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The biological control of aquatic weeds in South Africa: Current status and future challenges

Authors:
Martin P. Hill[1]
Julie Coetzee[2]

Affiliations:
[1]Department of Zoology and Entomology, Rhodes University, South Africa

[2]Department of Botany, Rhodes University, South Africa

Corresponding author:
Martin Hill,
M.hill@ru.ac.za

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Background: Aquatic ecosystems in South Africa are prone to invasion by several invasive alien aquatic weeds, most notably, *Eichhornia crassipes* (Mart.) Solms-Laub. (Pontederiaceae) (water hyacinth); *Pistia stratiotes* L. (Araceae) (water lettuce); *Salvinia molesta* D.S. Mitch. (Salviniaceae) (salvinia); *Myriophyllum aquaticum* (Vell. Conc.) Verd. (parrot's feather); and *Azolla filiculoides* Lam. (Azollaceae) (red water fern).

Objective: We review the biological control programme on waterweeds in South Africa.

Results: Our review shows significant reductions in the extent of invasions, and a return on biodiversity and socio-economic benefits through the use of this method. These studies provide justification for the control of widespread and emerging freshwater invasive alien aquatic weeds in South Africa.

Conclusions: The long-term management of alien aquatic vegetation relies on the correct implementation of biological control for those species already in the country and the prevention of other species entering South Africa.

Introduction

Aquatic ecosystems in South Africa have been prone to invasion by introduced macrophytes since the late 1800s, when water hyacinth, *Eichhornia crassipes* (Mart.) Solms-Laub. (Pontederiaceae), was first recorded as naturalised in KwaZulu-Natal (Cilliers 1991). Several other species of freshwater aquatic plants, all notorious weeds in other parts of the world, have also become invasive in many of the rivers, man-made impoundments, lakes and wetlands of South Africa (Hill 2003). These are *Pistia stratiotes* L. (Araceae) (water lettuce); *Salvinia molesta* D.S. Mitch. (Salviniaceae) (salvinia); *Myriophyllum aquaticum* (Vell. Conc.) Verd. (parrot's feather); and *Azolla filiculoides* Lam. (Azollaceae) (red water fern) (Hill 2003), which along with water hyacinth comprise the 'Big Bad Five' (Henderson & Cilliers 2002). Recently, new invasive aquatic plant species have been recorded which are still at their early stages of invasion, including the submerged species, *Egeria densa* Planch. (Hydrocharitaceae) (Brazilian water weed) and *Hydrilla verticillata* (L.f.) Royle (Hydrocharitaceae); the emergent species, *Sagittaria platyphylla* (Engelm.) J.G.Sm. and *S. latifolia* Willd. (Alismataceae); *Lythrum salicaria* L. (Lythraceae) (purple loosestrife), *Nasturtium officinale* W.T. Aiton. (Brassicaceae) (watercress); *Iris pseudacorus* L. (Iridaceae) (yellow flag); and *Hydrocleys nymphoides* (Humb. & Bonpl. ex Willd.) Buchenau (Alismataceae) (water poppy); and the new floating weeds, *Salvinia minima* Baker (Salviniaceae) and *Azolla cristata* Kaulf. (Azollaceae) (Mexican azolla); and the rooted floating *Nymphaea mexicana* Zucc. (Nymphaeceae) (Mexican water lily) (Coetzee et al. 2011a; Coetzee, Bownes & Martin 2011b). The mode of introduction of these species is mainly through the horticultural and aquarium trade (Martin & Coetzee 2011), and two issues contribute to the invasiveness of these macrophytes following establishment: the lack of co-evolved natural enemies in their adventive range (McFadyen 1998); and disturbance, the presence of nitrate- and phosphate-enriched waters, associated with urban, agricultural and industrial pollution that promotes plant growth (Coetzee & Hill 2012).

Aquatic weeds in South Africa are found throughout the country including the winter rainfall areas of the western part of the country, the more subtropical eastern parts and the cool, temperate areas of the Highveld plateau (Henderson 2001). Although the alteration of hydrological flows in South African river systems through the construction of impoundment walls, gauging weirs, culverts and low-water bridges where constant slow-flowing waters have facilitated population build-up and thus problems caused by aquatic weeds (Hill & Olckers 2001), infestations are also found in unimpacted habitats, such as *A. filiculoides* infestations in wetlands in the southern Free State and *I. pesudocorus* in wetlands of the Cape Peninsula. Here, we review the current status of

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aquatic weeds in South Africa, their socio-economic and environmental impacts and the benefits of their control.

Drivers of invasive aquatic plant invasions

It is important to understand the invasion biology of an organism, if effective control measures are to be implemented. Several authors (e.g. Bauer 2012; MacDougall & Turkington 2005) have grouped invasive alien species into three broad categories *viz.* (1) passengers, which are solely dependent on a disturbance for establishment and proliferation, and if the disturbance is removed, the invasion and associated impacts cease; (2) drivers of biodiversity loss, which include species that do not need any disturbance to establish; and (3) back-seat drivers whereby an initial disturbance is required for an invasive alien plant species to establish, but once established, even if the disturbance is removed, the invasion continues. Aquatic weed invasions in South Africa are examples of back-seat drivers. These invasive species rely on the broad ecosystem disturbance of slow-flowing permanent waters caused by impoundments and eutrophication which facilitates establishment and, linked with enemy release, allows them to proliferate, thereby gaining a competitive advantage over indigenous aquatic plants (Coetzee & Hill 2012). The resulting large continuous mats significantly impact all aspects of aquatic biodiversity and ecosystem functioning (see below).

Impacts of aquatic invasive plant invasions

Aquatic weeds cause various environmental (or ecological) and socio-economic impacts (which are in their majority negative), affecting floral and faunal diversity and ecosystem functioning and services. The impact mechanisms and effects of aquatic weeds differ between species, which is largely based on differences in their growth form and the habitat that they have invaded. We applied the generic impact scoring system (GISS) presented by Nentwig et al. (2016) to assess the impacts of eight water weed species in South Africa before and after biological control. This is not the intended use of GISS, which was designed to prioritise invasive alien species for control, but does allow a comparison and ranking of the impacts of water weeds in South Africa and an assessment of the success of the biological control programmes. GISS relies on published evidence and comprises 12 impact categories divided evenly between environmental and socio-economic impacts. Under the environmental impacts, the effect that the invasive alien species has on native fauna and flora, either directly or through competition, disease transmission, hybridisation and the ecosystem services, is rated. Under the socio-economic categories, the impact that the invasive alien species has on agriculture, forestry, infrastructure, human health and social well-being is scored. A six-level scoring system is applied (Nentwig et al. 2016):

0 – no data available, no impacts known, not detectable or not applicable
1 – minor impacts, only locally, only on common species and negligible economic loss
2 – minor impacts, more widespread, also on rarer species and minor economic loss
3 – medium impacts, large-scale, several species concerned, relevant decline, relevant ecosystem modifications and medium economic loss
4 – major impact with high damage, major changes in ecosystem functions, decrease of species and major economic loss
5 – major large-scale impact with high damage and complete destruction, threat to species including local extinctions and high economic costs

Table 1 presents an analysis of the socio-economic and environmental impacts caused by eight of the most invasive and well-studied species of aquatic weeds established in South Africa. The list of weed species chosen for this study was not exhaustive, but represents three of the main habits, free-floating species, emergent species and submerged species. Scoring systems have their flaws, in that they are constrained by time and locality, but provide valuable benchmarks. We, therefore, scored aquatic weeds in South Africa based on both the worst-case scenario and the current status (i.e. before and after biological control for the weeds that have biocontrol programmes), thereby presenting a measure of the value of biological control. The scores were based on published studies using South African data captured in review papers or chapters, except for *S. platyphylla, E. densa* and *H. verticillata*, where little data exist on their impacts in South Africa, and thus, we relied on data from elsewhere in the world (e.g. Adair et al. 2012; Langeland 1996; Yarrow et al. 2009). Where the

TABLE 1: The impact scores with level of confidence per impact categories of the GISS (Nentwig et al. 2016) for eight water weeds in South Africa, presenting the worst-case scenario in the absence of any biological control, and the current situation in South Africa, post biological control, where applicable.

Weed	Prior to biological control			Post biological control		
	Environmental impact (level of confidence)	Socio-economic impact (level of confidence)	Total	Environmental impact (level of confidence)	Socio-economic impact (level of confidence)	Total
Eichhornia crassipes	22 (2.67)	21 (3.00)	43 (2.83)	12 (2.50)	11 (2.67)	23 (2.58)
Pistia stratiotes	22 (2.67)	16 (2.83)	38 (2.75)	2 (3.00)	4 (2.83)	6 (2.92)
Salvinia molesta	22 (2.67)	16 (2.83)	38 (2.75)	2 (3.00)	4 (2.83)	6 (2.92)
Azolla filiculoides	20 (2.83)	20 (2.83)	40 (2.83)	0 (3.00)	0 (3.00)	0 (3.00)
Myriophyllum aquaticum	18 (2.83)	20 (2.83)	38 (2.83)	8 (2.83)	7 (2.83)	15 (2.83)
Sagittaria platyphylla	18 (1.30)	17 (1.30)	35 (1.30)	-	-	-
Egeria densa	21 (1.30)	21 (1.30)	42 (1.30)	-	-	-
Hydrilla verticillata	22 (1.30)	22 (1.30)	44 (1.30)	-	-	-

impact was unknown, largely because it was unstudied, the impact was assigned a neutral score of zero. Further, confidence limits were based on Nentwig et al. (2016) where 1 = low confidence (no empirical data or literature to support the impact score), 2 = medium confidence (no empirical data from South Africa, but literature from elsewhere to support the impact score) and 3 = high confidence (empirical and published data from South Africa support the impact score) (Appendix 1).

This analysis shows that of the floating macrophytes, *E. crassipes* had the biggest impact on aquatic ecosystems in South Africa, followed by *A. filiculoides*, *P. stratioes* and *S. molesta*. Although based on literature, this result is supported by annual field surveys throughout South Africa and is probably because of the fact that water hyacinth is the largest of the macrophytes that warrant control, it is the most widespread, we have studied its impacts (e.g. Coetzee, Jones & Hill 2014; Fraser, Martin & Hill 2016; Midgley, Hill & Villet 2006) and it has historically been the most difficult of the water weeds to control (e.g. Coetzee et al. 2011a; Hill 2003; Hill & Cilliers 1999). Although not considered to be under complete biological control (Klein 2011), the ecological and socio-economic impact of the weed has been significantly reduced through the introduction of eight biological control agents (Coetzee et al. 2011a; Paterson et al. 2016). On the contrary, the impacts of *A. filiculoides* on South African freshwater systems were quantified by Ashton and Walmsley (1984) and McConnachie et al. (2003). Based on this evidence, this weed achieved a score of 40 on the GISS, just below *E. crassipes*, and was considered more damaging than either *P. stratiotes* or *S. molesta* in the absence of biological control. Following the introduction of the highly successful agent, *Stenopelmus rufinasus* Gyllenhal (Coleoptera: Curculionidae), *A. filiculoides* no longer poses a threat to aquatic ecosystems of the country (Hill & McConnachie 2009; McConnachie et al. 2003; McConnachie, Hill & Byrne 2004); indeed, we could not find a single negative impact of this weed in this country and thus scores 0. Furthermore, biological control has significantly reduced the impact scores of *P. stratiotes*, *S. molesta* and *M. aquaticum*, highlighting the ecological and economic benefits of biological control.

Interestingly, the two submerged species analysed, *E. densa* and *H. verticillata*, recorded the two of the highest impact scores. This is largely because of their fairly recent invasion status in South Africa, and thus, we relied heavily on the published literature. Although *H. verticillata* is only confined to one site in South Africa (Coetzee et al. 2009b), and its impact at this site has not been quantified, its impact in the United States suggests that it should be given a very high priority in terms of impact and thus the need for control (Balciunas et al. 2002; Langeland 1996). The emergent species, *S. platyphylla*, scored the lowest in comparison with the other macrophytes possibly because it is a new invader still in the lag phase, not yet dominating the riparian zone, and is also not yet considered a major weed elsewhere in the world.

Impact of water weeds on biodiversity loss

Although the socio-economic impacts of water weeds have been fairly well reported (reviewed in Villamagna & Murphy 2010), there are very few specific examples that have documented their impacts on biodiversity. Below we present two case studies of the direct impact of water hyacinth on aquatic biodiversity in South Africa.

Case study 1: Midgley et al. (2006)

In this first case study, the benthic invertebrate community and algal biomass were sampled under water hyacinth mats and in water hyacinth-free water over a 13-month period, using artificial substrates in New Year's Dam, Eastern Cape Province, a cool temperate region of the country. The number of families and the number of individuals per substrate were significantly lower under the mats. Further, measures of biodiversity, including Shannon-Weiner diversity index, Margalef's richness index, Pielou's evenness index and chlorophyll *a*, were all significantly lower under water hyacinth mats than in water hyacinth-free zones, demonstrating the impact of water hyacinth on benthic biodiversity.

Case study 2: Coetzee et al. (2014)

Although similar to the previous study, this study aimed to determine whether the presence of water hyacinth altered the diversity and assemblage structure of benthic macroinvertebrates in a conservation area in a subtropical region of the country, the Nseleni Nature Reserve near Richard's Bay. The benthic macroinvertebrate assemblage was sampled over 1 year at five sites under water hyacinth mats and at five sites without water hyacinth in the Nseleni River. Once again, artificial substrates were placed beneath water hyacinth mats or in the open water to allow for colonisation by freshwater macroinvertebrates, and left for a period of 6 weeks, repeated on seven occasions over 10 months. Twenty-nine families comprising 18 797 individuals were collected, 817 (13 families) individuals were from under water hyacinth mat sites compared with 17 980 (27 families) individuals from open water sites. However, 98% of individuals collected were the invasive snail, *Tarebia granifera* L. (Thiaridae). This study again highlights that the presence of water hyacinth has a significantly negative impact on aquatic macroinvertebrate biodiversity, but in a conservation area.

Control of aquatic invasive plant invasions

In South Africa, water weeds have been controlled through the use of mechanical and manual removal, herbicide application and biological control. Although manual removal using rakes and pitchforks can be successful, it is labour intensive. Although one of the pillars of the Working for Water Programme of the Natural Resources Management

Programmes of the Department of Environmental Affairs is job creation through alien plant removal, this method is really ineffective for water weeds and this work force is better used on controlling terrestrial weeds in South Africa. Manual removal of submerged aquatic species such as *H. verticillata* and *E. densa* invariably leads to fragmentation of the weed mat and subsequent dispersal and increased infestation of the weed (Dayan & Netherland 2005).

Herbicidal control, using formulations containing the active ingredient glyphosate, is still used to control water hyacinth in some of the larger dams and river systems in South Africa. Herbicidal control of water hyacinth depends on skilled operators who maintain a long-term follow-up programme continually to control re-infestation from scattered plants and those germinating from seed. Therefore, any herbicide programme against the weed requires a commitment to an ongoing operation of unlimited duration. It is the lack of a follow-up regime that has often led to the failure of herbicidal control programmes (Hill & Olckers 2001). Although herbicide application is often used as part of an integrated management approach (Hill & Coetzee 2008), Hill, Coetzee and Ueckermann (2012) showed that a number of herbicide formulations used in South Africa were toxic to some of the biological control agents that have been released against this weed.

The biological control programme against water weeds in South Africa was initiated in 1973 and the weevil, *Neochetina eichhorniae* Warner, was released in 1974 (Cilliers 1991). Since that time, 13 agent species (11 insects, one mite and one pathogen) have been released against five weeds (Table 2). The biological control programme against water weeds in South Africa has been highly successful with four of the five weeds targeted (water lettuce, salvinia, parrot's feather and azolla) considered to be under complete control whereby no other control methods are required to keep the weed populations at a level where they no longer impact the aquatic biodiversity and water utilisation (see above) (Coetzee et al. 2011a). Although water hyacinth is not considered to be under complete biological control, in some areas biological control has controlled the weed, whereas in other areas it has reduced populations and impact such that alternative control methods such as herbicide applications are required far less frequently (Coetzee et al. 2011a; Hill & Cilliers 1999).

The biological control programme on water weeds in South Africa is co-ordinated through Rhodes University in collaboration with University of the Witwatersrand and the Plant Protection Research Institute of the Agricultural Research Council. This programme comprises about 7 research staff, 14 support and technical staff, and 12 postgraduate

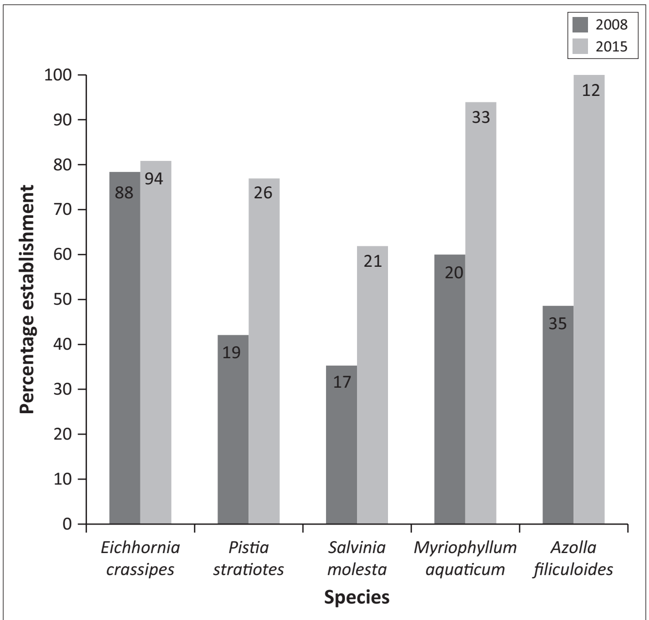
TABLE 2: Biological control agents released for the control of freshwater alien aquatic weed species in South Africa (after Klein 2011).

Target weed	Natural enemy	Feeding guild	Agent status	Weed status	Key references
Alismataceae					
Sagittaria platyphylla	*Listronotus appendiculatus* (Coleoptera: Curculionidae	Flower feeder	Under investigation	-	-
	Listronotus frontalis (Coleoptera: Curculionidae)	Tuber feeder	Under investigation	-	-
	Listronotus lutulentus (Coleoptera: Curculionidae)	Leaf feeder	Under investigation	-	-
	Listronotus sordidus (Coleoptera: Curculionidae)	Root crown feeder	Under investigation	-	-
Araceae					
Pistia stratiotes	*Neohydronomus affinis* (Coleoptera: Curculionidae)	Leaf and stem borer	Released 1985, extensive	Complete	Coetzee et al. 2011a
Azollaceae					
Azolla filiculoides	*Stenopelmus rufinasus* (Coleoptera: Curculionidae)	Frond feeder	Released 1997, extensive	Complete	McConnachie et al. 2004
Azolla cristata	*Stenopelmus rufinasus* (Coleoptera: Curculionidae)	Frond feeder	First recorded on this species in 2004, extensive	Substantial	Madeira et al. 2016
Haloragaceae					
Myriophyllum aquaticum	*Lysathia* sp. (Coloptera: Chrysomelidae)	Leaf feeder	Released 1994, extensive	Complete	Coetzee et al. 2011a
Hydrocharitaceae					
Egeria densa	*Hydrellia egeriae* (Diptera: Ephydridae)	Leaf miner	Under investigation	-	Coetzee et al. 2011b
Hydrilla verticillata	*Hydrellia purcelli* (Diptera: Ephydridae)	Leaf miner	Release permit issued	-	Coetzee et al. 2011b
Pontederiaceae					
Eichhornia crassipes	*Cercospora piaropi* (Mycosphaerellales: Mycosphaerellaceae	Leaf pathogen	Released 1992, considerable	Substantial	Morris, Wood & den Breeÿen 1999
	Cornops aquaticum (Orthoptera: Acrididae)	Lead feeder	Released 2011, establishment unconfirmed	-	Coetzee et al. 2011a
	Eccritotarsus catarinensis (Hemiptera: Miridae)	Leaf sucker	Released 1996, considerable	-	Coetzee et al. 2011a
	Eccritotarsus sp. nov. (Hemiptera: Miridae)	Leaf sucker	Released 2008, establishment unconfirmed	-	Paterson et al. 2016
	Megamelus scutellaris (Hemiptera: Delphacidae)	Leaf sucker	Released 2013, established		
	Neochetina bruchi (Coleoptera: Curculionidae)	Stem borer	Released 1990, considerable	-	Coetzee et al. 2011a; Hill and Cilliers 1999
	Neochetina eichhorniae (Coleoptera: Curculionidae)	Stem borer	Released 1974, considerable	-	Coetzee et al. 2011a; Hill and Cilliers 1999
	Niphograpta albiguttalis (Lepidoptera: Crambidae)	Petiole borer	Released 1990, considerable	-	Coetzee et al. 2011a; Hill and Cilliers 1999
	Orthogalumna terebrantis (Acari: Sarcoptiformes: Glamunidae)	Leaf miner	Released 1989, considerable	-	Coetzee et al. 2011a; Hill and Cilliers 1999
Salviniaceae					
Salvinia molesta	*Cyrtobagous salvinae* (Coleoptera: Curculionidae)	Stem borer	Released 1985, considerable	Complete	Cilliers et al. 2003; Coetzee et al. 2011a

students and postdoctoral fellows. The activities carried out by this research group include pre-release studies on new agents for several species, including *S. platyphylla*, *I. pseudocorus* and *E. densa*, and qualitative post-release evaluation studies on all of the weeds on which agents have been released. The most significant aspect of the post-release evaluation studies is an annual country-wide survey of all water weed sites (~450 infested water bodies) assessing weed and agent populations. These surveys that have been carried out since 2008 provide the guidance for the water weed biological control programme and a measure of success or failure.

Results of the surveys show that since 2008, there has been a substantial increase in the number of recorded invaded sites, but more importantly, the percentage of these sites where the respective biocontrol agents are present has increased significantly because of enhanced efforts to release agents from mass rearing centres (Figure 1). This has led to an increase in the control of the weeds and a reduction in their ecological and environmental impacts (Table 1). Another unintended benefit of these surveys is that they have served as an ideal early detection platform for additional freshwater invasive macrophytes. For example, since 2008, the number of locality records for *E. densa*, *S. platyphylla* and *I. pseudacorus* has increased (from 0 to 14, 16 and 14 sites, respectively) to the point that these species are no longer considered eradication targets (Wilson et al. 2013). All three species are now targets for biological control. On the contrary, *H. verticillata* remains confined to one system, Jozini Dam (KZN).

Some new developments arising from these field surveys since the 2011 review paper (Coetzee et al. 2011a) are presented below. Mass rearing and implementation also



The bars represent the percentage of sites infested by the weed where at least one control agent species was present. The value embedded in each bar is the number of sites invaded by each species.

FIGURE 1: Results of the first (2008) and most recent (2015) nationwide surveys on aquatic weeds in South Africa.

forms an important part of the research programme as in many areas of the country that are prone to cold winters and eutrophic waters, classical biological control is not as effective as an augmentive programme whereby high numbers of healthy agents are released at the onset of summer when field populations of the agents are low. Part of the mass rearing programme involves the employment of people living with disabilities (Weaver et al. 2016).

The biological control programme against *A. filiculoides* in South Africa using the Azolla specialist *S. rufinasus* has been highly successful (McConnachie et al. 2003, 2004). However, field surveys showed that the agent utilised another Azolla species, thought to be the native *Azolla pinnata* subsp. *africana* (Desv.) Baker, which contradicted the host specificity trials (Hill 1998). However, molecular analysis showed that what we thought was the native species, *A. pinnata subsp. africana*, was a new invasive species, *A. cristata* Kaulfuss, a close relative of *A. filiculoides* (Madeira et al. 2016). Field surveys have shown that *S. rufinasus* is capable of establishing populations on *A. cristata* in the warmer, eastern part of the country and will likely result in this plant never becoming highly invasive.

Most of the biological control research on water weeds is centred around water hyacinth, and the plant hopper, *Megamelus scutellaris* Berg (Hemiptera: Delphacidae), is the most recent agent to have been released in 2013. This agent has now established and is impacting the plant in the cooler areas of the country where the other agents have traditionally struggled to establish and have an effect (Coetzee, Byrne & Hill 2007). Recent molecular work has revealed that two separate populations of the mirid, *Eccritotarsus catarinensis* Carvahlo (Hemiptera: Miridae), collected from Brazil (collected in 1994) and Peru (collected in 1999), respectively, are in fact cryptic species (Paterson et al. 2016). Fortunately, these populations were kept separate and both subjected to impact and host specificity testing. However, this finding does show that the importation of multiple consignments of the same species for biological control should be conducted with caution.

Benefits of biological control of water hyacinth

Weed biological control has traditionally suffered from a lack of quantitative post-release evaluation studies that show economic or ecological benefit. Where the benefits of a biological control programme have been measured, it has focussed on economic benefits (e.g. Van Wilgen et al. 2004). For aquatic weeds, McConnachie et al. (2003) quantified the benefits of the biological control programme against red water fern using the weevil, *S. rufinasus* Gyllenhal, in South Africa and showed that the agent removed the impact of the weed on water supply, stock health and recreational activities (see above). Further, De Groote et al. (2003) demonstrated that the successful biological control of water hyacinth in southern Benin significantly increased the yearly income of the population of this region through increased crop and fish production. Also, Van Wyk and Van Wilgen (2002) compared the costs and benefits of three control interventions for *E. crassipes* and showed that biological control, along with integrated control, offered the best return on investment.

New threats to the aquatic environment

Coetzee et al. (2011b) highlighted the significance that the delays in promulgating appropriate legislation against a suite of new aquatic invaders could have in allowing their unmitigated establishment and spread in South African water bodies. In 2014, however, the promulgation of the *National Environmental Management: Biodiversity Act* (10/2004) (NEM:BA) and the publication of the Alien and Invasive Species List in 2014 resulted in the listing of 10 Category 1a aquatic plant species, including *H. verticillata*, *I. pseudacorus* and *S. platyphylla*; 16 Category 1b aquatic plant species, including *A. cristata* and *S. minima;* and one Category 2 aquatic plant species. This legislation will provide much needed impetus to curb the spread and impacts of this suite of invaders in South Africa. As these five species are no longer considered targets for eradication (Coetzee et al. 2011a, 2011b; Jaca & Mkhize 2015), biological control programmes have been initiated against these species and are currently at various stages of development: from surveying for potential natural enemies, in the case of *I. pseudacorus*; screening for host specificity in quarantine, in the case of *S. platyphylla* and *S. minima*; pending release of a suitable agent in the case of *H. verticillata*; to assessing the impact of an agent already released against *A. filiculoides* that has subsequently been found on *A. cristata* (Table 2).

Despite the NEM:BA legislation, there are a number of additional unlisted aquatic plant species whose introduction and establishment must be prevented at all costs. The role that pet traders, aquarists, boating enthusiasts and fishermen play in the spread of invasive aquatic species has been highlighted from around the world (Cohen et al. 2007; Maki & Galatowitsch 2004; Padilla & Williams 2004) and is a significant channel for the introduction and spread of aquatic plants throughout South Africa too (Martin & Coetzee 2011). Species such as *Cabomba caroliniana* Gray (Cabombaceae), *Alternanthera philoxeroides* Griseb. (Amaranthaceae) and *Stratiotes aloides* L. (Hydrocharitaceae) are widespread invaders elsewhere in the world (e.g. Julien et al. 2012; Schooler, Cabrera-Walsh & Julien 2009; Thiebaut 2007) and pose a threat to South African waterways, should they be introduced. Awareness and publicity programmes on potential new threats could go a long way in preventing their introduction and trade, as well as improved phytosanitory efforts and border control.

Discussion

Hill and Olckers (2001) critiqued the biological control programme on water hyacinth in South Africa. Although their emphasis was water hyacinth, the points made in that paper are pertinent to all invasive alien water weeds in South Africa. Hill and Olckers stated that there were four issues that mitigated against the sustainable biological control of water hyacinth; the injudicious use of herbicides that was antagonistic to the biological control agents; the cold winters in the temperate regions of the country that was deleterious to the build-up of agent populations; eutrophic waters that allowed the weeds to compensate for herbivory; and the fact that many of the systems infested by these weeds were small and lacked the necessary wind fetch to break up mats of agent infested weed. In the 15 years since the publication of Hill and Olckers, a considerable amount of research has been undertaken to better understand these four issues (summarised and reviewed in Byrne et al. 2010; Coetzee et al. 2011a, 2011b; Coetzee & Hill 2012). The implementation of this research has resulted in the release of additional agents that are better adapted to the diversity of habitats in South Africa (e.g. *M. scutellaris* which is able to establish on water hyacinth in cooler regions), and an emphasis on inundative releases of high numbers of agents at appropriate times of year (e.g. in spring and after herbicide application). This has been made possible through the construction of three mass-rearing facilities (City of Cape Town, Rhodes University and the South African Sugar Research Institute) that produce agents on demand.

The biological control programme against water weeds in South Africa has been highly successful, as measured by an increase in the number of sites under biological control, coupled with a significant reduction in the percentage cover of these weeds and a recovery of ecosystem services. However, unless the primary driver of disturbance (i.e. eutrophication by nitrates and phosphates) in aquatic ecosystems is addressed, we anticipate, rather than control, a succession of invasions by a suite of water weeds (Coetzee et al. 2011a, 2011b). Although we have shown that biological control has played a significant role in the recovery of aquatic biodiversity, these biodiversity benefits will be short-lived in impacted ecosystems unless an integrated catchment management approach is adopted which addresses eutrophication.

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Competing interests

The authors declare that they stand to gain no financial benefit from the publication of this article.

Authors' contributions

J.C. and M.P.H. contributed equally to the conception, analysis and writing of the article.

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Appendix 1

TABLE 1-A1: Summary of GISS detailed impact levels (Nentwig et al. 2016), for eight freshwater invasive alien aquatic weeds, in South Africa. Scoring was conducted in both the absence of biological control (BC) (worst-case scenario – no BC) and the presence of biological control (current status – BC), where applicable. References are included. Where there is a paucity on impact data and no implementation of biological control to date in South Africa, impacts realised elsewhere have been considered (i.e. for *Sagittaria platyphylla, Egeria densa* and *Hydrilla verticillata*).

Impact	Species and impact category	Description	Impact level, no BC	Confidence[a], no BC	Impact level, BC	Confidence[a], BC	References
Eichhornia crassipes							
1. Environmental impacts	1.1. On vegetation	Habitat alteration	5	3	3	2	Coetzee et al. 2009b; Villamagna and Murphy 2010
	1.2. On animals	Habitat alteration	5	3	2	3	Coetzee et al. 2009b, 2014; Midgley et al. 2006; Villamagna and Murphy 2010
	1.3. On competition	Space, light, nutrients	5	3	2	3	Coetzee et al. 2005, 2009b; Villamagna and Murphy 2010
	1.4. Transmission of disease	Provide habitat for vectors of disease	2	1	2	1	Mailu 2001; Villamagna and Murphy 2010
	1.5. Hybridisation	None	0	3	0	3	No indigenous *Eichhornia* spp
	1.6. Ecosystems	Ecosystem alteration	5	3	3	3	Coetzee et al. 2009b, 2014; Midgley et al. 2006; Van Driesche et al. 2010; Villamagna and Murphy 2010
Subtotal	-	-	22	2.67	12	2.5	-
2. Economic impacts	2.1. Agricultural production	Reduced irrigation	4	3	2	3	Fraser et al. 2016
	2.2. Animal production	Reduced irrigation	4	3	2	3	Fraser et al. 2016
	2.3. Forestry production	None	0	3	0	3	NA
	2.4. Human infrastructure	Bridges, weirs, hydropower, pumps	5	3	3	3	Hill 2003
	2.5. Human health	Disease vectors	3	3	2	1	Mailu 2001; Villamagna and Murphy 2010
	2.6. Human social life	Reduced water-based recreation	5	3	2	3	Center et al. 2002; Coetzee et al. 2009b
Subtotal	-	-	21	3	11	2.67	-
Total	-	-	43	2.83	23	2.58	-
Pistia stratiotes							
1. Environmental impacts	1.1. On vegetation	Habitat alteration	5	3	1	3	Diop, Coetzee and Hill 2010; Moore and Hill 2012; Neuenschwander et al. 2009
	1.2. On animals	Habitat alteration	5	3	0	3	Langa 2013; Neuenschwander et al. 2009
	1.3. On competition	Space, light, nutrients	5	3	0	3	Neuenschwander et al. 2009; Strange unpublished data
	1.4. Transmission of disease	Provide habitat for vectors of disease	2	1	0	3	Neuenschwander et al. 2009
	1.5. Hybridisation	None	0	3	0	3	Sole member of the Pistioidea
	1.6. Ecosystems	Ecosystem alteration	5	3	1	3	Coetzee et al. 2011a; Neuenschwander et al. 2009
Subtotal			22	2.67	2	3	
2. Economic impacts	2.1. Agricultural production	Reduced irrigation	4	3	1	3	Coetzee et al. 2011a; Neuenschwander et al. 2009
	2.2. Animal production	Reduced irrigation	3	3	0	3	Coetzee et al. 2011a; Neuenschwander et al. 2009
	2.3. Forestry production	None	0	3	0	3	NA
	2.4. Human infrastructure	Bridges, weirs, hydropower, pumps	3	3	1	3	Hill 2003
	2.5. Human health	Disease vectors	2	2	1	2	Neuenschwander et al. 2009
	2.6. Human social life	Reduced water-based recreation	4	3	1	3	Coetzee et al. 2011a; Neuenschwander et al. 2009
Subtotal	-	-	16	2.83	4	2.83	-
Total	-	-	38	2.75	6	2.92	-
Salvinia molesta							
1. Environmental impacts	1.1. On vegetation	Habitat alteration	5	3	1	3	Coetzee et al. 2011a; Doeleman 1989; Julien, Hill and Tipping 2009
	1.2. On animals	Habitat alteration	5	3	0	3	Coetzee et al. 2011a; Doeleman 1989; Julien et al. 2009
	1.3. On competition	Space, light, nutrients	5	3	0	3	Coetzee et al. 2011a; Doeleman 1989; Julien et al. 2009
	1.4. Transmission of disease	Provide habitat for vectors of disease	2	1	0	3	Coetzee et al. 2011a; Thomas and Room 1986

Table 1-A1 continues on next page →

TABLE 1-A1 (Continues...): Summary of GISS detailed impact levels (Nentwig et al. 2016), for eight freshwater invasive alien aquatic weeds, in South Africa. Scoring was conducted in both the absence of biological control (BC) (worst-case scenario – no BC) and the presence of biological control (current status – BC), where applicable. References are included. Where there is a paucity on impact data and no implementation of biological control to date in South Africa, impacts realised elsewhere have been considered (i.e. for *Sagittaria platyphylla, Egeria densa* and *Hydrilla verticillata*).

Impact	Species and impact category	Description	Impact level, no BC	Confidence[a], no BC	Impact level, BC	Confidence[a], BC	References
	1.5. Hybridisation	None	0	3	0	3	No indigenous Salviniaceae, sterile polyploid (Julien et al. 2009)
	1.6. Ecosystems	Ecosystem alteration	5	3	1	3	Coetzee et al. 2011a; Doeleman 1989; Julien et al. 2009
Subtotal	-	-	22	2.67	2	3	
2. Economic impacts	2.1. Agricultural production	Reduced irrigation	4	3	1	3	Coetzee et al. 2011a; Doeleman 1989; Julien et al. 2009
	2.2. Animal production	Reduced irrigation	3	3	0	3	Coetzee et al. 2011a; Doeleman 1989; Julien et al. 2009
	2.3. Forestry production	None	0	3	0	3	NA
	2.4. Human infrastructure	Bridges, weirs, hydropower, pumps	3	3	1	3	Hill 2003
	2.5. Human health	Disease vectors	2	2	1	2	Bennet 1966; Coetzee et al. 2011a; Thomas and Room 1986
	2.6. Human social life	Reduced water-based recreation	4	3	1	3	Coetzee et al. 2011a; Hill 2003; Julien et al. 2009
Subtotal	-	-	16	2.83	4	2.83	-
Total	-	-	38	2.75	6	2.92	-
Azolla filiculoides							
1. Environmental impacts	1.1. On vegetation	Habitat alteration	5	3	0	3	Hill and McConnachie 2009; McConnachie et al. 2003, 2004
	1.2. On animals	Habitat alteration	5	3	0	3	Hill and McConnachie 2009; McConnachie et al. 2003, 2004
	1.3. On competition	Space, light, nutrients	3	3	0	3	Hill and McConnachie 2009; McConnachie et al. 2003, 2004
	1.4. Transmission of disease	Provide habitat for vectors of disease	2	2	0	3	Hill and McConnachie 2009; McConnachie et al. 2003, 2004
	1.5. Hybridisation	None	0	3	0	3	Madeira et al. 2013, 2016
	1.6. Ecosystems	Ecosystem alteration	5	3	0	3	Hill and McConnachie 2009; McConnachie et al. 2003, 2004
Subtotal	-	-	20	2.83	0	3	
2. Economic impacts	2.1. Agricultural production	Reduced irrigation	5	3	0	3	Ashton and Walmsley 1984; Hill and McConnachie 2009; McConnachie et al. 2003, 2004
	2.2. Animal production	Reduced irrigation	5	3	0	3	Ashton and Walmsley 1984; Hill and McConnachie 2009; McConnachie et al. 2003, 2004
	2.3. Forestry production	None	0	3	0	3	NA
	2.4. Human infrastructure	Bridges, weirs, hydropower, pumps	3	3	0	3	Ashton and Walmsley 1984; Hill and McConnachie 2009; McConnachie et al. 2003, 2004
	2.5. Human health	Disease vectors	2	2	0	3	Hill and McConnachie 2009
	2.6. Human social life	Reduced water-based recreation	5	3	0	3	Ashton and Walmsley 1984; Hill and McConnachie 2009; McConnachie et al. 2003, 2004
Subtotal	-	-	20	2.83	0	3	-
Total	-	-	40	2.83	0	3	-
Myriophyllum aquaticum							
1. Environmental impacts	1.1. On vegetation	Habitat alteration	5	3	2	3	Cilliers 1999; Coetzee et al. 2011a
	1.2. On animals	Habitat alteration	3	3	1	3	Cilliers 1999; Coetzee et al. 2011a
	1.3. On competition	Space, light, nutrients	4	3	2	3	Cilliers 1999; Coetzee et al. 2011a
	1.4. Transmission of disease	Provide habitat for vectors of disease	2	2	1	2	-
	1.5. Hybridisation	None	0	3	0	3	Only female plants in SA (Henderson and Cilliers 2002)
	1.6. Ecosystems	Ecosystem alteration	4	3	2	3	Cilliers 1999; Coetzee et al. 2011a
Subtotal			18	2.83	8	2.83	
2. Economic impacts	2.1. Agricultural production	Reduced irrigation	5	3	2	3	Cilliers 1999; Coetzee et al. 2011a
	2.2. Animal production	Reduced irrigation	4	3	1	3	Cilliers 1999; Coetzee et al. 2011a
	2.3. Forestry production	None	0	3	0	3	NA
	2.4. Human infrastructure	Bridges, weirs, hydropower, pumps	4	3	1	3	Cilliers 1999; Coetzee et al. 2011a
	2.5. Human health	Disease vectors	3	2	1	2	Cilliers 1999; Coetzee et al. 2011a

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TABLE 1-A1 (Continues...): Summary of GISS detailed impact levels (Nentwig et al. 2016), for eight freshwater invasive alien aquatic weeds, in South Africa. Scoring was conducted in both the absence of biological control (BC) (worst-case scenario – no BC) and the presence of biological control (current status – BC), where applicable. References are included. Where there is a paucity on impact data and no implementation of biological control to date in South Africa, impacts realised elsewhere have been considered (i.e. for *Sagittaria platyphylla, Egeria densa* and *Hydrilla verticillata*).

Impact	Species and impact category	Description	Impact level, no BC	Confidence[a], no BC	Impact level, BC	Confidence[a], BC	References
	2.6. Human social life	Reduced water-based recreation	4	3	2	3	Cilliers 1999; Coetzee et al. 2011a
Subtotal	-	-	20	2.83	7	2.83	-
Total	-	-	38	2.83	15	2.83	-
Sagittaria platyphylla							
1. Environmental impacts	1.1. On vegetation	Habitat alteration	4	1	-	-	Adair et al. 2012; Chapman and Dore 2009
	1.2. On animals	Habitat alteration	4	1	-	-	Adair et al. 2012; Chapman and Dore 2009
	1.3. On competition	Space, light, nutrients	4	1	-	-	Adair et al. 2012; Chapman and Dore 2009
	1.4. Transmission of disease	Provide habitat for vectors of disease	2	1	-	-	Adair et al. 2012; Chapman and Dore 2009
	1.5. Hybridisation	None	0	3	-	-	Adair et al. 2012; Chapman and Dore 2009
	1.6. Ecosystems	Ecosystem alteration	4	1	-	-	Adair et al. 2012; Chapman and Dore 2009
Subtotal	-	-	18	1.33	-	-	-
2. Economic impacts	2.1. Agricultural production	Reduced irrigation	4	1	-	-	Adair et al. 2012; Chapman and Dore 2009
	2.2. Animal production	Reduced irrigation	4	1	-	-	Adair et al. 2012; Chapman and Dore 2009
	2.3. Forestry production	None	0	3	-	-	Adair et al. 2012; Chapman and Dore 2009
	2.4. Human infrastructure	Bridges, weirs, hydropower, pumps	3	1	-	-	Adair et al. 2012; Chapman and Dore 2009
	2.5. Human health	Disease vectors	2	1	-	-	Adair et al. 2012; Chapman and Dore 2009
	2.6. Human social life	Reduced water-based recreation	4	1	-	-	Adair et al. 2012; Chapman and Dore 2009
Subtotal	-	-	17	1.33	-	-	-
Total	-	-	35	1.33	-	-	-
Egeria densa							
1. Environmental impacts	1.1. On vegetation	Habitat alteration	5	1	-	-	Cabrera Walsh et al. 2013; Coetzee et al. 2011b; Yarrow et al. 2009
	1.2. On animals	Habitat alteration	4	1	-	-	Cabrera Walsh et al. 2013; Coetzee et al. 2011b; Yarrow et al. 2009
	1.3. On competition	Space, light, nutrients	5	1	-	-	Cabrera Walsh et al. 2013; Coetzee et al. 2011b; Yarrow et al. 2009
	1.4. Transmission of disease	Provide habitat for vectors of disease	2	1	-	-	Cabrera Walsh et al. 2013; Coetzee et al. 2011b; Yarrow et al. 2009
	1.5. Hybridisation	None	0	3	-	-	Lambertini et al. 2010
	1.6. Ecosystems	Ecosystem alteration	5	1	-	-	Cabrera Walsh et al. 2013; Coetzee et al. 2011b; Yarrow et al. 2009
Subtotal	-	-	21	1.33	-	-	
2. Economic impacts	2.1. Agricultural production	Reduced irrigation	5	1	-	-	Cabrera Walsh et al. 2013; Coetzee et al. 2011b; Yarrow et al. 2009
	2.2. Animal production	Reduced irrigation	4	1	-	-	Cabrera Walsh et al. 2013; Coetzee et al. 2011b; Yarrow et al. 2009
	2.3. Forestry production	None	0	3	-	-	Cabrera Walsh et al. 2013; Coetzee et al. 2011b; Yarrow et al. 2009
	2.4. Human infrastructure	Bridges, weirs, hydropower, pumps	5	1	-	-	Cabrera Walsh et al. 2013; Coetzee et al. 2011b; Yarrow et al. 2009;
	2.5. Human health	Disease vectors	2	1	-	-	Cabrera Walsh et al. 2013; Coetzee et al. 2011b; Yarrow et al. 2009
	2.6. Human social life	Reduced water-based recreation	5	1	-	-	Cabrera Walsh et al. 2013; Coetzee et al. 2011b; Yarrow et al. 2009
Subtotal			21	1.33	-	-	-
Total			42	1.33	-	-	-

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TABLE 1-A1 (Continues...): Summary of GISS detailed impact levels (Nentwig et al. 2016), for eight freshwater invasive alien aquatic weeds, in South Africa. Scoring was conducted in both the absence of biological control (BC) (worst-case scenario – no BC) and the presence of biological control (current status – BC), where applicable. References are included. Where there is a paucity on impact data and no implementation of biological control to date in South Africa, impacts realised elsewhere have been considered (i.e. for *Sagittaria platyphylla, Egeria densa* and *Hydrilla verticillata*).

Impact	Species and impact category	Description	Impact level, no BC	Confidence[a], no BC	Impact level, BC	Confidence[a], BC	References
Hydrilla verticillata							
1. Environmental impacts	1.1. On vegetation	Habitat alteration	5	1	-	-	Balciunas et al. 2002; Langeland 1996; Pieterse 1981; Souza 2011
	1.2. On animals	Habitat alteration	5	1	-	-	Balciunas et al. 2002; Langeland 1996; Pieterse 1981; Souza 2011
	1.3. On competition	Space, light, nutrients	5	1	-	-	Balciunas et al. 2002; Langeland 1996; Pieterse 1981; Souza 2011
	1.4. Transmission of disease	Provide habitat for vectors of disease	2	1	-	-	Balciunas et al. 2002; Langeland 1996; Pieterse 1981; Souza 2011
	1.5. Hybridisation	None	0	3	-	-	Balciunas et al. 2002; Langeland 1996; Pieterse 1981; Souza 2011
	1.6. Ecosystems	Ecosystem alteration	5	1	-	-	Balciunas et al. 2002; Langeland 1996; Pieterse 1981; Souza 2011
Subtotal			22	1.33	-	-	
2. Economic impacts	2.1. Agricultural production	Reduced irrigation	5	1	-	-	Balciunas et al. 2002; Langeland 1996; Pieterse 1981; Souza 2011
	2.2. Animal production	Reduced irrigation	5	1	-	-	Balciunas et al. 2002; Langeland 1996; Pieterse 1981; Souza 2011
	2.3. Forestry production	None	0	3	-	-	Balciunas et al. 2002; Langeland 1996; Pieterse 1981; Souza 2011
	2.4. Human infrastructure	Bridges, weirs, hydropower, pumps	5	1	-	-	Balciunas et al. 2002; Langeland 1996; Pieterse 1981; Souza 2011
	2.5. Human health	Disease vectors	2	1	-	-	Balciunas et al. 2002; Langeland 1996; Pieterse 1981; Souza 2011
	2.6. Human social life	Reduced water-based recreation	5	1	-	-	Balciunas et al. 2002; Langeland 1996; Pieterse 1981; Souza 2011
Subtotal	-	-	22	1.33	-	-	-
Total	-	-	44	1.33	-	-	-

[a], Confidence limits based on Nentwig et al. (2016) where 1 = low confidence – no empirical data or literature to support the impact score; 2 = medium confidence – no empirical data from South Africa, but literature from elsewhere to support the impact score; 3 = high confidence – empirical and published data from South Africa support the impact score.