boundary conditions. This involved intricate spatial averaging. For simplicity's sake, studies in literature only demonstrate the derivation of the delay term for a one-dimensional domain, only mentioning that it should be possible to carry out numerical simulations in higher space dimensions. At the time of writing, the author could find no other examples in literature of a mathematical model incorporating such a range of complexities for two interacting species. This study therefore contributes to the body of knowledge by understanding the aspects involved in the modelling of interacting species in general, not just specific to the modelling of water hyacinth and weevil interactions.

3. *The derivation of suitable plant and weevil diffusion coefficients.*

   At the time of this study, no explicit measurements of the dispersal rates of the plant and weevil species over time could be obtained from literature. The derivation of suitable parameter values for the diffusion coefficients for water hyacinth and the mobile stages of the *N. eichhorniae* weevils from the limited information available on the respective dispersal patterns from previous studies, may therefore be deemed as a new contribution.

4. *The detailed description of the implementation of the spatio-temporal model in* MATLAB.

   The detailed discussion of the implementation of the spatio-temporal model in a bounded, two-dimensional spatial domain in MATLAB may aid as a valuable foundation for future implementations of mathematical models describing similar plant-herbivore interactions. At the time of this study, studies in literature in which the implementation of a two-species spatio-temporal model in a bounded, two-dimensional spatial domain was discussed, were very limited. The author addressed the challenge of implementing time-dependent solutions for partial derivatives and provided a method for implementing two-dimensional spatial averaging for a bounded domain by means of using the spatial averaging kernel for the unbounded case and manually accounting for the effect of each reflecting boundary. The implementation of frequent releases and fluctuating temperatures was also discussed.

5. *The construction of a cost-benefit function for water hyacinth biological control.*

A cost-benefit function was constructed, in which the cost of a specific BCA release strategy was compared to the benefit of that strategy, in terms of the value of water saved. The daily amount of water saved was measured in terms of the difference in evapotranspiration from the initial water hyacinth population, prior to the application of biological control, and the current water hyacinth population. In a recent study, only estimates of the average evapotranspiration from water hyacinth populations in the long term has been used in cost-benefit analyses. The contribution of a detailed daily measurement of the evapotranspiration from water hyacinth used in the cost-benefit analysis in this study provides a more accurate representation of the benefit that may be drawn from biological control of water hyacinth.

6. *Practical recommendations for efficient and cost-effective BCA release strategies in water hyacinth management.*

   Numerical and sensitivity analyses resulted in easily interpretable results and practical recommendations for BCA releases in water hyacinth infested areas, which include suggestions on when releases should be commenced, as well as the best frequency, distribution and magnitude of BCA releases, yielding cost-effective control of the water hyacinth weed in the Cape Town region. The model may easily be adapted to obtain release suggestions for other regions as well. Analyses further provided target values for the cost per BCA which may yield economically viable results for researchers when the value of water saved is considered as a benefit of biological control.

7.3 Possible future work

Several suggestions are made with respect to possible future research emanating from the work presented in this thesis (in fulfillment of Thesis Objective VI).

7.3.1 Recommendations for future entomological research

The collection of more thorough field data or data from laboratory experiments may assist to more accurately estimate some of the parameter values assumed in the spatio-temporal model presented in Chapter 4.

Investigate the movement behaviour and dispersal rate of *N. eichhorniae* weevils

The model presented in this study assumes that, based on previous studies [91] and field observation, only the old larval and adult stages of the weevil's life cycle are mobile. At the time of this study, information regarding the effectiveness with which old larvae and adult weevils disperse between neighbouring locations was limited. The old larval diffusion coefficient was derived from a study by Wilson [91] in which the observation was made that third instar larvae move between plants with a probability of $p = 0.065$, independent of plant size or nutrients, while the adult diffusion coefficient was derived from a study by Haag [30] where it was observed that, even in the absence of flight muscles, adult weevils are able to move between adjacent plants over a distance of at least 4 m in a course of one month. Information about adult movement over longer distances is still lacking. The studies, however, did not explicitly measure dispersal rates over time, and therefore the assumed values for the diffusion coefficients used in this thesis are only rough estimates. In order to incorporate a higher level of biological realism into the model, more information with respect to the possible range of movement, as well as how fast weevils disperse over some spatial domain and how it is influenced by temperature, is required.

Measure the Allee-effect threshold

At the time of this study, no experimental values were available for the Allee-effect threshold and a conservative minimum threshold for weevil reproduction of $a = 3$ adults/m^2 had to be assumed. More information on the minimum required number of BCAs/m^2 for reproduction is needed in order to be able to measure the efficiency of different BCA release strategies more accurately.

Acquire more in-depth information on the old larval damage rate and density-dependent factor

Parameter values for the rate of damage caused by old larvae, $c_{L_2}(\theta)$, and density-dependent scaling factor, J_{L_1}, were obtained from previous studies by Wilson [91]. These values, however, were only estimates. While the addition of stage-specific processes makes the model more biologically realistic, the accuracy of the model may be improved when more information on these parameters is obtained.

7.3.2 Recommendations for possible future modelling work

During the construction of the mathematical model presented in Chapter 4, simplifying assumptions were made in order to describe a part of a real-world process. The model should therefore not be considered as a complete or exact representation of real-world water hyacinth and weevil interactions, but rather as an approximation. The model may be refined by improving on the assumptions made or using better techniques or modelling approaches. Possible future modelling work may include the following suggestions.

Incorporate stochasticity into temperature fluctuations

The growth, oviposition, damage, development, survival, mortality and evaporation rates used in the model are temperature dependent. In this study, however, a constant average temperature was assigned to each month without any fluctuations within a given month. The temperature on a specific day may rather be estimated by means of a probability distribution of temperature for each month.

Incorporate long-range dispersal of water hyacinth and adult weevils

The spatio-temporal model developed in Chapter 4 assumes only local dispersal of water hyacinth and adult weevils within a bounded, isolated, continuous spatial domain, while no dispersal between different spatial domains was considered. During certain seasons or under specific physiological conditions, *N. eichhorniae* adult weevils may develop flight muscles and be able to fly and migrate between different spatial domains infested with water hyacinth [16, 26, 65]. This seems to be quite rare and, even after extensive research, the exact factors influencing wing muscle development remain difficult to pinpoint [7]. Furthermore, wind, water streams, boats, birds and other animals may unintentionally assist in spreading water hyacinth plants into other areas [37, 69]. Although it is reasonable to assume local dispersal of water hyacinth and adult weevils, some individuals may disperse over considerable distances across different domains. A case of possible immigration of *N. eichhorniae* adult weevils to a study site in Texas from nearby (60 m) areas infested with water hyacinth has been reported [26]. An understanding of the development of flight muscles is necessary to be able to manage weevils effectively. Adjustments may be made to the model in order to account for the possibility of plant and weevil dispersal between fragmented landscapes.

Investigate alternative modelling approach for distinct stages of growth and dispersal

The reaction-diffusion model presented in Chapter 4 assumes plant growth and dispersal, as well as weevil reproduction and dispersal, occur simultaneously. Reaction-diffusion models have been successfully used to model the spread of plant and animal populations [55]. However, for populations where the stages of dispersal and reproduction are clearly distinguished and occur at discrete intervals, reaction-diffusion models appear to give unrealistic representations of the population dynamics. In these cases, another type of mathematical model based on integro-difference or integro-differential equations[1] may yield a more realistic description of the spatial dynamics [55]. In these models, an integral represents dispersal or interaction between spatial locations. A weight function (known as a kernel), describing the relative importance of nearby individuals compared with distance ones, is assigned to the integral [46]. When model assumptions are adjusted to incorporate the possibility of distinct stages of reproduction and dispersal for both plant and weevil, the use of an integro-differential equation modelling approach may be investigated in order to accurately represent these discrete processes.

Explore new options for the locations of recurring releases

The frequent release approach adopted in this study consists of re-releasing BCAs at constant points in the domain for as long as there exist sufficient plant densities before releasing at a neighbouring position. Since numerical solutions in Chapter 5 indicated that density dependence limits the success of biological control release strategies when large numbers of *N. eichhorniae* weevils occur at the same position, it may be insightful to explore the outcome of avoiding previous points of release as far as possible by performing recurring releases at different positions of the domain instead of at the same location until the weed is eradicated at that location, aiming to get as close as possible to a uniform distribution of BCAs across the water hyacinth infested area, while still accounting for accessibility constraints.

Expand on the characteristics of the domain

In this study, only domains of rectangular shape are considered as representative approximations of the considered water hyacinth infested areas. In order to expand on realism, the model may be adapted to incorporate domains of different shapes or fragments, where the large, continuous domain is divided into a number of smaller patches of lower total area, isolated from each other by areas of dissimilar habitat. The use of geographic information system (GIS) to import detailed spatial and geographical data of a specific release site may be considered.

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[1] An integro-differential equation is an equation that involves both integrals and derivatives of a function [89].

Quantify and incorporate further benefits of biological control

Besides the gains to be obtained from the effective control of water hyacinth in terms of water saving, there are many other advantages, which include the conservation of biodiversity, increased catchment stability, a greater potential for ecotourism, reduction in health risks and direct job creation through the control programmes [42]. These benefits are difficult to quantify and, until now, the total economic and socio-economic benefits of water hyacinth control programmes are yet to be adequately described in economical terms [73]. The incorporation of further benefits pertaining to the control of water hyacinth in the cost-benefit analysis presented in this study may support a more comprehensive assessment of cost-effective biological control strategies, as well as a demonstration of the full socio-economic worth of control programmes, which in turn may validate the continued funding of such programmes.

Determine the existence of equilibrium states and/or limit cycles in the system

Due to the complexity of the model presented in this study, the equilibrium states, where the population densities remain unchanged over time, are yet to be determined. Seasonal variation may mean that the densities observed are not the same as the equilibrium densities that would be observed in a stable environment. The existence of limit cycles, wherein the population densities undergo well-defined cyclic changes in time with fixed amplitudes [45], may also be an insightful subject of investigation.

Consider integrated control strategies

In practice, two or more control methods are often applied in an attempt to achieve better control of water hyacinth. In South Africa, integrated control of water hyacinth often consists of a combination of biological and herbicidal or mechanical control. Herbicide application and mechanical removal programmes are known to limit the success of biological control by removing the BCA populations along with the water hyacinth infestations. When cleared or treated water bodies are re-infested after these removals, the enemies are absent, resulting in rapid and abundant growth of the weed [31, 32, 81]. The incorporation of integrated control strategies into the mathematical model may aid in determining the optimal, most cost-effective combination of control methods.

Adapt model to compare the effect of different BCAs

The model presented in this study only considers the interaction between water hyacinth and the *N. eichhorniae* weevil as BCA. The model may be adapted for different water hyacinth BCA species in order to evaluate the efficiency of and determine cost-effective release strategies for different BCAs in the control of water hyacinth.

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