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Mind the gap: the delayed recovery of a population of the biological control agent *Megamelus scutellaris* Berg. (Hemiptera: Delphacidae) on water hyacinth after winter

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Abstract

Cold winter temperatures significantly affect the biological control effort against water hyacinth, *Pontederia (= Eichhornia) crassipes* Mart. (Pontederiaceae), in more temperate regions around the world. The population dynamics of the planthopper *Megamelus scutellaris* Berg. (Hemiptera: Delphacidae), a newly released biological control agent of water hyacinth, were recorded on the Kubusi River in the Eastern Cape Province (South Africa) over 15 months to determine the population recovery post-winter. *Megamelus scutellaris* incurred a severe population decline at the onset of winter when the water hyacinth plants became frost damaged. The combined effect of a population bottleneck and low minimum winter temperatures (6.12°C) below the agent's lower developmental threshold (11.46°C) caused a post-winter lag in agent density increase. Subsequently, the maximum agent population density was only reached at the end of the following summer growing season which allowed the water hyacinth population to recover in the absence of any significant biological control immediately post-winter. Supplementary releases of agents from mass-reared cultures at the beginning of the growing season (spring) is suggested as a potential method of reducing the lag-period in field populations in colder areas where natural population recovery of agents is slower.

Introduction

Water hyacinth (*Pontederia* (= *Eichhornia*) *crassipes* Mart. (Pontederiaceae), Pellegrini *et al*., (2018)) is a free-floating perennial aquatic weed that has become invasive in many waterways in the tropical, subtropical and some temperate regions of the world, including South Africa. Water hyacinth is considered the most damaging aquatic weed and is included among the world's 100 worst invasive species (Lowe *et al*., 2000). The plants grow vegetatively to form dense mats, which lead to reduced aquatic biodiversity due to shading and subsequent lowered dissolved oxygen concentrations in the water column (Midgley *et al*., 2006; Coetzee *et al*., 2014). Water hyacinth reduces water quality through the build-up of sulphur dioxide beneath the mats, and quantity through evapotranspiration, putting great stress on water resources, particularly in water-scarce countries such as South Africa (Fraser *et al*., 2016; Arp *et al*., 2017).

Attempts to combat the spread of water hyacinth have led to the implementation of biological control programmes in many countries around the world, including Papua New Guinea, the USA, China and South Africa (Cofrancesco *et al*., 1985; Cilliers, 1991; Julien and Orapa, 1999; Jianqing *et al*., 2001) where the most commonly released biological control agents are the two congeneric weevils, *Neochetina eichhorniae* Warner and *N. bruchi* Hustache (Coleoptera: Erirhinidae). While the weevils are effective in tropical regions of the world (Julien and Orapa, 1999; Cock *et al*., 2000), successful control is limited in cooler, more temperate areas where water hyacinth has invaded, prompting importation and release of additional agents in these regions. In South Africa, a further seven biological control agent species (including several arthropods and a pathogen) have been released (Cilliers, 1991; Hill and Coetzee, 2017), but despite this high number, success has been limited compared to other countries. The high nutrient status of the rivers and dams in South Africa, which are among the most eutrophic in the world, significantly enhance the rate of water hyacinth growth, thus reducing the impact of the current suite of biological control agents (Coetzee and Hill, 2012). Reductions in the populations of established biological control agents also occur in response to the improper, or overuse of non-specific chemical herbicides, as well as from stochastic events such as flooding. In these situations, plants with agents are removed,

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but infestations regenerate from seeds in the absence of biological control agents (Hill and Olckers, 2001; Coetzee *et al.*, 2011).

In addition, Hill and Olckers (2001) identified cold winters as having a significant negative impact on the successful biological control of water hyacinth. Cold weather offers a significant metabolic challenge to insects and decreases in temperature can lead to reduced survival, fecundity and feeding frequency (Kingsolver, 1989). Certain parts of the USA, such as California, Louisiana and Texas have documented that cold winters are deleterious to control efforts (Grodowitz *et al.*, 1991; Moran *et al.*, 2016). Further, Coetzee *et al.* (2009) concluded that the mirid, *Eccritotarsus catarinensis* (Carvalho) (Hemiptera: Miridae) would not be suitable for release in parts of the USA above 35°N latitude, as the severe winter temperatures would significantly limit the survival of the insects. Biological control agents of water hyacinth introduced from the tropical areas of South America experience a climatic mismatch in some regions of their introduced range, and this is expected to have a negative effect on their establishment and population growth during the winter in temperate regions (Byrne *et al.*, 2010). Furthermore, as the growing season ends, the nutritional quality of the host-plants declines, and in areas prone to frost, water hyacinth leaves turn brown and die. This winter dieback leaves only the crown of the plant and its submerged roots intact, removing a significant proportion of the available food supply and habitat for the host-specific herbivores (Madsen *et al.*, 1993). The combined effect of low temperatures and poor food quality leads to high levels of mortality among biological control agents, causing seasonal population bottlenecks. As a result, few to no progeny are produced over winter and, hence, agent populations in frost-affected areas typically only reach damaging levels near the end of the growing season (Hill and Cilliers, 1999). This lag-period means that water hyacinth can regrow rapidly during spring and summer with limited impact from biological control (Hill and Cilliers, 1999).

To account for stochastic changes and seasonal variation, new agents which have shorter generation times to build-up populations rapidly post-winter have been targetted. *Megamelus scutellaris* Berg. (Hemiptera: Delphacidae), a host-specific natural enemy of water hyacinth collected from Argentina, was found to be most likely to fulfil the required niche and was tested for host-specificity and cleared for release in the USA in 2010 (Tipping *et al.*, 2011; 2014), and in South Africa in 2013 (Coetzee, 2013). *Megamelus scutellaris* is a multivoltine phloem-feeding insect with a short generation time and overlapping generations (Sosa *et al.*, 2005; 2007). Studies have shown that *M. scutellaris* is highly effective as a biological control agent in both greenhouse experiments and field settings (Coetzee, 2013; Moran *et al.*, 2016; Miller *et al.*, 2019). However, research on the thermal tolerance of this species conducted by May and Coetzee (2013) concluded that *M. scutellaris* was climatically incompatible with certain high altitude sites around South Africa, which experienced cold winters with frosting events. On the other hand, Tipping *et al.* (2014) noted that, while *M. scutellaris* performed poorly in areas in the USA with very hot summers, the agent has overwintered for at least 3 consecutive years in Gainesville, Florida (29°22′51.9″N 82°13′20.6″W) despite multiple days of below-freezing winter temperatures.

This study aimed to monitor *M. scutellaris* population dynamics in a cold temperate region of South Africa to determine its response to cold winters and the subsequent recovery in the following spring and summer. The Kubusi River in the Eastern Cape Province (South Africa) was selected because it is the water hyacinth biological control site in the country that experiences the coldest winters (Byrne *et al.*, 2010), and it was the first field site where *M. scutellaris* was released in South Africa and has persisted since that time (pers. obs.). Based on the results, improved management strategies that counter the effects of cold temperatures on water hyacinth biological control in cooler regions of the world can be developed.

Materials & methods

Study site

The Kubusi River, near Stutterheim in the Eastern Cape of South Africa, (32°33′54.0″S 27°29′21.1″E; 774 m AMSL) is heavily infested with water hyacinth, often experiencing 100% cover in the summer. Since the late 1990s, release efforts at the Kubusi River facilitated the establishment of permanent, self-perpetuating populations of the biological control agents *E. catarinensis* and both water hyacinth weevil species, *N. eichhorniae* and *N. bruchi*. This is the coldest site where biological control agents have established on water hyacinth in South Africa making this site thermally important (Byrne *et al.*, 2010). The climate of the area is characterized as temperate (minimum mean temperature = 5.09°C; maximum mean temperature = 27.22°C), with year-round rainfall and cold winters which can experience up to 56 days of frost each year (Byrne *et al.*, 2010).

Data collection

The site was sampled monthly for 15 months from May 2017 until August 2018. Plant and insect data were collected from the same site on the system each month and the data were compared with temperature and rainfall data received from the nearby Dohne Weather Station approximately 3 km away from the study site (fig. 1) (S 32°32′02.4″ E 27°28′01.2″, 901 m AMSL) (www.weathersa.co.za). A study by Coetzee (2012) concluded that the microclimate at the Kubusi River and the Dohne Weather Station climate were not significantly different and, therefore, these data could be used as a proxy for the climate at the study site.

Plant health and fecundity measurements

The population structure and establishment potential of a biocontrol agent are determined, in part, by the quality and quantity of its host plant. Therefore, plant parameters were measured monthly from ten randomly selected water hyacinth plants from within the site. The measured plant parameters were adapted from Coetzee and Hill (2012) and included: (1) the length of the longest live petiole, which is a measure of plant height, (2) total root length which is an indication of nutrient status and intra-species competition, (3) the number of ramets (daughter plants) which determine the extent of clonal reproduction, and (4) the number of photosynthetically active leaves on each plant, which is a measurement of host-plant quality and as a determinant of possible feeding sites for *M. scutellaris*. Feeding damage is difficult to detect at the plant level at agent densities recorded over the study period, particularly in high nutrient water (Miller *et al.*, 2019), therefore damage was not measured in this study as the focus of the study was the population dynamics of the insect, in particular after winter. A thorough post-release

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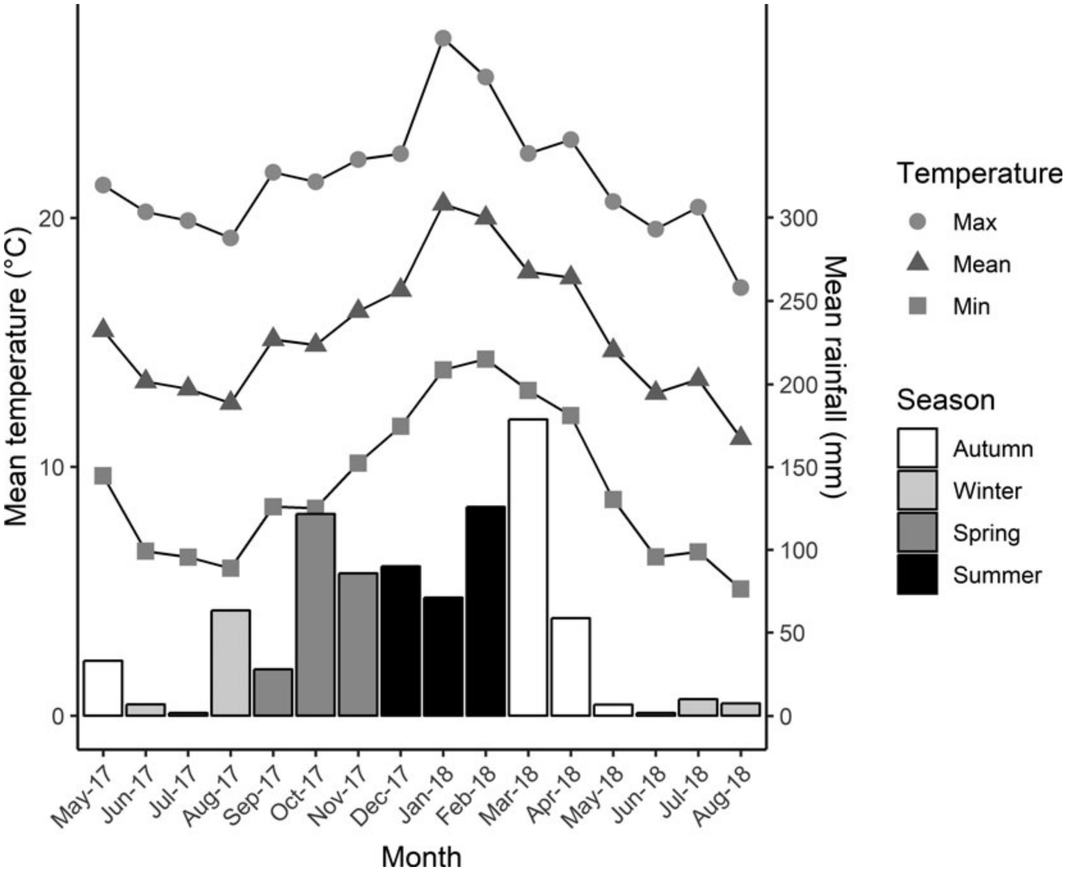

Figure 1 Monthly minimum, maximum and mean temperature (lines) and total monthly rainfall (bars) by season from the Dohne Weather Station near the Kubusi River throughout the study.

evaluation is currently being conducted on this agent in South Africa, and this study forms part of the larger study.

Each month, three randomly selected 0.25 m^2 quadrats of biomass were also removed from within the water hyacinth mat (see online supplementary material fig. 1), and the contents of each quadrat were separated into above water biomass (green leaves and petioles), below water biomass (roots) and dead biomass and these were weighed to determine the wet weight per unit area. The number of individual plants per quadrat was also recorded.

Megamelus scutellaris *population measurements*

The density of *M. scutellaris* present at the site on the Kubusi River was determined using a purpose-built sampler (see online supplementary material fig. 2), which was adapted from the 'Minteer Method' (C. Minteer, unpublished) which has been used to measure aquatic insect numbers on floating aquatic macrophytes in the USA. The sampler used here was devised from a 70 L black plastic bin from which the bottom was removed and into which a thin metal wire cross-wise frame was built. The sampler was placed over water hyacinth plants in the water and pushed down, submerging the plants. The wires kept the plants underwater, allowing *M. scutellaris* nymphs and adults present on the water hyacinth to float up onto the water's surface and the side of the bucket where they could be counted. No differentiation was made between the nymphs or adults in the analysis. This was repeated 10 times in different parts of the site at wading depth at intervals of approximately between 5 and 10 m. The sample size was considered representative of the population as water hyacinth is a uniform clonal species. Standard errors of the mean plant growth parameters were within 5% of each other confirming that measuring ten plants were representative of the population. Data on other biological control agents present on the water hyacinth were recorded, but these data form part of a long-term study which was not the focus of this study. Research has shown that there are no negative interactions between *M. scutellaris* and the different species of biological control agents on water hyacinth (Petela, 2018).

Statistical analyses

All statistical analyses were completed using RStudio v 3.4.3 (R Core Team, 2017). To find a comparative method of measuring the insect density, the data were transformed from a measure of insects per sample to insects m^{-2} by equating the circular area of the base of the sampler to a square metre, yielding a conversion factor of

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

According to the Shapiro–Wilks test for normality, the data were not normally distributed, so non-linear statistics apply. The data were analyzed using a negative binomial generalized mixed-effects model (GLMM) (Bolker *et al.*, 2009) to determine

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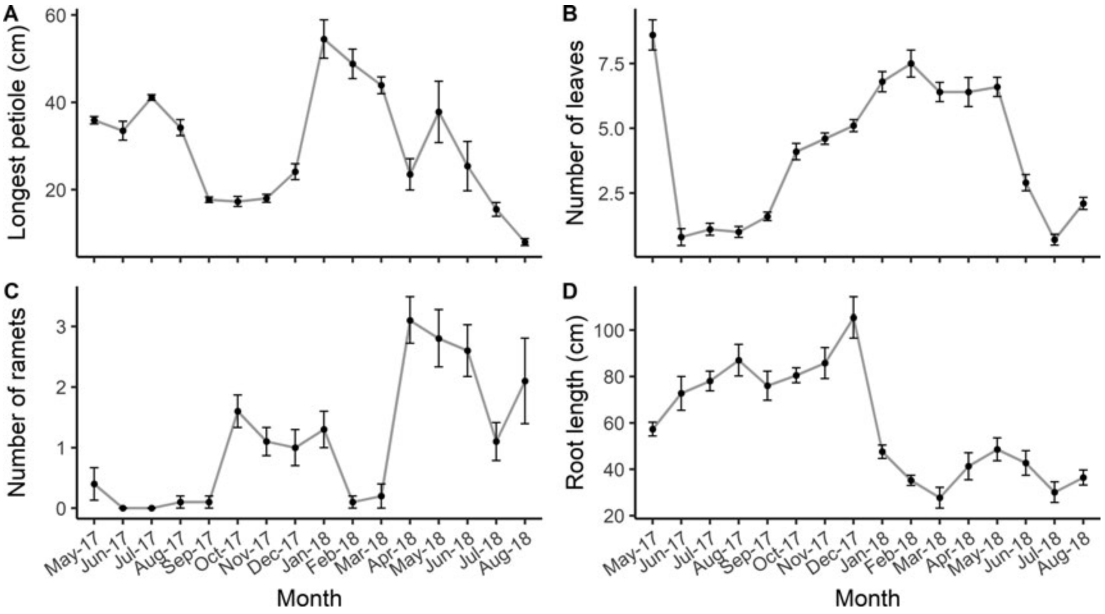

Figure 2 Mean (a) length of the longest petiole (cm), (b) number of leaves per plant, (c) number of ramets per plant and (d) root length of water hyacinth plants in the Kubusi River between May 2017 and August 2018. Error bars = ± S.E.

how climate and the availability of food (number of leaves) impacted the density of *M. scutellaris.* Month was specified as a random effect as the data were collected from the same site over many months. The fixed effects included the minimum temperature, season and the number of leaves on each plant. The most supported model was selected using a stepwise backward selection process and AICc scores (Burnham &Anderson, 2002) and models were considered if they were within 7 AICc points of this model (ΔAICc = 0). In addition, for every extra parameter added to the model (K), 2 AICc points were added to account for potential overfitting of the model. Model diagnostics checks performed in the 'DHARMa' package in R (Hartig, 2020), indicated that the model specification was appropriate. The log-likelihood values were also used to determine the maximum likelihood of the model.

Results

Plant population dynamics

Over the 15-month sampling period, the length of the longest petiole fluctuated greatly depending on the season. On average, the plants were tallest during mid-summer, January 2018 (54.48 ± 4.38 cm) and shortest during late winter, August 2018 (8.00 ± 0.80 cm) (fig. 2a). The mean number of leaves per plant was greatest in May 2017, with a mean of 8.6 ± 0.58 leaves per plant. However, in both years, leaf number decreased rapidly after May as a result of frosts in June, reducing the number of viable leaves in the canopy to the annual minimum of 0.8 ± 0.33 leaves per plant. The annual minimum in 2018 occurred a month later than in 2017, with 0.7 ± 0.21 leaves per plant in July 2018 (fig. 2b).

The ramet production was reduced to almost zero over the winter of 2017, with only a few plants bearing any daughter plants. However, the number of ramets produced over the winter of 2018 was much higher, with a mid-winter mean of 2.8 ± 0.47 and 2.6 ± 0.43 ramets for May and June 2018 respectively, whereas only 0.4 ± 0.27 were recorded during May 2017, and none in June 2017 (fig. 2c). The highest number of ramets were recorded in April 2018, with a mean of 3.1 ± 0.38 ramets per plant. Root length varied over time and between seasons. The longest roots were recorded in December 2018, during mid-summer (105.28 ± 8.78 cm), while the shortest roots occurred in late summer, March 2018, at 27.7 ± 4.48 cm (fig. 2d).

The above water biomass peaked in January 2018. At the highest point, the above water biomass was 15.67 ± 3.84 kg m^{-2} (fig. 3a). There was a marked decrease in the above water biomass as winter set in, leading to annual minima of 4.33 ± 0.88 kg m^{-2} in October 2017 and 2.07 ± 0.52 kg m^{-2} in August 2018. However, the below water biomass, which is an indicator of nutrients and intraspecific competition, was variable between months, but there was a generally decreasing trend in the root biomass throughout the study. The maximum root biomass of 12.67 ± 3.53 kg m^{-2} was measured in June 2017, decreasing steadily to a mean minimum in August 2018 of 1.87 ± 0.92 kg m^{-2} (fig. 3b). The lowest root biomass also coincided with the lowest above water biomass in August 2018.

Old leaves and petioles that had senesced or been damaged by winter frosts formed the dead biomass. The amount of dead biomass present at each sampling interval was variable and did not follow a seasonal trend. The mass of dead material did, however, decrease sharply in January 2018 to 2.13 ± 0.58 kg m^{-2}, which coincided with a marked increase in live biomass (fig. 3c). The least dead biomass was recorded in July 2018 (0.13 ± 0.13 kg m^{-2}), and the greatest mass of dead material was recorded equally in June and November 2017, both measuring 7.67 kg m^{-2} (±1.45 and ± 0.33 respectively) (fig. 3d).

The highest density of plants was recorded during December 2017, with 74.67 ± 9.33 plants m^{-2}, while the lowest plant density occurred at the end of winter in August 2018, with only 28.00 ± 4.00 plants m^{-2}. Both the number of leaves per plant ($y = 0.72x - 2.5$, $F_{1,14} = 25.85$; $P < 0.001$; $R^2 = 0.62$) and the above water biomass ($y = 0.76x - 0.3$; $F_{1,14} = 14.16$; $P = 0.002$; $R^2 = 0.47$) were significantly correlated with the minimum recorded temperature

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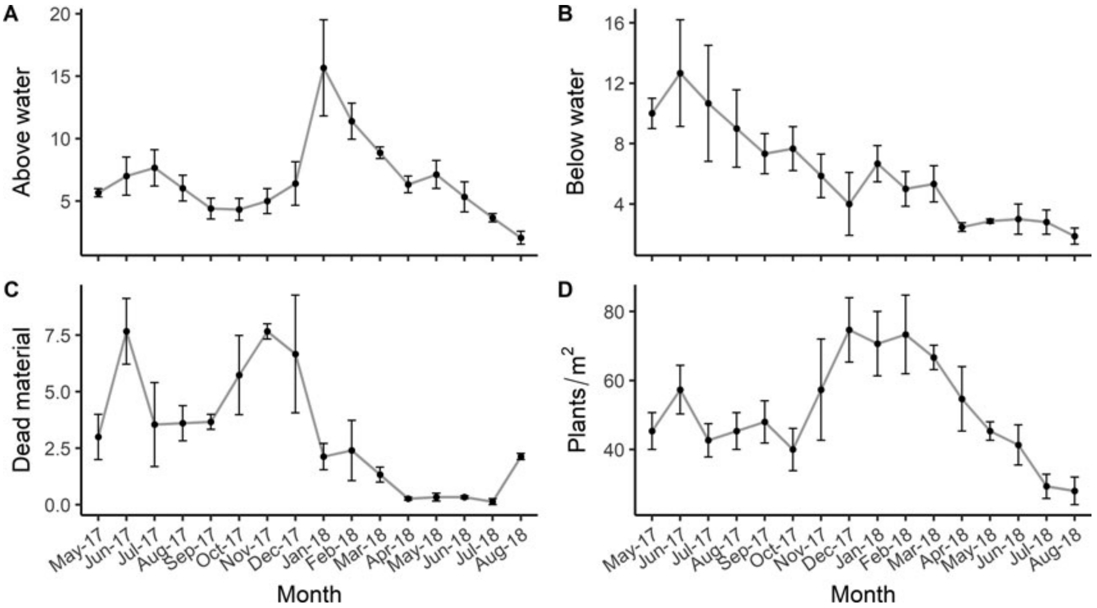

Figure 3 Mean (a) above water biomass (kg m^{-2}) (b) below water biomass (kg m^{-2}), (c) dead biomass (kg m^{-2}) and (d) number of plants m^{-2} of water hyacinth plants in the Kubusi River between May 2017 and August 2018. Error bars = ± S.E.

(see online supplementary material fig. 3). In this instance, we used the minimum temperature as it is a limiting factor to the growth of both *M. scutellaris* and water hyacinth.

Seasonal interactions between insect and plant populations

The number of insects per square metre followed seasonal and climatic trends. During the spring of 2017, the insect density was low (mean numbers of insectsm^{-2} ranging between 0 and 1.08 insects between September and December 2017) (fig. 4). By April 2018, late summer/early autumn, the insect numbers had increased to their maximum recorded density of 605.34 ± 111.91 insects m^{-2}. The insect numbers were also higher in the winter months of 2018 than they were in the winter of 2017, with a mean of 11.47 ± 3.92 insects m^{-2} in 2017 compared to 230.45 ± 16.57 insects m^{-2} in 2018.

The change in the density of *M. scutellaris* was associated with both the number of leaves per water hyacinth plant and the above water biomass (fig. 4a). The number of leaves increased rapidly post-winter, showing signs of recovery between September and October 2017, while the *M. scutellaris* population recovery lagged until it reached a maximum population density in April 2018 (fig. 4a). Biomass decreased initially in early summer as the new plants began to grow, but, by the late summer, the biomass rapidly increased (fig. 4b). Importantly, the maximum density of *M. scutellaris* lagged until after the biomass and the number of leaves had reached their maxima. Both the insect density and the number of leaves declined sharply at the start of winter in June of 2017 and 2018. Biomass began to decline in autumn, prior to the first frosts.

The best-supported model determined that season was the most influential variable affecting the density of *M. scutellaris* at the Kubusi River (Table 1) (see online supplementary material Table 1 for AIC table). Between seasons, the density of *M. scutellaris* was 876% higher in autumn than in summer ($z = 2.425$, $P = 0.015$) (fig. 5), while winter densities were 248% higher than summer ($z = 0.856$, $P = 0.392$), but this was not a significant difference according to the model. Density decreased significantly between summer and spring, reducing insect populations by 99% ($z = -2.601$, $P = 0.009$).

Discussion

Understanding how biotic and abiotic factors influence the population dynamics of a biological control agent is key to the success of invasive plant management programmes. The results of this study indicate that the population of *M. scutellaris* varies over time and between seasons. Even though the season was the most influential factor affecting the population density of the insect at the Kubusi River, changing seasons also have a direct impact on the growth and quality of the host plant, both of which directly affect the post-winter recovery of host-specific insect herbivores. Host plant quality was considerably reduced in the winter, particularly with the onset of frost, which had deleterious effects on plant vigour and leaf quality. Grodowitz *et al.* (1991) found the same trend with the onset of winter in Texas, which lead to a dramatic decrease in the population of the weevil *N. eichhorniae* from a maximum population density of 55 weevils m^{-2} to a minimum of 8 weevils m^{-2} for 5 months, however, *N. eichhorniae* were found to overwinter as larvae, and larval populations increased over winter.

Although low winter temperatures negatively affect both water hyacinth and *M. scutellaris*, the water hyacinth plants were able to recover more rapidly at the Kubusi River. However, the population of *M. scutellaris*, which was significantly reduced each winter by a severe winter bottleneck, was unable to mirror the rapid population growth rate of its host plant until later in the growing season, by which time the plants were able to recover with only a negligible impact from biological control. The mirid *E. catarinensis* and both water hyacinth weevil species, *N. eichhorniae* and *N. bruchi*, also only re-emerged after an extended post-winter lag-period, with adult mirids and weevils only modelled to emerge by late October (Byrne *et al.*, 2010). This is a 2-month lag between the onset of spring and the recovery of the natural enemy

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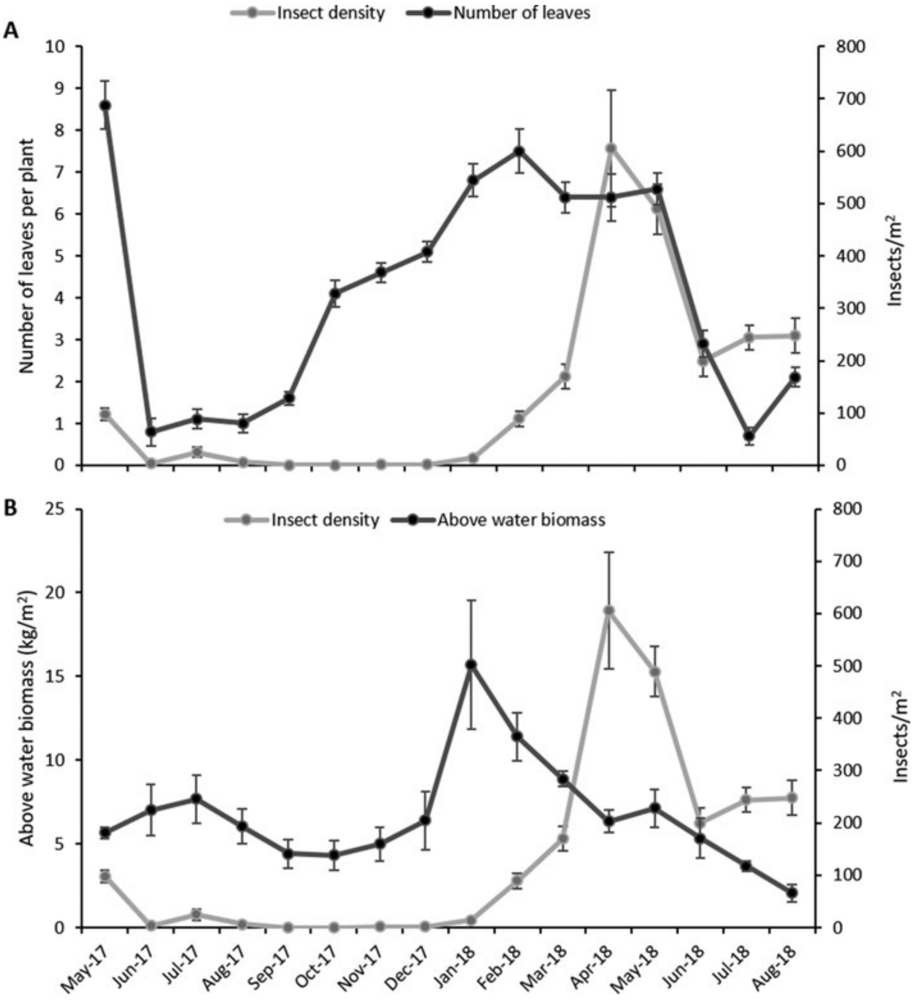

Figure 4 The relationship between *Megamelus scutellaris* density, (a) leaf number and (b) above water biomass on Kubusi River between May 2017 and August 2018. Error bars indicate S.E.

Table 1. Fixed effect variables in the best supported negative binomial generalized mixed-effects model for *Megamelus scutellaris* density. Values in bold are significant ($P < 0.05$).

	Estimate	Standard error	*z*-value	*p*-value
Intercept	2.815	0.891	3.158	**0.002**
Autumn	2.792	1.152	2.425	**0.015**
Winter	0.921	1.077	0.856	0.392
Spring	−4.345	1.671	−2.601	**0.009**

Month was specified as a random effect to account for non-independence between monthly surveys.

populations (Byrne *et al*., 2010). Elsewhere, it has been found that *M. scutellaris* was able to overwinter successfully through multiple winters at cooler sites in California in the western USA, as well as in Florida, despite several nights where temperatures were below freezing (Tipping *et al*., 2014; Moran *et al*., 2016). Successful establishment was more likely if there was riparian vegetation offering shaded areas to the insects to buffer the effects of rapid diel temperature fluctuations (Tipping *et al*., 2014).

The lag-period in post-winter recolonization by biological control agents was initially proposed by Hill and Olckers (2001) to be a hindrance to all of the water hyacinth natural enemies released in South Africa, as well as being one of the reasons that complete control of water hyacinth has not yet been achieved through biological control. These results document this relationship for the first time in the field and are an indicator of the accuracy of the predictions which suggested that biological control agent populations that are reduced by cold winters will only recover completely nearer the end of the growing season. The lower developmental threshold (t_0) reported by May and Coetzee (2013) for *M. scutellaris* is 11.458 °C, below which development ceases. However, the minimum temperature did not exceed t_0 between May 2017 and December 2018, and only between January and April 2018 was the mean temperature high enough to facilitate the development of *M. scutellaris*. This short period of development time also coincides with, and may explain, the greatest increases in the populations of the insects at the Kubusi River. The results of a similar study which monitored the seasonal population density of both *Neochetina* species on the Kubusi River closely reflected those presented here, where the adult weevil density remained at or near zero over winter and peaked during late summer and early autumn, only to collapse again with the first frosts (Byrne *et al*., 2010). The same trend was reported by both Moran *et al*. (2016) and Hopper *et al*. (2017) who found *M. scutellaris* population densities to be temperature-dependent in California, peaking between October and November. The peak in density coincided with late summer/early autumn in the northern hemisphere, and the population declined again over winter when temperatures were close to the reported t_0. Hopper *et al*. (2017) also

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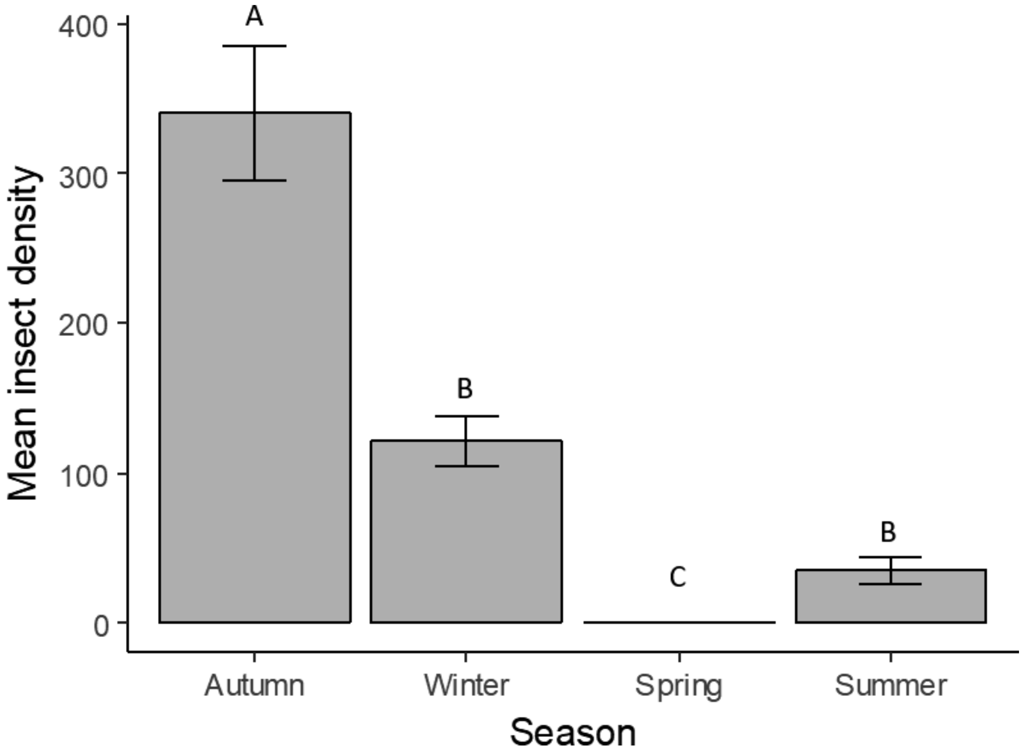

Figure 5 Seasonal mean insect density m^{-2} at the Kubusi River between May 2017 and August 2018. Error bars indicate S.E. Significant differences are indicated by a different letter ($P < 0.05$).

determined that, among other water hyacinth biological control agents, the presence of a climatic mismatch as well as the lag phase in post-winter agent recovery are major factors responsible for biological control efforts on water hyacinth not being as successful in the USA as in other parts of the world.

However, one of the major benefits of using *M. scutellaris* as a natural enemy of water hyacinth in South Africa is that it is multivoltine with a fast generation time (Sosa *et al.*, 2005; 2007). Yet, the low temperatures experienced by these insects in the field still has the effect of prolonging their developmental time to as much as 65.6 days (at 19°C) from egg to adult, where, under ideal conditions, *M. scutellaris* can complete its development in 39.42 days at 27°C (May and Coetzee, 2013). Furthermore, from observations in the field, *M. scutellaris* was often the first biological control agent to appear post-winter, and in the greatest numbers – particularly after major environmental disturbances, such as drought. *Megamelus scutellaris* is able to co-exist with other biological control agents, and can even increase the damage caused by other agents (Petela, 2018). Therefore, competition is unlikely to be the reason that *M. scutellaris* was able to recolonize faster than the other water hyacinth biological control agents at the site. Furthermore, evidence from sites in California suggests that the presence of *M. scutellaris* contributed to a 27% reduction in overall leaf number on water hyacinth at a temperate site in Folsom, California, USA (Moran *et al.*, 2016). Additionally, *M. scutellaris* has been shown to vector phytopathogenic fungi which contribute to reduced plant biomass and daughter plant production (Sutton *et al.*, 2016).

This study has determined that *M. scutellaris* can overwinter successfully in the coldest water hyacinth biological control site in South Africa and that our results are consistent with those recorded in temperate sites in the northern hemisphere. Furthermore, overwintering populations faced a significant lag-period before their densities built up to a sufficient size in the late summer, as a result of temperatures below the developmental threshold of the insect, as well as due to the reduction of above-water plant biomass and leaf tissue as a food source over winter. Certain factors, such as fewer frost days, can lead to small populations of *M. scutellaris* remaining throughout the winter (pers. obs), thus reducing the bottleneck effect and allowing faster post-winter population increases. However, emphasis needs to be placed on understanding the anthropogenic drivers of water hyacinth invasions, such as eutrophication and excessive herbicide application (Coetzee & Hill, 2012; Hill *et al.*, 2012).

We recommend that, where water hyacinth is present in temperate regions of the world, augmentative releases of biological control agents should be made in early spring as soon as the plants show signs of recovery (September–October) to reinforce existing overwintering populations and reduce the effect of the lag-periods between the onset of the plant growing season and the increase in the biological control agent populations. Long-term post-release evaluations, in turn, are required at these sites to monitor population numbers so that successes can be recorded and biological control agent populations can be monitored and manipulated if needed.

Supplementary material. The supplementary material for this article can be found at http://doi.org/10.1017/S0007485320000516

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conclusion or recommendation expressed in this material is that of the authors and the NRF does not accept any liability in this regard. The authors also acknowledge gratefully the assistance of Mr Z Maseko for his assistance in the field, and Dr G Sutton for his valuable advice and assistance with the statistical analyses.

References

Arp RS, Fraser G and Hill MP (2017) Quantifying the economic water savings benefit of water hyacinth (*Eichhornia crassipes*) control in the Vaalharts irrigation scheme. *Water SA* **43**, 58–66.

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH and White JS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* **24**, 127–135.

Burnham KP and Anderson DR (2002) *Model Selection and Multimodel Inference*. New York, NY: Springer New York.

Byrne M, Hill MP, Robertson M, King A, Jadhav A, Katembo N, Wilson J, Brudvig R and Fisher J (2010) Integrated Management of Water Hyacinth in South Africa: Development of an integrated management plan for water hyacinth control, combining biological control, herbicidal control and nutrient control, tailored to the climatic regions of South Africa. *Water Research Commission TT 454/10*, 1–302.

Cilliers CJ (1991) Biological control of water hyacinth, *Eichhornia crassipes* in South Africa. *Agriculture, Ecosystems & Environment* **37**, 207–217.

Cock MJW, Day R, Herren H, Hill MP, Julien MH, Neuenschwander P and Ogwang J (2000) Harvesters get that sinking feeling. *Biocontrol News and Information* **21**, 1–8.

Coetzee JA (2012) Meteorological weather station data can be used in climate matching studies of biological control agents. *Biocontrol Science and Technology* **22**, 419–427.

Coetzee, J.A. (2013) Permission to release the planthopper, *Megamelus scutellaris* Berg. (Hemiptera: Delphacidae), a potential biological control agent of water hyacinth, *Eichhornia crassipes*. *Release Application to the Department of Environmental Affairs*, 34 pp.

Coetzee JA and Hill MP (2012) The role of eutrophication in the biological control of water hyacinth, *Eichhornia crassipes*, in South Africa. *BioControl* **57**, 247–261.

Coetzee JA, Byrne MJ, Hill MP and Center TD (2009) Should the mirid, *Eccritotarsus catarinensis* (Heteroptera: Miridae), be considered for release against water hyacinth in the United States of America? *Biocontrol Science and Technology* **19**, 103–111.

Coetzee JA, Hill MP, Byrne MJ and Bownes A (2011) A review of the biological control programmes on *Eichhornia crassipes* (C. Mart.) Solms (Pontederiaceae), *Salvinia molesta* DS Mitch. (Salviniaceae), *Pistia stratiotes* L. (Araceae), *Myriophyllum aquaticum* (Vell.) Verdc. (Haloragaceae) and *Azolla filiculoides* Lam. (Azollaceae) in South Africa. *African Entomology* **19**, 451–468.

Coetzee J, Jones R and Hill M (2014) Water hyacinth, *Eichhornia crassipes* (Pontederiaceae), reduces benthic macroinvertebrate diversity in a protected subtropical lake in South Africa. *Biodiversity and Conservation* **23**, 1319–1330.

Cofrancesco, A.F., Stewart, R.M. and Sanders, D.R. (1985) The impact of *Neochetina eichhorniae* (Coleoptera: Curculionidae) on waterhyacinth in Louisiana. In *VI International Symposium on Biological Control of Weeds, 6 August 1984*. Canada, Agriculture Canada, p. 525.

Fraser G, Hill M and Martin J (2016) Economic evaluation of water loss saving due to the biological control of water hyacinth at New year's Dam, Eastern Cape province, South Africa. *African Journal of Aquatic Science* **41**, 227.

Grodowitz MJ, Stewart RM and Cofrancesco AF (1991) Population dynamics of waterhyacinth and the biological control agent *Neochetina Eichhorniae* (Coleoptera: Curculionidae) at a southeast Texas location. *Environmental Entomology* **20**, 652–660.

Hartig (2020) DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.2.7. http://florianhartig.github.io/DHARMa/.

Hill MP and Cilliers CJ (1999) A review of the arthropod natural enemies, and factors that influence their efficacy, in the biological control of water hyacinth, *Eichhornia crassipes* (Mart.) Solms-Laubach (Pontederiaceae), in South Africa. *African Entomology, Memoir No. 1*, 103–112.

Hill MP and Coetzee JA (2017) The biological control of aquatic weeds in South Africa: current status and future challenges. *Bothalia* **47**, e1–e12.

Hill, M.P. and Olckers, T. (2001) Biological control initiatives against water hyacinth in South Africa: constraining factors, success and new courses of action. In *Second Meeting of the Global Working Group for the Biological and Integrated Control of Water Hyacinth*, 9–12 October 2000, Beijing, China, ACIAR, pp. 33–36.

Hill MP, Coetzee JA and Ueckermann C (2012) Toxic effect of herbicides used for water hyacinth control on two insects released for its biological control in South Africa. *Biocontrol Science and Technology* **22**, 1321–1333.

Hopper JV, Pratt PD, McCue KF, Pitcairn MJ, Moran PJ and Madsen JD (2017) Spatial and temporal variation of biological control agents associated with *Eichhornia crassipes* in the Sacramento-San Joaquin river Delta, California. *Biological Control* **111**, 13–22.

Jianqing, D., Ren, W., Weidong, F. and Guoliang, Z. (2001) Water hyacinth in China: its distribution, problems and control status. In *Second Meeting of the Global Working Group for the Biological and Integrated Control of Water Hyacinth*, 9–12 October 2000, Beijing, China, ACIAR, pp. 29–32.

Julien, M.H. and Orapa, W. (1999) Successful biological control of water hyacinth (Eichhornia crassipes)in Papua New Guinea by the weevils *Neochetina bruchi* and *Neochetina eichhorniae* (Coleoptera: curculionidae). In Spencer, N.R. (ed), *Proceedings of the X International Symposium on Biological Control of Weeds*. Bozeman, MT, USA: Montana State University, p. 1027.

Kingsolver JG (1989) Weather and the population dynamics of insects: integrating physiological and population ecology. *Physiological Zoology* **62**, 314–334.

Lowe, S., Browne, M., Boudjelas, S. and De Poorter, M. (2000) *100 of the World's Worst Invasive Alien Species: A Selection From the Global Invasive Species Database*. Auckland, New Zealand: Invasive Species Specialist Group 2017, p. 12.

Madsen, J.D., Luu, K.T. and Getsinger, K.D. (1993) Allocation of Biomass and Carbohydrates in Waterhyacinth (*Eichhornia crassipes*): Pond-Scale Verification. *Technical Report A-93-3*. US Army Corps of Engineers Waterways Experiment Station Vicksburg, MS.

May B and Coetzee JA (2013) Comparisons of the thermal physiology of water hyacinth biological control agents: predicting establishment and distribution pre-and post-release. *Entomologia Experimentalis et Applicata* **147**, 241–250.

Midgley JM, Hill MP and Villet MH (2006) The effect of water hyacinth, *Eichhornia crassipes* (Martius) SolmsLaubach (Pontederiaceae), on benthic biodiversity in two impoundments on the New Year's river, South Africa. *African Journal of Aquatic Science* **31**, 25–30.

Miller BE, Coetzee J and Hill M (2019) Chlorophyll fluorometry as a method of determining the effectiveness of a biological control agent in post-release evaluations. *Biocontrol Science and Technology* **29**, 1118–1122.

Moran PJ, Pitcairn MJ and Villegas B (2016) First establishment of the planthopper, *Megamelus scutellaris* Berg, 1883 (Hemiptera: Delphacidae), released for biological control of water hyacinth in California. *Pan-Pacific Entomologist* **92**, 32–43.

Pellegrini MOO, Horn CN and Almeida RF (2018) Total evidence phylogeny of Pontederiaceae (Commelinales) sheds light on the necessity of its recircumscription and synopsis of *Pontederia* L. *PhytoKeys* **108**, 25–83.

Petela, N. (2018) *Interactions between three biological control agents of water hyacinth, Eichhornia crassipes (Mart.) Solms (Pontederiaceae): the planthopper Megamelus scutellaris Berg (Hemiptera: Delphacidae), the sap-sucking mirid Eccritotarsus eichhorniae Henry (Heteroptera: Miridae), and the weevil Neochetina eichhorniae Warner (Coleoptera: Curculionidae)* (Rhodes University Masters thesis), 109 pp.

R Core Team. (2017) R: A language and environment for statistical computing. *R Foundation for Statistical Computing* 3.4.3.

Sosa AJ, Marino De Remes Lenicov AM, Mariani R and Cordo HA (2005) Life history of *Megamelus scutellaris* with description of immature stages (Hemiptera: Delphacidae). *Annals of the Entomological Society of America* **98**, 66–72.

Sosa AJ, Cordo HA and Sacco J (2007) Preliminary evaluation of *Megamelus scutellaris* Berg (Hemiptera: Delphacidae), a candidate for biological control of waterhyacinth. *Biological Control* **42**, 129–138.

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Sutton GF, Compton SG and Coetzee JA (2016) Naturally occurring phytopathogens enhance biological control of water hyacinth (*Eichhornia crassipes*) by *Megamelus scutellaris* (Hemiptera: Delphacidae), even in eutrophic water. *Biological Control* **103**, 261–268.

Tipping PW, Center TD, Sosa AJ and Dray FA (2011) Host specificity testing and potential impact of *Megamelus scutellaris* (Hemiptera: Delphacidae) on water hyacinth *Eichhornia crassipes* (Pontederiales: Pontederiaceae). *Biocontrol Science and Technology* **21**, 75–87.

Tipping PW, Sosa A, Pokorny EN, Foley J, Schmitz DC, Lane JS, Rodgers L, McCloud L, Livingston-Way P, Cole MS and Nichols G (2014) Release and establishment of *Megamelus scutellaris* (Hemiptera: Delphacidae) on Waterhyacinth in Florida. *Florida Entomologist* **97**, 804–806.

https://doi.org/10.1017/S0007485320000516 Published online by Cambridge University Press