Salvinia molesta D. Mitch. (Salviniaceae): impact and control

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Abstract

Salvinia molesta D.S. Mitchell (Salviniaceae) (giant salvinia), a floating aquatic fern of Brazilian origin, has been dispersed to much of the tropical and subtropical parts of the world since the mid-1900s, where it is invasive and damaging. Herbicide application and mechanical control of this weed are labor intensive and expensive, but biological control using the host-specific weevil, *Cyrtobagous salviniae* (Calder and Sands), provides an effective and sustainable solution. The weevil was first released as a biological control agent onto *S. molesta* in Australia in 1980 and has subsequently been released in further 22 countries affected by the weed. The biological control program against *S. molesta* has been an extraordinary success story where a single weevil species has resulted in the weed no longer being considered invasive in most countries in a relatively short time of under 3 years. Biological control in temperate regions of the world might require more time than in tropical and subtropical regions, and this difference is presumed to be due to greater winter mortality. Nevertheless, inundative releases of the weevil early in the growing season have resulted in more effective control and less dependence on herbicide applications. However, there are new records of infestations of *S. molesta* in particular in Africa, and these sites must be prioritized for biological control.

Keywords: biological control, *Cyrtobagous salviniae*, giant salvinia, invasive aquatic fern, socioeconomic and environmental impacts

Review methodology: The review was conducted using the literature accumulated by both authors over the last 20 years, in the form of books, book chapters, and journal articles, as well as "gray literature." Additional searches in Google and Google Scholar were made, using the keywords: *Salvinia molesta* impacts; *Cyrtobagous salviniae*; biological control of *Salvinia minima*; and chemical control of *Salvinia molesta*.

Introduction

Salvinia molesta D. Mitch. (Salviniaceae) is a ubiquitous aquatic invader, named after Antonio Maria Salvini (1633–1729). The species name *molesta* is derived from the Latin *molestus*, which highlights its weediness as it is a nuisance across the world, invading natural water bodies as well as artificial impoundments [1, 2]. This aquatic fern is native to a relatively small area in southeastern Brazil (between latitudes 24°050 S and 32°050 S) at elevations up to 900 m, where it forms part of the floating and emergent vegetation in wetlands, natural lagoons and swamps, slow moving rivers, and stream margins, as well as artificial impoundments and irrigation and drainage channels [3].

Over the last century, *S. molesta* has spread widely throughout the world, becoming an invasive alien species in many regions. Indeed, in 2013, *S. molesta* was elected as the one of the 100 of the World's Worst Invasive Alien Species to replace the Rinderpest virus, which was declared eradicated in the wild in 2010 [4]. The species is widespread in Africa (occurring in over 20 countries), the Indian subcontinent, Southeast Asia, Australia, New Zealand, the southern USA, and some Pacific islands [2]. The first population established outside the native range was in

Sri Lanka in 1939 where it was introduced via the Botany Department of the University of Colombo [5]. It was later recorded growing in Australia in 1952 and in Lake Kariba, Zimbabwe, in 1961 [6]. The weed was first reported in the USA from South Carolina in 1995 [7] and has since become established in at least 12 states [8]. It is also widely distributed across southern and southeastern parts of Asia, Papua New Guinea, New Caledonia, French Polynesia, Fiji, and New Zealand in the south Pacific [2]. *S. molesta* is reported from Europe including Austria, Belgium, France (Corsica), Germany, Italy, Israel, the Netherlands, and Portugal, but it is not clear if these records represent established populations [9]. The low winter temperatures characteristic of Europe may be the only factor restricting its growth and spread, despite most of the catchment systems being eutrophic and the fact that there is high commercial trade in this plant in the aquarium and water-garden industries [9].

In most countries where *S. molesta* is invasive, it has been classified as a noxious weed, and its culturing and movement are prohibited [9]. In the USA, *S. molesta* is on the Federal Noxious Weed List as governed by the Noxious Weed Act of 1974, which restricts movement of the weed across state lines without a permit [2]. *S. molesta* is a Weed of National Significance in Australia because of its invasiveness and its severe environmental, economic, and social impacts [2], while in New Zealand, *S. molesta* is listed on the National Plant Pest Accord prohibiting it from sale and commercial propagation and distribution. The species was excluded from a consolidated list in New Zealand by Howell [10] due to its absence from conservation land. In South Africa, the presence of the weed dates to the early 1900s, and it is listed as a Category 1b weed that has to be controlled under the National Environmental Management: Biodiversity Act (No. 10 of 2004) (NEMBA). Most African countries such as Botswana, Namibia, Zambia, and Zimbabwe recognize *S. molesta* as a noxious aquatic plant, but there is lack of legislation to deal with it; however, control measures against it are in place [2]. In Europe, *S. molesta* has been on the European Plant Protection Organization (EPPO) List of Alien Invasive Plants since 2012; and in 2016, it was identified as a priority for risk assessment, which subsequently concluded that *S. molesta* had a high phytosanitary risk to the endangered area [9] and was added to the EPPO A2 List of pests recommended for regulation (https://gd.eppo.int/taxon/SAVMO/categorization).

S. molesta is known by a variety of names, which include Kariba weed due to its successful invasion of Lake Kariba (Zimbabwe) in 1959 (then the world's largest man-made water reservoir), African pyle, African payal, water fern, giant salvinia (USA), giant azolla, and Australian azolla (Philippines) [11, 12]. It is part of a larger group of *Salvinia*, the *Salvinia auriculata* Aublet (Salviniaceae) complex, whose species have trichomes that form an "egg beater" or "cage," in comparison to other members of the genus whose trichomes are pointed. *S. molesta* was initially identified as a form of *S. auriculata,* until 1972, when it was reclassified as *S. molesta* by Mitchell (1972) based on the shape of the male sporocarps, which hang from the rhizome [1, 2, 13].

Due to the socioecological and economic impacts of this weed, various control measures have been implemented against it, including chemical, mechanical, and biological control. Although biological control by the weevil, *Cyrtobagous salviniae* Calder and Sands (Coleoptera: Curculionidae), has proved to be highly successful [11, 14–18], there has been less control achieved in areas where the weed grows as an understory species [19]. Shallow waters that occur in the shade provide a haven for *S. molesta* to establish, and when combined with the effect of falling water levels or eutrophication, the nuisance proportions of the weed may increase [19, 20]. Biological control in temperate regions is also variable [21–23] because agent population growth rate declines in winter [24]. Here we review the various impacts of this aquatic invasive, the measures used for its control, as well as recent developments highlighting factors influencing or constraining success of control.

Biological and ecological factors promoting invasiveness

S. molesta is considered one of the world's worst weeds because of its high mobility, tolerance to environmental stress, exponential growth rate, and level of difficulty to control [25–27]. It is a sterile pentaploid, reproducing by means of vegetative reproduction where viable fragments give rise to new plants [2]. *S. molesta* has a high growth rate and three distinct growth stages. During the primary growth stage, or the initial plant invasion stage, *S. molesta* produces smaller leaves (1.5 cm) and has long internodes, and floating leaves are flat on the water's surface, whereas leaves in the secondary growth stage are larger in width (2 cm), slightly cupped, and partially in contact with the water's surface [28]. The tertiary growth stage is the mat-forming stage and the only stage to bear sterile sporocarps [28]. The leaves are much larger in width (6 cm), intricately folded along shorter internodes, and sometimes do not come in contact with the water's surface [28]. At this stage, as plants mature into the tertiary growth stage, the dense mats expand and restrict access to the water body for commercial, agricultural, and recreational activities [22, 25, 27].

High light intensities coupled with high water temperatures and nutrient supply promote the growth of *S. molesta* [5]. The optimal temperature for *S. molesta* growth is 30°C, while no growth occurs below 10°C or above 40°C [29]. The exposure of *S. molesta* to adverse conditions with temperatures below −3°C and above 43°C may kill the plant [2], but in tropical regions, the impact of temperatures above 40°C is ameliorated by the buffering effect of water [30]. Plants exposed to low temperatures usually succumb to frost but may survive if covered by other *S. molesta* plants, or other vegetation, or protected by the temperature-buffering effect of water.

The weed also has the capacity to regenerate after being exposed to stresses such as frosts, droughts, and extreme heat with new leaves appearing on seemingly dead, brown weed mats. Buds can retain viability in dry and very hot conditions if they are sheltered within a multilayered weed mat [2].

Water nutrient quality affects *S. molesta* growth and therefore invasion. When nutrients are optimal, *S. molesta* is dark green with vigorous growth and characterized by wedge-shaped plants. Long, thin, yellowish plants often indicate poor water nutrient quality, and although this results in reduced invasiveness, it may also reduce the success of biological control [31]. Under ideal temperatures of 30°C and high nutrient levels, doubling of the infestation size can occur in about 3 days [31]. Once the water surface is covered, the *S. molesta* mats thicken vertically and may reach layers 0.5–1 m thick.

Invasion commonly occurs in disturbed areas, such as drainage or irrigation canals, rice paddies, artificial lakes, and hydroelectric reservoirs, or any other man-made structure that alters the hydrological flow of the water body [5]. In natural settings, the dispersal of *S. molesta* is mediated by water flow or wind, and by animals, which utilize natural water courses such as birds (worldwide), capybara (South America), hippopotamus (Africa), and water buffalo (Australasia) [2]. The spread of *S. molesta* is through viable fragments (nodes or apical buds), which are responsible for giving rise to new plants. Boats and vehicles that enter infested waters also act as agents of dispersal of *S. molesta* to new areas. The weed has also been widely spread by humans via the aquarium trade as water garden plants may be contaminated with propagules of the weed, thus enhancing its spread across the world [2].

Impact

Ecologically, mats of *S. molesta* cause similar problems to those caused by excessive growth of other floating macrophytes. The dense mats restrict photosynthesis in the water below, killing submerged plants through light deprivation [32]. The mats also lower water flow and turbulence of water, reducing the amount of oxygen that enters the water column; together with a reduction in photosynthesis, the oxygenation of the water column is limited, and dissolved oxygen (DO) is reduced, leading to anoxic conditions [2]. Additionally, decaying *S. molesta* that sinks to the bottom consumes DO, and the resultant reduction of oxygen in the water is characterized by high concentrations of carbon dioxide and hydrogen sulfide in the water [5, 14], leading to acidification of the waterway [2]. Increases in organic matter raise the sediment level, which reduces depth [22]. Fish nurseries and other breeding pools are affected as shallow nurseries have higher temperatures and decreased nutrients [22].

The high growth rate of *S. molesta*, coupled with the slow rate of decomposition, leads to the locking up of essential nutrients within its plant tissues, and this in turn impedes the process of nutrient cycling. Phytoplankton and macrophytes are thus deprived of the nutrients, which are essential in their role as primary producers, and other higher trophic levels are negatively affected [5]. Mat formation can have negative impacts on native animals and plants more generally by significantly altering aquatic habitats and therefore ecosystem structure and function in its exotic range. For example, the esthetic value and functioning of the Senegal River Delta, a World Heritage Site under the Ramsar Convention, and home to a variety of birds, many endemic to that region was eroded as a result of a *S. molesta* invasion [16]. A recent example of the ecological impacts of a *S. molesta* invasion comes from Malaysia [33]. Lake Tungog is one of 27 oxbow lakes once part of the Kinabatangan River in Sabah Malaysia, providing numerous ecological services to the region. It is a breeding ground for many fish and endangered wildlife, such as the Oriental darter (*Ardea purpurea*), Storm's stork (*Ciconia stormi*), and three species of otter. Since the 1990s, *S. molesta* has invaded every oxbow lake in the region, following natural flooding events that allowed it to spread to new areas. In the Lake Tungog itself, the weed threatens a vast array of native aquatic flora and fauna species. In turn, *S. molesta* is a major threat to three species of otter and a host of rare waterbirds, as these species no longer have access to the water or their natural source of food. Furthermore, Lake Tungog plays a vital role in restocking the neighboring river system with fish, especially during the annual wet season, when floods cause the lake and nearby river to merge. The presence of *S. molesta* has significant environmental impacts, not only in the lake itself, but also in the surrounding floodplain, threatening the collapse of the entire food web and ecosystem.

S. molesta also has economic impacts on human livelihoods where mats restrict utilization of both artificial and natural impoundments, as well as rivers for recreational and agricultural activities [34]. Losses in livestock have occurred due to drowning in infested waters. Occasionally, plants of various species will colonize thick *S. molesta* mats, forming "floating islands" of vegetation or mixed sudd communities, which hamper activities such as water abstraction, watering of domestic animals, docking of boats, and recreation [35].

In regions with livelihoods dependent on aquaculture and water transport, severe losses are incurred due to these infestations where there is disruption of water traffic, commercial, and sport fishing [2]. In the agro-based economies of low rainfall regions, *S. molesta* blocks irrigation pipes and fills in irrigation canals by accelerating siltation rates. For example, rice production in Sri Lanka was severely affected because *S. molesta* actively competes with crops for space and nutrients. The Department of Agriculture in Sri Lanka estimated losses in the affected areas to have been about 2%–3% [14]. *S. molesta* infestations in Senegal also led to a shift in the supply of rice where there was little of the product on the market. This raised prices for consumers, while production costs for the farmers increased due to the factoring in of abatement costs [16]. In this regard, the cost of living for people in these affected areas is raised.

Drinking water supply and quality is negatively affected, especially in terms of odor, color, and turbidity, which tend to increase cost of water purification for the responsible authorities [34]. The largest temperate infestation of *S. molesta* in Australia is the invasion of the Hawkesbury River, located north west of Sydney, New South Wales. The infestation has had significant impacts on Sydney's water supply because the catchment provides most of the city's water from the Warragamba Dam, as well as agriculture in the catchment, which generates AUS$1 billion annually, and recreation and fishing [36].

Health costs are also incurred because infestations of the weed may harbor vectors of diseases. The resurgence of mosquito borne diseases such as malaria, filariasis, Dengue fever, and encephalitis is concerning where control of these diseases also raises health costs for the affected countries, such as in Sri Lanka, where about 30% of the health budget of 1987 was dedicated to controlling mosquito borne diseases [14].

Control of *S. molesta*

While manual, mechanical, and chemical control may provide temporary relief, particularly in small infestations, biological control using the host-specific natural enemy, *C. salviniae,* has proven to be a highly effective method for control of *S. molesta* around the world. Nonetheless, experience in Australia has shown that management and control of *S. molesta* require site-specific applications where priorities depend on the prevailing climate, the nature and use of the water body, extent of the infestation, and the available resources for the undertaking [36] and may therefore require a combination of strategies for effective control.

Mechanical control

Manual and mechanical control entails the physical harvesting of the weed, by hand or using machines. Physical removal is aided using booms to accumulate or control the location of mats. These methods have been used in many instances, although rarely with great success and always at great expense. Costs of the management activities may range from $500 to $2400 per day in the USA [37] and far exceed the benefits accrued from the application of this control option as the weed growth rates are higher than the removal rates. Lack of follow-up management and monitoring results in a resurgence by the remaining plants [29].

There are very few instances where complete control of the weed by this method has been possible and are limited to new infestations where small amounts of *S. molesta* are detected early or small infestations on enclosed water bodies of up to 1 ha in area [36]. Follow-up measures are therefore essential to guard against reinvasion by new plants or resurgence by the missed plants [2]. Post-treatment monitoring is rarely undertaken due to the costs associated with it, and as such, mechanical control usually fails to provide sustainable control in the long term [11].

Lake Tungog in north-east Borneo, an oxbow lake and an important feature in the wetlands surrounding the lower reaches of the famous Kinabatangan River, was recently invaded by *S. molesta*. It is the center of Tungog Rainforest Eco Camp (TREC) (www.mescot.org), in Kinabatangan, Sabah Malaysia, run by Kopel-Mescot, which focuses on community-based ecotourism that connects four surrounding villages and encourages villagers to be part of the conservation and restoration of the surrounding rainforests and waterways [38]. Following floods in 2001, *S. molesta* invaded the lake and quickly covered the system. Kopel-Mescot received aid from the non-profit organization, Land Empowerment Animals People (LEAP), and the Alexander Abraham Foundation for restoration, which until recently, provided funds for the physical removal of *S. molesta* through containment and manual/mechanical removal, which was considered successful as it limited *S. molesta* infestations in the lake [38]. Unfortunately, the funds ran out, and *S. molesta* reinvaded the lake from plants left behind. The socioecological importance of restoring the lake was made known through a crowdfunding campaign in 2015 (https://www.crowdfunder.co.uk/borneo-lake-restoration-programme), which appealed for funds for continued physical removal. Despite receiving some funds, the program was not successful. Subsequently, a biological control program using *C. salviniae* was initiated in 2016, with the first release made in 2018, and results from sampling in 2019 suggest that the weevils have established (Gretchen Coffman, USF, pers. comm.).

Chemical control

Herbicide use has contributed to the control of *S. molesta* in a number of countries across the world. The first use of chemicals to control the plant was made in Sri Lanka in the 1940s in rice paddies and waterways using pentachlorophenol, while paraquat became the herbicide of choice from the late 1960s and 1970s to control *S. molesta* in Kenya, Botswana, Zimbabwe, Sri Lanka, Australia, and Papua New Guinea [25]. Since then, a number of different herbicides, surfactants, and detergents have been used *S. molesta* control. In Australia, diquat, glyphosate, calcium dodecyl benzene sulfonate, and orange oil have been used [36], while in New Zealand, fluridone was trialed in tank studies [39]. At concentrations lower than 100 mg/l, plants were not consistently killed, and because fluridone is very slow acting, effective control requires contact with the plants for 30–90 days [40]. Diquat and 2,4-dichlorophenoxyacetic acid (2,4D) were used in South Africa but are no longer permitted leaving glyphosate as the only registered herbicide there [2]. Chemical control is the primary means of control in the USA, but it is an expensive and often difficult option that must be conducted on a continual basis to achieve a significant reduction in *S. molesta* biomass. Here, permitted herbicides include diquat dibromide, fluridone, glyphosate, and several chelated copper compounds, which have been screened for: efficacy [26, 41, 42]; to evaluate spray volume [43]; and to determine the influence of seasonality/time of year on control [44]. While fluridone is regarded as one of the safer options, it is also the most expensive, with estimated costs of $2292.13/ha in 1999 [45]. Glyphosate is also relatively slow acting and as a result of expensive. For example, *S. molesta* treated with glyphosate applied at a rate of 8.97 kg/ha averaged 78.3% mortality after 28 days, in comparison to diquat applied at 1.12 kg/ha, which resulted in 100% mortality [26].

Herbicide application is usually made using hand guns, boom sprayers, and aircraft. When managing isolated or small plant infestations, chemical control is the most rapid control method [25]; however, as mat increases in coverage and thickness, chemical control becomes costly and often requires multiple applications throughout a growing season. In addition, herbicides are indiscriminate, affecting nontarget plants.

There are a number of limitations to this control method, the most significant of which is most probably the cost of chemicals alone, which, in 2009, were estimated to be in the range of US$210–US$900 per ha [2]. In addition, reduced accessibility to weed infestations, high costs of materials, and time consuming application of treatments often requiring repeated applications raise the costs significantly [2]. Herbicide uptake by the plant is also limited by the morphology of the leaves as the rows of trichomes on the upper surface of the *S. molesta* fronds act as a waterproof barrier to herbicides. The addition of wetting agents is therefore required before the application of a contact herbicide can be made, which also raises the costs of control even further and causes up to 20% mortality of the biological control agent, *C. salviniae* [46]. Although herbicides may have very rapid depleting effects against the weed biomass, in the long run, they do not provide a cost effective and environmentally friendly solution to the weed problem as post-treatment monitoring is not always conducted, repeated application is required, and nontarget plants are often affected too [25].

Biological control

Biological control relies on suitably host-specific natural enemies (biocontrol agents), mainly plant-feeding insects and mites, and pathogens that are sourced from their respective countries of origin to suppress the invasiveness of the targeted weeds, and is an ecologically sound method that aims to maintain weed populations at acceptable levels [47]. Floating macrophytes, including *S. molesta*, are particularly susceptible to biological control with a number of successful cases throughout the world. *S. molesta* has been brought under complete biological control by a single agent, *C. salviniae*, in a number of countries in as little as 2 years, to a point where it no longer threatens aquatic ecosystems [2, 48].

The native range of *S. molesta* was not known until 1978 because it was not considered a separate species from the *S. auriculata* complex. Therefore, the first surveys for biocontrol agents were conducted in the native range of *S. auriculata* in Trinidad, British Guyana, and Brazil, where three species were selected for host-specificity testing; *Cyrtobagous singularis* Hustache (Coleoptera: Curculionidae), the moth *Samea multiplicalis* Guenee (Lepidoptera: Pyralidae), and a grasshopper *Paulinia acuminata* De Geer (Orthoptera: Pauliniidae) [49]. However, it was only once the native range of *S. molesta* was known that additional surveys for natural enemies in Brazil in 1979 revealed the most effective control agent, *C. salviniae*.

Following host specificity testing, *C. singularis, S. multiplicalis,* and *P. acuminata* were released against *S. molesta* in Zambia and Botswana but failed to control the weed [50]. A weevil thought to be *C. singularis* was released in Australia in 1980 where it established and successfully controlled *S. molesta*. This weevil had been collected in southeastern Brazil on *S. molesta* and showed greater success in control than the Trinidad specimens, which was attributed to it being a different biotype to the ones collected from *S. auriculata*. In 1983, this weevil was reported to be a different species and was reclassified as *C. salviniae* Calder and Sands (Coleoptera: Curculionidae) [50].

Cyrtobagous salviniae

The morphology and biology of *C. salviniae* are extensively covered in Ref. [50] and summarized in Ref. [2]. Here, aspects of the weevil's biology that contribute to its success (or failure) as a biocontrol agent are covered. Forno *et al.* [51] conducted studies at 25.5°C, where adults mated more than once from 5 days after emergence and pre-oviposition behavior were observed between 6 and 14 days. Oviposition sites are commonly feeding holes in young unopened leaves or developing "roots" below the unopened leaves. Eggs normally hatch after 10 days at temperatures greater than 19°C [2, 23, 51]. Larvae complete three instars during their development, which takes between 14 and 28 days depending on the prevailing temperature. Larval development is optimal between 21°C and 30°C with nitrogen levels within host plant tissue being a major factor [51]. Development may occur at temperatures as low as 16.3°C under laboratory conditions [52]. After the third instar, larvae spin a cocoon of root hairs, which they attach to the "roots" below the water surface, and pupal development takes about 12 days at 25°C [52]. After eclosion, adult weevils are found on or among leaves, or underwater among the "roots" where they breathe by means of a plastron [51]. Adults feed at temperatures between 13°C and 33°C, but if daily maximum temperatures remain below 20°C for several months, weevil populations are unlikely to persist [31]. Thus, the temperature at which the weevils can initiate reproduction and complete their developmental stages is crucial to their success as biological control agents [53].

C. salviniae is a very effective herbivore of *S. molesta* where both adults and larvae inflict serious damage to the plants. The grazing behavior can stimulate the plants to produce more buds in a drive to compensate for the loss of buds, but these are also subsequently eaten [2]. The compensatory reaction by the weed eventually depletes the plant's resources and reserves, leading to a reduction in growth rate, and eventually a halt. Adults mostly feed on tender apical buds, leaves, and roots, preventing growth, whereas larvae tunnel inside the rhizome and destroy the plant structure in the process. Tertiary stage *S. molesta* suffers damage almost solely on buds due to adult feeding, while terminal leaves of primary and secondary plants are also prone to damage [54]. Feeding rates increase with an increase in temperature, while increases in nitrogen have no effect on feeding rates [51]. High plant nitrogen serves to stimulate oviposition, and both oviposition and feeding mostly occur nocturnally [55, 56]. Weevil damage is evident in the form of a gradually expanding brown patch on a weed mat. The brown *S. molesta* becomes water logged after the destruction of the aerenchyma tissue and sinks to the bottom of the water body creating a patch of open water [2].

Although *C. salviniae* is gregarious, with population's densities of 300 adults and 900 larvae/m^2 considered necessary to achieve a desirable level of control [29, 57], it is a relatively slow disperser until high populations deplete food resources, and then flight dispersal occurs due to scarcity of food [25]. In optimal conditions, weevils can reach these population densities, which allow them to deplete plants much faster than the plants can compensate for damage, leading to starvation of the weevils. Cycles of population build ups and crashes occur, rarely ever achieving a total equilibrium between host and herbivore [36].

The control of *S. molesta* in many tropical and subtropical countries has been achieved through the release of *C. salviniae* in the affected areas [13, 25, 57], and it is now the first choice strategy, at times applied in conjunction with other management options. In Australia, *C. salviniae* was introduced from Brazil in 1980 and released at Lake Moondarra near Mount Isa [13] where the weevil population of a few thousand expanded, clearing about 30,000 t of *S. molesta* in 1 year [1]. Subsequent releases in tropical and subtropical Australia resulted in consistent successes [36].

Following the great success in control in Australia, *C. salviniae* was introduced to Namibia, Botswana, and Zambia in 1983. *S. molesta* invaded Botswana via the Zambezi River in 1948 and became a serious weed in the Kwando/Linyanti/Chobe River systems on the border between Botswana and Namibia, severely hampering the fishing, hunting, and photographic industries in these systems. *C. salviniae* was released on the Namibian side of the Kwando/Linyanti in December 1983, and by 1987, the infestations on these systems had declined to the point where they were no longer considered a threat [15].

Another success story in the tropics is the control of *S. molesta* in Papua New Guinea (PNG) in the early 1980s. The weed entered the floodplain of the Sepik River in PNG in the early 1970s covering many lakes and channels. At the height of the infestation, villages were abandoned because inhabitants were unable to fish or access their local markets and schools [25]. In 1982, *C. salviniae* was introduced to one lagoon, and over the next 2 years, 900,000 adults were redistributed manually among another 130 lagoons and lakes [25]. The time taken for weevils to spread throughout a lagoon and for the weed to be controlled was generally 12–18 months, depending on the area of invasion, its thickness, and its mobility when blown by the wind, and an equilibrium appeared to be reached when *S. molesta* mats were reduced to less than 1% of former population densities. Within 2 years of releasing *C. salviniae* in PNG, *S. molesta* was reduced to 2 km^2 scattered across many lagoons, and village life had returned to pre-invasion normality [25].

S. molesta biological control in South Africa commenced with the release of *C. salviniae* in 1985. Next to *Pontederia crassipes* (Mart.) [≡*Eichhornia crassipes* (Mart.) Solms-Laub.] (Pontederiaceae), *S. molesta* was considered the most problematic aquatic invader in South Africa [17]. The proven success of the control measures in Australia, Papua New Guinea, and Namibia ensured the direct introduction of *C. salviniae* into South Africa in September 1985, from Eastern Caprivi, Namibia without going through the usual host specificity tests after Australian research had proved the weevil to be host specific [58]. Control of the weed was achieved throughout the country, even when faced with concerns that there would be limited success in the temperate regions [17]. At the end of the 1990s, successful biological control of *S. molesta* was achieved, and it was concluded that no further control measures were necessary, with the exception of further releases of the weevil to newly infested sites [17, 18].

In conclusion, those tropical and subtropical countries that have implemented biological control of *S. molesta* using *C. salviniae* have experienced successful control; temperate regions, however, have had fewer successes across a large scale, including Australia and the USA (Table 1).

Biocontrol in temperate regions

Successful biological control of *S. molesta* is limited by two main factors—temperature and plant quality [31]. When neither is limiting (e.g., in some tropical areas), populations of *C. salviniae* increase, spread quickly, and can affect control in less than a year [66]. However, in cooler regions, lower temperatures are more important influencing agent development, survival, and overwintering and therefore time taken for control [31, 51] (Table 2).

Table 1. Biological control of *S. molesta* by the weevil, *C. salviniae*; country and year of first release and the documented time to achieving control of the weed (updated from Refs. [59, 60], using personal knowledge and literature searches).

Country	Year	Level of control achieved (time between release and control)
Australia	1980	Excellent (13 months to 4 years) [25]
Botswana	1984	Excellent (1–5 years) [61]
Congo, Democratic Republic	2000	Excellent (less than 2 years) [62]
Fiji	1991	Good [59]
Ghana	1996	Good [59]
India	1983	Excellent (less than 3 years) [63]
Indonesia	1997	Unknown
Kenya	1991	Good [59]
Ivory Coast	1998	Unknown
Malaysia	1989	Good (14 months) [59]
Mali	2004	No establishment
Mauritania	2000	Excellent (18 months) [47]
Namibia	1984	Excellent [64]
Papua New Guinea	1982	Excellent (11 months to 2 years) [25]
The Philippines	1991	Unknown
Senegal	2001	Excellent (18 months) [47]
South Africa	1985	Excellent (1–3 years) [65]
Sri Lanka	1986	Excellent (usually 12–24 months) [66]
Togo (Republique Togolaise)	2001	Unknown
Uganda	2017	Excellent (Molo and Ogwang, pers. comm.)
The USA	2001	Moderate to excellent [67]
Zambia	1981	Excellent [59]
Zimbabwe	1992	Excellent (2 years)

Table 2. Effect of climate on biological control of *S. molesta* by *C. salviniae* (from Ref. [36]).

Climate	When to release *C. salviniae*	Time taken to control	Effect of control	Follow ups required
Tropical monsoon	End of wet season	Generally 12–24 months	Reduces *S. molesta* to an acceptable low level	Usually not required. Re-release if monitoring indicates weevils are not present, possibly after monsoonal flushing
Subtropical	All year round. Avoid releasing in cooler months	Generally 18–36 months	Reduces *S. molesta* to an acceptable low level	Usually not required. Re-release if monitoring indicates there is no presence of weevils
Temperate	Early spring. Avoid releasing after midsummer	3–4 years (in the absence of other interventions)	Reduces *S. molesta* to an acceptable low level, but in some areas other control methods will be required in addition to biocontrol	Re-release if monitoring after winter indicates there are no weevils present

In the southeastern USA, biological control of *S. molesta* has been limited by cold winters to southern regions [21]. *S. molesta* was first detected in the USA in 1995 from South Carolina, followed by reports from Louisiana and Texas in 1998 [68], and is currently reported from 17 states in the USA, with the most recent reports from Arkansas in 2008, and the Virgin Islands in 2012 (https://nas.er.usgs.gov/queries/FactSheet.aspx?speciesID=298). *C. salviniae* collected from *S. minima* in Florida was released in Louisiana and Texas in 1999 [67, 69], and then later, it was imported from Australia and established in western Louisiana and eastern Texas in 2001 [67]. In northern Louisiana and Texas, however, *C. salviniae* did not establish after release attempts in 2010–2011 after populations suffered high winter mortality [23]. This prompted investigations into the cold tolerance of *C. salviniae* from colder regions in its native range, further south in the Lower Paraná-Uruguay Delta (LPUD), South America, in an attempt to justify releasing a more cold adapted population. Indeed, populations of weevils from this region exhibited greater survival at 0°C, faster mean chill coma recovery time, and lower mean super-cooling point (SCP) than weevils from southern Louisiana populations [70] and suggested that this population should be considered for managing *S. molesta* in temperate regions.

However, overwintering weevil populations were later found in northern Louisiana in 2015, years after the initial releases, suggesting that these populations had developed cold tolerance mechanisms at these locations [24]. Phenotypic plasticity of *C. salviniae* could therefore be important for sustaining insect populations in the short term, while in the long term, Cozad *et al.* [24] suggested that efforts should focus on implementation of the foreign ecotype of *C. salviniae* from the Lower Paraná-Uruguay Delta, investigated by Russell *et al.* [70]. Alternatively, exposing populations of the weevil to artificial or natural winter refugia may provide microclimates for insect survivability and aid in long-term management of *S. molesta* [70]. Another tactic could be laboratory cold-hardening over a number of generations, followed by releases to climatically unsuitable areas to improve establishment and overwintering success. Ultimately, *C. salviniae* is able to suppress *S. molesta*, including at more temperate locations that regularly experience below freezing temperatures during the winter. Despite the weevil's ability to disperse on its own and find new infestations, mass rearing of insect colonies for redistribution to new infestations is needed in more temperate areas to provide sustainable control of this *S. molesta*.

Plant quality influences biocontrol success

Success of biological control of *S. molesta* is dependent on a number of additional abiotic site conditions that influence the growth of *S. molesta,* including conductivity, salinity, pH, light intensity, and perhaps most importantly, the abundance of nitrogen [1]. While these factors regulate the growth and population dynamics of *S. molesta* in the absence of natural enemies [71], they induce phenotypic differences in the plants [31], which affect developmental rates, survival, and fecundity of *C. salviniae* [67].

Room [1] explored the effects of two water-nitrogen concentration levels and climate at three latitudes on *S. molesta* population dynamics, as well as damage inflicted by weevil feeding. The populations of the weevils increased faster on plants with high nitrogen content because female fecundity increases with tissue nitrogen concentration [31]. Larval tunneling within the plant rhizomes usually leads to the destruction of many sections of rhizome when there is low plant tissue nitrogen concentration (less than 1.5% dry weight), and fewer sections of rhizome are destroyed at higher tissue nitrogen concentrations [31]. In areas where high temperatures occur, combined with high nitrogen in water, control of *S. molesta* is achieved in contrast to low temperature and nitrogen sites. Occurrence of high temperatures and nitrogen favors high population growth rates for *C. salviniae* and therefore control of *S. molesta* [22].

While successful control of *S. molesta* has been achieved at a number of sites in South Africa, post-release evaluations between 2008 and 2015 revealed a number of new sites where control was less successful [18]. In South African waterbodies, the amount of shade impedes biological control of *S. molesta*, where plants growing in the shade suffer less damage than those exposed to the sun. Resurgences of the weed therefore result from the reserve of plants growing in the shade, thus presenting a continuous challenge even after successful control [32]. Even though *S. molesta* remains under good biological control in South Africa, larger and shaded sites require intermittent strategic management, such as augmentative releases of *C. salviniae* [18].

Disease threatens biological control success

The effectiveness of *C. salviniae* introduced to South Africa could be reduced as a result of infection by the parasitic green alga, *Helicosporidium* sp. [72–74]. *Helicosporidium* sp. infection was first detected by White *et al.* [72] from field-collected adults of *C. salviniae* in South Africa in the early 2000s. Subsequent field surveys in 2018/2019 to collect *C. salviniae* from a number of sites throughout the country showed that *Helicosporidium* sp. infection was found at every site sampled, and 92.15%–100% of the insects per site were infected (T. Mpephu, unpublished data). However, at this stage, it is uncertain what impact this disease has on the weevil population.

Integrated control

In the USA, where many managers rely on short-term effectiveness of control methods, such as lake drawdowns and large-scale applications of herbicides, which are not environmentally friendly, efforts to integrate control methods of *S. molesta* have been limited. Biological control using *C. salviniae* is another tool in the toolbox for plant managers, but very little information is available on the direct and indirect impacts of herbicides on the weevils. Recent research in the USA has focused on evaluating recently registered, lower-risk aquatic herbicides and surfactants, which are applied at very low use rates and concentrations and possess a high degree of selectively against target plants, thereby minimizing damage to desirable vegetation [75, 76]. Mudge *et al.* [77] investigated the interactions of some of these newer herbicides, surfactants, and *C. salviniae* for control of *S. molesta* and found that weevil mortality varied between 5% and 47% depending on the herbicide and surfactant used, but more importantly, that all weevil and herbicide treatments (alone or combination) resulted in reductions of 52% to 97% in *S. molesta* biomass 4 weeks after their treatments.

Integrated control of *S. molesta*, particularly in the USA where biological control does not provide the rapid results required by water managers, could go a long way in reducing the need to broadcast spray herbicides across large invaded water bodies. Ultimately, weed management decisions in the USA are context driven; for example, a lake manager for a hydroelectric plant or a pond manager for duck hunting has more incentives and significant resources to control *S. molesta*. Mudge *et al.* [77] highlighted the potential for the use of contact or systemic herbicide in invaded systems where *C. salviniae* has been released and recommend that lower herbicide rates in combination with weevils to decrease costs should be investigated, with the outcome of increased weevil survival as more plant material will be available for weevil longevity.

Conclusion

The origin and impact of *S. molesta* are well documented [2]. The success of *C. salviniae* as a biological control agent has been repeated in a range of countries, climates, and habitats (including disturbed habitats), and there have been no reported adverse nontarget effects on other organisms during or following biological control of *S. molesta*. New sites of infestation (e.g., Cameroon, Uganda and Borneo, Malaysia) have been reported, and the first priority for the management of *S. molesta* at these sites should be the release of *C. salviniae*. However, in more temperate regions, particularly in the southern USA, where the success of biological control of *S. molesta* is confounded by slow population growth rates, and where control relies on broad-scale herbicide applications, more prudent approaches combining biological and herbicidal control technologies to achieve rapid biomass reduction and long-term control are being explored [77].

Quantifying success in classical weed biological control programs is difficult, requiring considerable resources over a long-time period, and they are therefore largely neglected, or superficially conducted [78, 79]. Although it is generally accepted that an effective program should reduce the density of the invasive weed to below a pre-determined ecological, economic, or social threshold [80], the assumption is that the system returns to a pre-invasion state, which might not be the case. There are very few studies that have monitored aquatic ecosystem recovery post-biological control (e.g., [81]). Thus, the challenge for aquatic weed biological control globally is to embark on post-release evaluation programs in which the responses of ecosystems following the reduction of a weed's competitive advantage through biological control are measured and compared to the pre-invasion state.

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