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INVASIVE SPECIES III

Review Paper

Maintenance management and eradication of established aquatic invaders

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Abstract Although freshwater invasions have not been targeted for maintenance management or eradication as often as terrestrial invasions have, attempts to do so are frequent. Failures as well as successes abound, but several methods have been improved and new approaches are on the horizon. Many freshwater fish and plant invaders have been eliminated, especially by chemical and physical methods for fishes and herbicides for plants. Efforts to maintain invasive freshwater fishes at low levels have sometimes succeeded, although continuing the effort has proven challenging. By contrast, successful maintenance management of invasive freshwater plants is uncommon, although populations of several species have been managed by biological control. Invasive crayfish populations have rarely been controlled for long. Marine invasions have proven far less tractable than those in fresh water, with a few striking eradications of species detected before they had spread widely, and no marine invasions have been substantially managed for long at low levels. The rapid development of technologies based on genetics has engendered excitement about possibly eradicating or controlling terrestrial invaders, and such technologies may also prove useful for certain aquatic invaders. Methods of particular interest, alone or in various combinations, are gene-silencing, RNA-guided gene drives, and the use of transgenes.

Keywords Biological control · Chemical control · Gene drive · Gene-silencing · Pheromone · Sterile male

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Introduction

Occasional opinions are voiced that attempts to eradicate any established invaders—terrestrial or aquatic—or to manage them are largely futile and expensive (e.g., Vince, 2011). "Eradication" connotes total removal of all individuals of an entire population from a discrete area not contiguous with other occupied areas, whereas "maintenance management" is simply controlling the population at acceptably low levels. In fact, great progress has been achieved in both eradicating and managing terrestrial invaders (Simberloff et al., 2018; Veitch et al., 2019), although much of this progress is largely unpublicized in either scientific or lay media. Some successes come from incremental improvements in existing technologies (Clout & Williams, 2009; Simberloff, 2009) and some from different directions entirely or great advances in an existing method (e.g., Campbell, 2002). However,

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the scientific literature has many fewer reports of successful control strategies for aquatic invasive species. An example of this disparity is provided by the 2017 IUCN conference in Dundee, Scotland (Veitch et al., 2019). This conference, nominally about controlling island invasives, included many presentations on continental invasions as well. The 108 papers and 70 additional abstracts dealt with management of 50 terrestrial species (5 rodents, 7 other mammals, 8 birds, 7 herptiles, 16 plants, 5 insects, and 2 other invertebrates). By contrast, 25 aquatic species were treated (2 mammals, 7 herptiles, 5 fishes, 3 plants, 5 crayfish, and 3 other invertebrates). Of the actual management projects described (not including policy papers), 90 were on terrestrial species and 11 on aquatic ones.

A widespread perception is that freshwater and especially marine invasions are much harder than terrestrial ones to manage (e.g., Francis & Pyšek, 2012; Moorhouse & Macdonald, 2015). One major reason is that, because they are always or intermittently underwater, aquatic invaders are harder to see. Also some techniques useful in terrestrial settings (especially various physical and mechanical techniques) are more difficult to apply. The connectivity of many water bodies is often cited as a problem; for instance, invaders may easily recolonize a cleared area following treatment, and some management techniques, particularly chemical and biological control, present risks to non-target organisms, including humans in the case of chemical control (e.g., Francis & Chadwick, 2012; Francis & Pyšek, 2012). However, the connectivity issues also pertain to managing terrestrial invaders. Among well-known terrestrial invasion corridors are railroads and their rights-of-way (e.g., Mack, 1981) and roads and their verges (e.g., Brisson et al., 2010). The details of the issues vary from case to case in both terrestrial and aquatic environments.

Freshwater invasions, particularly in small, circumscribed water bodies, have been the target of far more eradication and maintenance management attempts than marine invasions. Part of the reason is that many marine species are "cryptogenic": they occupy entire coasts of one or more than one ocean, lack substantial fossil records, and might have been transported by early seafarers (Carlton, 1982, 1996; Darling & Carlton, 2018). It is thus likely that, in many regions, some marine species that are introduced are not recognized as such and therefore are not targeted for management. Another reason fewer marine invasions are targets of eradication or management is that, even when their non-native status is known, their impacts may not be recognized until they are substantial and the invasion is widespread (Locke & Hanson, 2009). Although it may be difficult to determine if the presence of certain species in freshwater bodies results from natural range expansion or anthropogenic introduction (e.g., Fuller et al., 1999), for myriad freshwater species the introduced status is certain or nearly certain owing to a combination of historical records, geographical considerations, and paleontological and/or molecular genetic research. Another factor complicating attempts to control marine invaders is the frequent difficulty of delimiting the boundary of the invasion, so it is often not evident what area would need to be treated to eradicate or to manage a marine invader. This is not an issue in small, discrete freshwater bodies. Finally, unless a marine invasion is in the intertidal zone, physical management will involve divers and mechanical management will entail use of machines, nets, or traps underwater. Physical management of invaders in terrestrial systems is far less logistically challenging and has recorded many successes (Pickart, 2011), and for some freshwater systems, water bodies can be drained or drawn down to facilitate controlling invasions.

A complication in assessing eradication is that the term is often used colloquially, even by scientists, to mean simply substantial control but not removal, or total removal of all individuals from only one part of a continuous area occupied by a population (Simberloff, 2003). Other times, a failed eradication can become a maintenance management success if the same method used in an eradication attempt, if used repeatedly on an ongoing basis, succeeds in substantially reducing the population of an invader.

This paper reviews efforts to eradicate or manage aquatic and marine invaders, emphasizing successes as well as failures. The technologies employed and their evolution are described, as are new methods currently in development, especially those relying on advances in molecular genetics.

Eradication

Freshwater

The iconic successful aquatic mammal eradication was that of the nutria, *Myocastor coypus* (Molina, 1782), from a large region of southeastern England, a meticulously planned and well-funded government trapping effort lasting ten years (Gosling, 1989; Gosling & Baker, 1989). An ambitious trapping project loosely modeled on the British effort was initiated by a partnership of federal and state agencies and non-governmental organizations (NGOs) in 2002 to eradicate nutria from the Delmarva Peninsula and adjacent Chesapeake Bay, USA (Kendrot, 2014). As of September 2019, it is believed to have succeeded, but verification procedures are continuing (Anonymous, 2019). Two small nutria populations, in California and Indiana, USA, were eradicated earlier (Carter & Leonard, 2002). In the Outer Hebrides, an ongoing traping project by the European Union, Scottish government agencies, and NGOs to eradicate American mink, *Neovison vison* (Schreber, 1777), from a series of islands eliminated them from Uists (North Uist, Benbecula and South Uist) and set the stage for an attempt to remove them from other islands (Roy, 2011; Roy et al., 2015). An important innovation is the use of detector dogs to locate dens. By 2019, it was believed that the larger islands of Lewis and Harris were almost if not wholly mink-free, and a new population in the Uists was being removed (Macleod et al., 2019; Scottish National Heritage, 2019). The American mink was also eradicated from 989 km^2 Hiiumaa Island (Estonia) by trapping between 1998 and 2000 in a government project (Maran, 2003). Between 1932 and 1939, the muskrat, *Ondatra zibethicus* (Linnaeus, 1766), was eradicated in Great Britain (Sheail 1988; Gosling & Baker 1989), although the substantial non-target mortality rate suggests that the government campaign, which relied on trapping, might have to be conducted differently if it were undertaken nowadays (Usher, 1986). A similar government trapping campaign initiated in 1933 to eradicate muskrat from Ireland succeeded by 1935 (Fairley, 1982).

Rytwinski et al. (2019), reviewing freshwater fish removal projects for 39 species in 28 genera, tallied 77 attempted eradication attempts and another 12 projects in which either eradication or maintenance management was the stated goal. The majority of these eradication projects reported success, although Rytwinski et al. (2019) questioned the adequacy of the evidence in many cases. Most projects used one main technology, but others used combinations [e.g., chemical plus physical methods (including electrofishing)]. A subsequent report of several eradication projects in Norway, all successfully completed by means of piscicides, adds three more genera and species (Bardal, 2019). Environmental DNA analysis to help determine whether an eradication has been successful or whether further effort is needed has been employed in a government project using trapping and biological control to eradicate topmouth gudgeon, *Pseudorasbora parva* (Temminck and Schlegel, 1846) in English ponds (Davison et al., 2017) and could be employed to the same end for other aquatic eradication projects in clearly bounded locations.

Although Rytwinski et al. (2019) did not focus on the reasons why eradication was attempted, several of the cited papers, or follow-up studies, reported substantial benefits from successful projects. For instance, eradication by federal and university researchers of non-native trout populations by gillnetting from three California lakes resulted in significant increases in populations of a declining frog of conservation concern, *Rana muscosa* Camp, 1917 (Knapp et al., 2007). Another reported consequence of a freshwater fish eradication was eradication of a parasite from a region by eradicating native host fish populations. A Norwegian government agency eradicated the monogenean salmon fluke, *Gyrodactylus salaris* Malmberg, 1957, a damaging non-native parasite in Norway of wild Atlantic salmon (*Salmo salar* Linnaeus, 1758), by eradicating salmon populations with rotenone, then reintroducing salmon from other locations that are parasite-free (Sandodden et al., 2018).

Several attempts have been mounted to eradicate invasive crayfish populations by various methods (Holdich et al., 1999; Stebbing et al., 2014; Sandodden, 2019). Successes have been reported for three of these, consisting of eradication of the signal crayfish, *Pacifastacus leniusculus* (Dana, 1852), from small ponds and streams by use of synthetic pyrethroids. Two of these projects were mounted in Norway by a government agency (Sandodden & Johnsen, 2010; Sandodden, 2019) and one in Scotland by government agencies in cooperation with an NGO (Ballantyne et al., 2019). Populations of the hairy marron crayfish, *Cherax tenuimanus* (Smith, 1912), endangered in its native Australia, were eradicated by a government agency from two small ponds near Auckland by draining the ponds (Gould, 2005; Duggan & Collier, 2018). Many projects aimed at eradicating crayfish also explored the possibility of maintenance management, and they will be discussed in this context below. An apparently successful project by an interstate government agency to eradicate quagga mussels (*Dreissena bugensis* Andrusov, 1897) from a small Pennsylvania lake by means of ionic copper was recently reported (Hammond & Ferris, 2019). The Japanese copepod *Sinodiaptomus valkanovi* Kiefer, 1938 was eradicated in Bulgaria by destruction of the constructed pond in which it was found, and the copepod *Boeckella symmetrica* Sars G.O., 1908, possibly introduced from Australia, was eradicated in a New Zealand quarry by infilling (Branford & Duggan, 2017).

For freshwater fish invasions (Rytwinski et al., 2019) and terrestrial mammal invasions of islands (DIISE Partners, 2014), comprehensive reviews have been published of the details and outcomes of attempted eradications. Woldendorp & Bomford (2004) lamented the absence of a comprehensive review of attempts to eradicate weeds, a lacuna that still has not been filled for weeds in general or for aquatic plants in particular, although recent reviews of management approaches for aquatic plants (Hussner et al., 2017; Hofstra et al., 2018) provide many examples. Although no project of the scale of the nutria eradication in England has succeeded, certainly many small populations of invasive aquatic plants have been eradicated by chemicals, hand-pulling, suction pumps, bottom-shading, biological control, draining or drawdown of small water bodies, and various combinations of these techniques: e.g., *Myriophyllum spicatum* L. by draining a water body (Thurston County Department of Water and Waste Management, 1995), *Nymphoides geminata* (R.Br.) Kuntze (Clayton, 1996) by means of a polyethylene covering, *Nymphoides peltata* (S.G. Gmel.) Kuntze (Champion & Clayton, 2003), *Lagarosiphon major* (Ridl.) by hand-weeding, suction-pumping, and lining the bottom of a water body (Clayton, 1996; Bickel, 2012; De Winton et al., 2013; Champion & Wells, 2014), *Egeria densa* Planch. by biological control (Rowe & Champion, 1994; Champion & Wells, 2014), *Ceratophyllum demersum* L. by biological control (De Winton et al., 2013; Champion & Wells, 2014), *Menyanthes trifoliata* L. (Champion & Clayton, 2003), *Hydrilla verticillata* (L. f.) Royle by herbicide treatment (Kratville, 2013; Anonymous, 2017), *Potamogeton perfoliatus* L. (Champion & Clayton, 2003), *Alternanthera philoxeroides* (Mart.) Griseb. by herbicide treatment (Gunasekera & Bonila, 2001; Schooler, 2012), *Pistia stratiotes* L. (Champion & Clayton, 2003), *Zizania palustris* L. (Champion & Clayton, 2003), and probably *Ludwigia grandiflora* (Michx.) Greuter & Burdet by hand-weeding (Hussner et al., 2016). An interesting feature of some eradications was the role of biological control, which aims not for eradication but for a long-term, stable persistence of the target pest in low density. Grass carp, *Ctenopharyngodon idella* (Valenciennes, 1844), which are generalized herbivores and thus need not rely on a particular target species to persist, eradicated *E. densa* from a small New Zealand lake, after which the carp were removed, and *H. verticillata* from a slightly larger lake (Hofstra et al., 2018) in government projects.

An enormous literature on different projects and methods used on aquatic plants will be addressed below with respect to maintenance management, but several points require mention here. (1) Most of the literature on aquatic plant eradication deals also with maintenance management by the same methods, and several failed eradications have led to more or less effective long-term maintenance management. (2) Many aquatic plant projects denoted “eradication” would not technically qualify as eradication because they targeted only a part of the invasive population that is not discrete. Thus, even if the project is viewed as a success, reinvasion is certain and the project becomes one of maintenance management, if “eradication” is again undertaken. Rapid recolonization also occurs with some discrete populations: e.g., the eradication of *M. spicatum* noted above was quickly followed by reinvasion because of a public boat ramp, leading to implementation of a maintenance management program (M. Swartout, pers. comm., 2003).

Marine

The record for successful eradications of marine invaders is far skimpier than that for freshwater invasions and is largely restricted to intertidal invasions or those in shallow water near shore. A joint operation by a state agency, commercial mariculture facilities, and academic scientists eradicated the South African sabellid polychaete worm, *Terebrasabella heterouncinata* Fitzhugh & Rouse, 1999, which parasitizes abalone and other gastropods, at an intertidal site in California, with volunteers removing 1.6 million potential hosts, thereby breaking the infection cycle (Culver & Kuris, 2000). An intertidal invasion of the brown alga *Ascophyllum nodosum* (Linnaeus) Le Jolis, 1863 on the western side of San Francisco Bay was similarly removed by hand by volunteers mobilized by state and federal agencies (Miller et al., 2004), although another, larger invasion on the east side of the bay was discovered in 2008, and a similar eradication attempt was mounted (Anonymous, 2008). However, the species was again detected at the site in 2017; it is uncertain whether these individuals descend from those targeted by the earlier attempt, which then was a failure, or represent a new introduction from discarded packing material used for bait from Maine (G. Ruiz, pers. comm, 2020).

A larger, subtidal eradication was that of the Caribbean black-striped mussel, *Mytilopsis sallei* (Recluz, 1849), discovered near three marinas in 1999 in Cullen Bay (12.5 ha), Darwin Harbor, Australia, before it had spread further (Bax et al., 2002). In a joint project of the Northern Territory government and national government agencies, within nine days the bay had been quarantined and treated with liquid bleach and $CuSO_4$, and the mussel population was eradicated. In addition, all 27 ships that had left the harbor since the discovery were examined, as were all 400 ships that had been in the marinas since the hypothesized date of the invasion. A cooperative operation by federal, state, and local agencies as well as private groups and NGOs eradicated the marine alga *Caulerpa taxifolia* (M.Vahl) C. Agardh, 1817 between 2000 and 2002 from two sites in California, a lagoon and a series of small ponds connected to a harbor, by means of bleach (5% sodium hypochlorite) and chlorine released under tarpaulins anchored on the bottom under water (Anderson, 2005; Muñoz, 2016). In South Australia, a state agency eradicated *C. taxifolia* from an artificial marine water body by temporarily replacing salt water with freshwater (Walters, 2009).

In 2000, attached sporophytes of the invasive non-native seaweed *Undaria pinnatifida* (Harvey) Suringar, 1873 were found on a recently sunk trawler off the coast of Chatham Island, New Zealand. A commercial firm commissioned by a government agency quickly subjected these sporophytes to a heat treatment that killed all sporophytes and gametophytes and prevented further colonization of the region (Wotton et al., 2004). The eradication of the mussel *Perna perna* (Linnaeus, 1758) from a deep soft-sediment site in central New Zealand, coordinated by a government ministry, exemplifies the difficulty of such projects and the importance of the invasion being restricted to a small site. It required 227 dredge tows covering 94% of a 13-ha site, and 35 tons of material dredged from the seabed were deposited in a landfill (Hopkins et al., 2011). For all four of these subtidal eradications, a key aspect of their success was that the invasion was recent and the assumption that it was still restricted to a small area proved to be correct.

Against these few reported successful eradications of marine invaders are many accounts of failed attempts (Ojaveer et al., 2014), and no doubt failures are proportionally under-reported in the literature (Locke & Hanson, 2009). Among such failed eradication projects are those targeting *C. taxifolia* in France (Meinesz, 1999), *U. pinnatifida* in many nations (Wallentinus, 2007), the brown seaweed *Sargassum muticum* (Yendo) Fensholt, 1955 in the United Kingdom (Critchley et al., 1986), the ascidian *Didemnum vexillum* Kott, 2002 in New Zealand (Pannell & Coutts, 2007) and the United Kingdom (Sambrook et al., 2014), and the whelk *Rapana venosa* (Valenciennes, 1846) off the coast of Brittany (Mann et al., 2004).

As for why eradication of marine invaders has so rarely succeeded, failure to act quickly enough, before an invasion has spread, is doubtless a major factor and can be due to failure to detect the invader quickly enough, failure to identify it as non-native, or absence of adequate literature to suggest that it will be consequential (Locke & Hanson, 2009). Perception of the public and policymakers that marine environments are “open” and thus an eradication attempt is unlikely to reach all individuals of the invading species also plays a role (Thresher & Kuris, 2004). As noted above, the fact that marine invaders (except for intertidal ones) are underwater makes their detection and any management procedures more difficult than for terrestrial species, and for much of the marine environment delimiting the invaded area is particularly difficult. It is striking that, for the four successful subtidal eradications described above, evidence suggested that the invasion was very recent, and for *C. taxifolia* the targeted sites were substantially closed to the larger marine environment.

Maintenance management

Maintenance management requires a long-term commitment to maintain populations of an invasive species at a low level and to thus minimize damage. Innumerable projects, both terrestrial and aquatic, have substantially lowered populations of targeted invaders, but ultimately control foundered because the effort was not sustained, usually because the ongoing cost of the project was deemed unsustainable or interest in management waned once the targeted population was reduced by the initial effort. Another hindrance to successful long-term maintenance management is the possibility of continuing reinvasion of a managed site from an unmanaged site, an issue that of course depends on the spatial extent of the invasion and effective connectivity between sites.

Freshwater

Populations of American mink have been successfully maintained at low levels by trapping in a large region of mainland Scotland beginning in 2006 through a partnership comprising a government agency, a national park, and local fisheries boards and capitalizing on recruitment and training of a corps of enthusiastic volunteers (Bryce et al., 2011; Raynor et al., 2016). This project is maintained despite ongoing reinvasion from nearby areas. Perhaps the key factor in its success is the perception of many stakeholders that aggressive management is feasible and in their interest, and this program is cited as an example of both the importance of engaging many stakeholders and how this may be achieved (Shackleton et al., 2019).

In their review of freshwater fish eradication projects cited above, Rytwinski et al. (2019) also reviewed projects aiming for maintenance management of invasive freshwater fishes, identifying 69 such projects reported in the literature. They included another 12 projects for which the goal was either eradication or maintenance management and a failed eradication that conferred some sustained control was therefore viewed as successful maintenance management. Their original authors deemed many of these projects successes, although Rytwinski et al. (2019) questioned the validity of this classification in most cases. Whereas eradication attempts entailed physical and chemical methods with approximately equal frequency, only four maintenance management projects used chemicals and most used physical methods, especially electrofishing and netting.

Holdich et al. (1999) list several attempts to control invasive crayfish by mechanical or physical means, some of which substantially reduced the population, often at great expense, but none of them were consistently implemented over the long term. Several chemicals have been tested for efficacy with more or less promising results (Holdich et al., 1999), but expense and non-target impacts are a concern for many of these, and sequestering of a toxin that will then be ingested by a predator on crayfish can be an issue. Gherardi et al. (2011) and Stebbing et al. (2014) reported little success from an array of attempts to control non-native crayfish by draining water bodies, mechanical or physical means, and chemicals, pointing in many cases to the importance and expense of maintaining a program that is initially successful. A sense of the effort required to control a crayfish population over the long term was provided by an experiment by university researchers, who removed 91,930 individuals of *Orconectes rusticus* (Girard, 1852) from a 64 ha Wisconsin lake over eight years by intensive trapping, with 1,300–15,000 trap-days per year, plus regulated sport fishing. Four years after the project ended, *O. rusticus* densities remained low, suggesting that a surge of very heavy trapping could suffice to reduce crayfish populations for years (Hansen et al., 2013).

Aldridge et al. (2006) and Costa et al. (2012) have proposed the use of “BioBullets,” tiny beads consisting of a biocide surrounded by a nutrient shell that masks the presence of the toxin, to control fouling by populations of zebra mussel, *Dreissena polymorpha* (Pallas, 1771), that interfere with municipal and industrial operations. The mussel ingests the beads by filter-feeding, the lipid shell is digested away, and the biocide, potassium chloride, kills the mussel. However, the utility of the method in open water for conservation purposes is questionable because non-target organisms can also be killed as they ingest the beads.

Maintenance management of invasive non-native aquatic plants by mechanical or physical harvest has usually proven futile except in very small, contained water bodies because of rapid regrowth of remnants or recolonizers, which often manifest prodigious productivity. When commitment and funding decline after an initially successful program to control a population, an invasion may reestablish itself quickly (Hofstra et al., 2018). The problem is exemplified by numerous attempts to control water hyacinth, *Eichhornia crassipes* (Mart.) Solms, by such means. Biomass doubling time for water hyacinth varies greatly depending on environmental context but is as short as four days, with a growth rate of 228 metric tons/ha/year (Newete & Byrne, 2016). In fact, such high productivity is a key factor in a century-long litany of failures to sustain reduction of water hyacinth in many African nations by various combinations of mechanical, chemical, and biological methods (Kitunda, 2018). Water hyacinth also exemplifies the context-dependency of the efficacity of many management methods. Biological control of a massive invasion in Florida failed (Schardt, 1997), while the same biological control agent succeeded in substantially reducing water hyacinth in Lake Victoria, possibly aided by weather associated with an El Niño event (Wilson et al., 2007). By contrast, the herbicide 2,4-D controls water hyacinth well in Florida (Schardt, 1997). Several authors have suggested that chemical and biological control of water hyacinth could be fruitfully combined. For instance, in Florida, Tipping et al. (2017) propose that two established biological control agents could allow a lower frequency of treatments with 2,4-D.

Context-dependency is also exemplified well by efforts to manage alligator weed (*A. philoxeroides*). Introduction of the alligator weed flea beetle *Agasicles hygrophila* Selman and Vogt, 1971 in Florida in the 1960s has been termed “the world’s first aquatic weed success story” (Buckingham, 1996), and in fact the beetle continues to control alligator weed in aquatic habitats in Florida. However, it has proven unable to do so in more northerly locations and in terrestrial habitats (Allen et al., 2007; Lu & Ding, 2010; Schooler, 2012). Thus, researchers have sought management based on mechanical and chemical methods (Dugdale & Champion, 2012), but neither approach has proven effective in the long term (Schooler, 2012).

The review by Hussner et al. (2017) emphasizes the striking context-dependency of efforts to eradicate invasive aquatic plants or to control them in the long term but features several rough generalizations. Ceteris paribus, submerged species have been more difficult to manage than floating species. In both instances, facilitation of dispersal of plant fragments or seeds by physical and mechanical methods is a frequent problem, and except for hand-weeding and certain suction dredges, these methods are not species-specific. The range of management options is often determined by laws and regulations—e.g., ability to use certain herbicides or to release certain biological control agents. Many invasive aquatic plant populations have been greatly reduced by a range of herbicides (cf. Madsen, 1997), but long-term maintenance can be thwarted by both the ongoing expense and the evolution of resistance. For instance, in Florida, invasive *H. verticillata* had been controlled well by the herbicide fluridone until three different strains evolved that are resistant to fluridone as well as to chemically similar herbicides (Michel et al., 2004; Puri et al., 2009). In Florida hydrilla is a vegetatively reproducing female clone, but resistance nevertheless evolved by means of somatic mutations (Michel et al., 2004).

With respect to classical biological control, several successful examples exist in addition to water hyacinth and alligator weed, but so far these have all been on emergent or floating species rather than submersed species. Introduced fishes, especially grass carp (*C. idella*), have frequently been employed to control invasive aquatic plants, but the fact that they are not selective means that, depending on the management goal, they may be unsuitable. Grass carp have even been used along with tench (*Tinca tinca* Linnaeus, 1758) in successful eradication of *E. densa* in a small lake, but both fish species were removed with rotenone after the eradication to prevent herbivory of native plants (Rowe & Champion, 1994). In sum, Hussner et al. (2017) stress that many variations exist on the themes of mechanical/physical control, chemical control, and biological control, but that contexts differ among cases and determine both the feasibility of maintenance management and the methods most likely to succeed.

Marine

I can find few attempts at sustained maintenance management of a marine invader, and no example manifesting success in the long term. The problems are exemplified by many failed attempts to control *U. pinnatifida* (Epstein & Smale, 2017). Manual removal requires the ongoing expense of divers, and even if the invaded area is isolated, monthly assiduous hand-removal misses microscopic stages that create the equivalent of a persistent local "seed bank" (Hewitt et al., 2005). A joint project of federal agencies and a regional council attempted to use augmentative biological control to manage an *Undaria* invasion of a rocky reef in New Zealand, translocating into the target site over 50 individuals/m^2 of a primarily herbivorous native sea urchin, *Evechinus chloroticus* (Valenciennes, 1846), known to devastate kelp beds. After 17 months, urchin densities had greatly declined, indicating that ongoing translocations would likely be needed to maintain a decrease in *Undaria* (Atalah et al., 2013). In addition, *Evechinus* grazes on many non-target native species in canopy-forming algae and understory assemblages of plants and animals. In Kāne'ohe Bay, Hawaii, in an operation by a state agency in collaboration with an NGO and academic researchers, outplanted hatchery-raised native sea urchins, *Tripneustes gratilla* (Linnaeus, 1758), have been deployed to control the red alga *Kappaphycus* Doty (several clades) that smothers coral reefs (Westbrook et al., 2015) with sufficient success that the project is now being extended to Waikiki (Anonymous, 2020). In Kāne'ohe Bay, urchin deployment is supplemented by divers wielding a powerful vacuum ("Super Sucker") over the alga (Detisch, 2018).

Perhaps the most widely bruited proposal for physical control of a marine invader is the contention that the western Atlantic invasion by lionfishes, *Pterois volitans* (Linnaeus, 1758) and *P. miles* (Bennett, 1828), can be controlled through spearing and/or netting by trained divers or volunteers, or by lionfish "derbies." Both enthusiasts and skeptics agree that wide-scale control throughout their entire invasive range is unattainable by this means, but Green et al. (2014) and Côté et al. (2014) suggest that this method can maintain lionfish populations on local reefs at relatively innocuous densities. They tested the approach in a controlled experiment conducted by NGO and university scientists with monthly culling by trained divers for 1.5 years on a series of Bahamian reefs (Green et al., 2014), rejected the contention that culling-induced lionfish behavioral shifts defeat the method (Côté et al., 2014), and found evidence from six single-day derbies that such events can often suppress densities below levels detrimental to native fish populations (Green et al., 2017). However, these are all so far short-term efforts, and Barbour et al. (2011) argue that sustained intense pressure would be needed to effect long-term control. Andradi-Brown et al. (2017a, b) argue that substantial mesophotic lionfish populations (depths of 30–150 m) on reefs will limit the effectiveness of this method because of diving restrictions and that yet-to-be determined technologies would be needed to supplement diving for consistent control.

Outside-the-box technologies

The methods for eradication and maintenance management described in the previous sections generally fall into three categories—physical/mechanical (e.g., hand-weeding, dredging), chemical (e.g., herbicides, piscicides), and biological (biological control). These categories have dominated control efforts for terrestrial as well as aquatic invasions. For terrestrial invasions, two other approaches derive from "thinking outside the box": pheromonal control and sterile male technique. They have long been used for certain invasive insect pests and are only recently being discussed or developed for use on aquatic invaders—almost exclusively the sea lamprey, *Petromyzon marinus* Linnaeus, 1758. In addition, one relatively recent mechanical tool—robots—has been added to the arsenal for terrestrial invasions and is under development for at least one marine invader. Also, several novel methods based on genetic manipulation have recently been developed and have already been deployed for a few terrestrial invaders, exciting both tremendous optimism and also controversy, but these are so far only a minor part of the discussion for aquatic invasions. Table 1 lists these "outside-the-box" technologies.

Table 1 Outside-the-box technologies for control of biological invasions, and example of proposed aquatic target for each

	Suggested target
Non-genetic technologies	
Robots	Lionfish (*Pterois* spp.)
Pheromones	Sea lamprey (*Petromyzon marinus*)
Sterile male technique	Sea lamprey (*Petromyzon marinus*)
Genetic technologies	
Gene-silencing	Common reed (*Phragmites australis*)
Skewed sex ratio	Brook trout (*Salvelinus fontinalis*)
Transgenes	Zebra mussel (*Dreissena polymorpha*)
Gene-editing	Zebra mussel (*Dreissena polymorpha*)

Non-genetic methods

Proposals abound to use robotics to aid conservation, including in a freshwater or marine environment. For instance, an Australian team has created COTSbot, a robot equipped with an injection arm, to find and kill crown-of-thorns starfish, *Acanthaster planci* (Linnaeus, 1758), on the Great Barrier Reef, and another Australian team has created a driver-steered machine that clears fouling organisms from ship hulls (Martinez et al., 2020). Robots in Service of the Environment (www.robotsise.org, accessed 1/22/20) has developed a robot to find and harvest lionfish (*Pterois* spp.). Whether such robots, autonomous or assisted, can be developed to eradicate or effectively manage an aquatic invader at a feasible cost remains to be seen, but it would be well to bear in mind that even 20 years ago most people rejected the feasibility of self-driving automobiles.

Pheromones have long been used in managing invasive insects, especially lepidopterans, primarily by mating disruption or by attract-and-kill methods. Two pheromones of the anadromous sea lamprey (*P. marinus*) have been detected and characterized with an eye towards aiding in managing this invader in the Laurentian Great Lakes. A pheromone produced by larval sea lampreys attracts adults to streams for reproduction (Vrieze & Sorensen, 2001; Li et al., 2018), and a mating pheromone produced by males attracts females (Li et al., 2002; Johnson et al., 2009, 2013). Both pheromones have undergone extensive research as well as laboratory and field-testing that indicates they could potentially contribute greatly to the current, moderately successful integrated method of lamprey control in the Great Lakes, which relies heavily on lampricides, barriers, and traps (Johnson et al., 2013; Thresher et al., 2019). Sorensen & Johnson (2016) review the great number of pheromones and other semiochemicals that fish species in addition to sea lampreys have been shown to use for various purposes: sex pheromones, attraction, species recognition cues, advertisement, imprinting, alarm cues, reproductive priming. The difficulties of developing such semiochemicals to control invasive fishes are substantial—especially the facts that these fish signals typically have several components and that they disperse and become greatly attenuated in open waters. Testing such chemicals on target pests is also more challenging for fishes than for insects. Nevertheless, Sorensen & Johnson (2016) point out that development of such methods in species other than the sea lamprey could substantially aid management of invasive fish species that cannot be adequately controlled with the limited toolbox currently available.

The existence of sex pheromones has been demonstrated for two famously invasive crayfish, the red swamp crayfish, *Procambarus clarkii* (Girard, 1852) (Ameyaw-Akumfi & Hazlett, 1975) and the signal crayfish (Stebbing et al., 2003), but pheromone-baited traps for both species (Stebbing et al., 2004; Aquiloni & Gherardi, 2010), although attracting adult males, did not do so to the extent that they were deemed promising for development as a control method (Stebbing et al., 2014). Several other pheromones have been discovered in crayfish that appear to be potentially useful in managing invasive populations (Stebbing et al., 2014), but research along these lines has not been reported.

As with pheromones, the sterile male technique (also known as SIT—sterile insect technique) has long been used to manage and even occasionally eradicate populations of invasive insects, especially dipterans. And again as with pheromones, the target for the greatest effort in this direction for an aquatic invader is the sea lamprey in the Great Lakes. After research established the efficacy of an injected chemosterilant in virtually eliminating viable offspring of treated males (Twohey et al., 2003), a field test began in 1991 in which sterile males were released into 33 streams flowing into Lake Superior and also the St. Marys River, which flows from Lake Superior into Lake Huron (Bravener & Twohey, 2016). The program in Lake Superior was discontinued in 1997, having produced conflicting results: it confirmed the ability to trap and sterilize males, that the resultant males were competitive, and viable eggs and larvae were reduced, but the adult population in Lake Superior did not decline. However, the experiment continued through 2010 in the St. Marys River, at which point it was terminated, primarily because of the greatly improved technology of using the lampricide Bayluscide, unanswered questions about the efficacy of the sterile male program in the St. Marys River, and the inability to increase the number of sterilized males, which might have resolved some of the questions about efficacy (Bravener & Twohey, 2016). A particular assessment problem was posed by the fact that use of Bayluscide increased the impact of the sterile males by increasing their proportion relative to untreated males but confounded an attempt to estimate the independent effect of the sterile male releases. However, ongoing field experiments continue, including a 3-year project initiated in 2017 using sterile males instead of lampricides in three Michigan rivers (Breen, 2017). Aquiloni et al. (2009) reported promising results of an experiment to sterilize male *P. clarkii* crayfish that nevertheless retained their competitiveness, but this approach appears not to have been followed up in crayfish management.

Technologies based on genetics

Gene-silencing is among a series of suggested genetics-based technologies to control invasive species. This approach entails interrupting or suppressing expression of a gene at the transcriptional or translational levels and is primarily achieved by preventing translation. This is usually accomplished by ribonucleic acid interference (RNAi) by rendering messenger RNA molecules unstable or inaccessible through introduction to the cells of double-stranded RNA (dsRNA). Much research on the technology has been engendered by the belief that it may aid in treating human disease (Titze-de-Almeida et al., 2017) and increase agricultural productivity, including by attacking terrestrial plant pests. Most previously published research on the latter approach focused on getting targeted species to eat food on which dsRNA had been deposited and then managing for enough of the dsRNA to pass through the digestive system and into the targeted cells. However, Monsanto in 2017 received U.S. government approval to distribute seed corn that bypassed part of this sequence by means of a transgene in the corn that silences key genes in western corn rootworm (*Diabrotica virgifera virgifera* J.L. LeConte, 1868) when the insect attacks the plant (Bachman et al., 2013; Zhang, 2017). DuPont filed a patent application in 2016 for a similar method of using gene-silencing to attack pest stinkbugs, including the invasive brown marmorated stinkbug, *Halyomorpha halys* (Stål, 1855) (McGonigle et al., 2016). Perhaps most remarkably to date, Leonard et al. (2020) have engineered the genome of a symbiotic gut bacterium (*Snodgrassella alvi* Kwong & Moran, 2013) of the honey bee (*Apis mellifera* Linnaeus, 1758) to express dsRNA sequences for genes of the varroa mite (*Varroa destructor* Anderson & Trueman, 2000), a devastating bee parasite. This activates the mite's RNAi mechanism, which destroys those sequences in the mite, thus killing it. An important consideration regarding gene-silencing is that specific applications need not entail genetic changes. If a gene-silencing agent is simply deposited on a plant for an herbivore to eat, this would not constitute a heritable change and thus trigger considerations and regulations for dealing with such changes. If, on the other hand, the method involves a genetic change such as an inserted transgene, a substantially more rigorous permitting process may be entrained. Development of a method to produce sterile fish by gene-silencing for aquaculture purposes was motivated by exactly this regulatory consideration (Wong & Zohar, 2015).

A US government agency is exploring using gene-silencing for landscape-level control of *Phragmites australis* (Cav.) Trin. ex Steud. (Martinez et al., 2020), but the most substantial research effort on gene-silencing for aquatic species is on crustaceans, where the method has already been applied in aquaculture (to produce all-male prawns) and proposed for potential management of invasive populations (Ventura & Sagi, 2012; Sagi et al., 2013). Lezer et al. (2015) have addressed the issue of the safety of the method in light of likely escapes from aquaculture, while Savaya-Alkalay et al. (2018) have suggested that all-male prawns produced by gene-silencing may be safe and effective biological controls for invasive snails. Research on applications of gene-silencing in molluscs lags behind that in crustaceans, but sufficient information exists to suggest this subject is ripe for exploration (Owens & Malham, 2015). A potential impediment to using gene-silencing to manage invasive species, including aquatic ones, is that many of the techniques and products developed in this field are protected by patents (Campbell et al., 2015).

Another approach was adumbrated by Hamilton (1967), who suggested in a classic paper that warping the sex ratio towards one sex or the other (which he envisioned as occurring by meiotic drive) could actually drive a population to extinction, and he pointed out that such a process might be useful in pest insect control. At the time, before the advent of transgenes, there was no apparent technology to produce such an effect. However, in 2006, a proposal to skew the sex ratio of invasive fishes by means of hormone treatment (Gutierrez & Teem, 2006) inspired much interest. The plan, exemplified by a model based on Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758), and extended to Asian carp (Teem & Gutierrez, 2010), entails continued production (by means of hormone treatment already employed in aquaculture) and release of sex-reversed YY males. Schill et al. (2016) developed a breeding scheme for brook trout, *Salvelinus fontinalis* (Mitchill, 1814), that, combined with estradiol treatment, produced such sex-reversed YY individuals. After simulations to estimate the numbers of individuals needed to affect invasive populations (Schill et al., 2017), the team introduced these sex-reversed YY fish into four streams occupied by non-native brook trout; for two of these streams, brook trout numbers were first reduced by electrofishing (Kennedy et al., 2018). The released fish survived and reproduced in sufficient proportion to suggest that the method may be feasible for eradicating some invasive brook trout populations, particularly if the resident population is first reduced by electrofishing, piscicides, or other means.

The potential use of transgenes to control or even eradicate invasive species first received enormous attention with the advent of Oxitec's Friendly™ *Aedes aegypti* (Linnaeus, 1762) mosquito, in which a transgene renders females flightless (i.e., lethal in nature) when raised on a diet without tetracycline, which inactivates the gene (Fu et al., 2007). Reports on the project and especially news of the unpublicized field-testing of the mosquito on Grand Cayman Island elicited concern about lack of regulation (Angulo & Gilna, 2008) and unintended consequences (Enserink, 2010). However, in the wake of the spread of the zika virus to the western hemisphere, resistance to release of this engineered mosquito dissipated (Rutkin, 2016; Servick, 2016), although widespread concern about release of all genetically modified organisms persists, especially among environmental activists (Resnik, 2018). The Oxitec Friendly™ mosquitoes are raised in an environment with tetracycline, females are discarded, and males are released in great number to mate with wild-type females, whose offspring then carry the transgene and are believed to die—in other words, a version of the sterile male technique. Oxitec is proceeding to develop similar versions for several other pest Diptera and Lepidoptera (https://www.oxitec.com/en/our-technology, accessed January 30, 2020), although the finding that genes from the Friendly™ mosquito have been recovered in a natural population in Brazil (Evans et al., 2019) demonstrates that at least a small percentage of offspring carrying the transgene survive and has spurred continuing concern over the safety of the technology.

Transgenic research has been ongoing in aquatic species at least since 1982, when Vielkind et al. (1982) injected tumor genes from one strain of the platy-swordfish complex (*Xiphophorus maculatus* [Günther, 1866] and *X. helleri* Heckel, 1848) into a tumor-free strain. Soon thereafter, Zhu et al. (1985, 1986) transferred the human growth hormone gene into goldfish (*Carassius auratus* L. 1758) and loach (*Misgurnus anguillicaudatus* [Cantor, 1842]). Since then, transgenic fishes of several species have been used in medical research (e.g., Hall et al., 2007) and environmental toxicology (e.g., Winn, 2001), but especially in attempts to grow bigger fish (e.g., Devlin et al., 1995) or fishes with relatively more muscle tissue and less fat (e.g., Lee et al., 2008). The GloFish, zebra danios (*Danio rerio* [F. Hamilton, 1822]) with transgenes producing fluorescent colors from various aquatic invertebrates, attracted interest from both hobbyists seeking the flashiest aquarium fish and scientists concerned with potential environmental impacts (Knight, 2003). Transgenic molluscs and crustaceans have been produced for various purposes (Chen et al., 2015). However, to date I have not encountered a sustained project to produce a transgenic form for use in managing invasive populations of an aquatic or marine species with the exception of a project, described in the following paragraph, that required a further technological advance.

The advent of CRISPR-Cas9 gene-editing technology and recognition of its potential use in controlling populations of invasive species (Esvelt et al., 2014), as well as continuing refinements and improvement of the technology (e.g., Cohen, 2018; Hu et al., 2018), have served only to heighten enthusiasm about the potential for managing or even eradicating invasive populations. Many authors have focused on the possibility of using CRISPR-Cas9 gene drives to manage invasive terrestrial species (e.g., Harvey-Samuel et al., 2017; Moro et al., 2018), and two well-funded projects are proceeding, Target Malaria for *Anopheles* mosquitoes (https://targetmalaria.org/) and GBIRd for invasive rodents (https://www.geneticbiocontrol.org/). Invasive aquatic species have received much less attention. However, the U.S. Bureau of Reclamation in 2017 announced US$100,000 in prize money in a competition for methods to eradicate zebra and quagga mussels in open water (https://www.usbr.gov/research/challenges/mussels.html) and in 2018 awarded the main prize to a project to introduce a transmissible cancer found in soft-shell clams (*Mya arenaria* Linnaeus, 1758) into zebra mussels, potentially with the aid of CRISPR-Cas9 to knock out a tumor-suppressing gene that acts at mitosis (https://www.usbr.gov/newsroom/newsrelease/detail.cfm?RecordID=63426, https://invasivemusselcollaborative.net/wp-content/uploads/2019/03/Suhr-Biomilab-Eradication-of-Invasive-Mussels.pdf). Transmissible cancers, though rare in nature, have arisen twice in Tasmanian devils, *Sarcophilus harrisii* (Boitard, 1841), and have quickly threatened the species with extinction (Stammnitz et al., 2018).

The feverish activity surrounding RNA-guided gene drives, particularly CRISPR-Cas9, has increased concern about unintended consequences of attempts to eradicate populations of invasive species. For instance, a group of prominent conservation scientists and environmentalists released a manifesto at the World Conservation Congress in 2016 advocating never using gene drive technology for conservation purposes (Anonymous, 2016). A report by the U.S. National Research Council (National Academies of Sciences, Engineering, and Medicine, 2016) and a United Nations Treaty (Callaway, 2018) both recognized potential unintended consequences, particularly transfer of a driven gene into an untargeted species, but advised proceeding with caution with testing, including field-testing. Although natural selection will act against any gene drive lowering the fitness of its bearers, mathematical models suggest that, in small populations, the evolutionary race between population reduction to extinction and evolved resistance to the drive will often end in extinction (Noble et al., 2018). This observation has led some of the originally most enthusiastic advocates of the use of the technology for this purpose to call for a substantial delay in deployment while methods are developed to “call back” or halt a drive that is leading to an unintended consequence (Esvelt & Gemmell, 2017). A further concern is that, as gene drive technology becomes increasingly accessible and affordable, either well-meaning individuals without the oversight of projects such as Target Malaria and GBIRd, or persons with more nefarious goals, will be able to engineer and liberate a gene-drive-laden propagule that turns out to be disastrous (Cohen, 2016; Baumgaertner, 2018).

Discussion

In addition to eradication and maintenance management, a third option in dealing with an established non-native population is to do nothing (Clayton, 1996; Simberloff, 2002). Assessment of this option should distinguish between two cases: recent invasions that have not yet spread widely and longstanding invasions distributed over substantial areas. These are extremes and various sorts of intermediate cases exist, but they capture the range of important considerations.

Supporting this option in discussions of particular recent, localized invasions, the fact that most invasions are not known to have harmful impacts is often cited. This is true, but two important considerations should give one pause in choosing this option (Simberloff, 2014). First, many invasions undergo a lag, during which an established population remains small and quite restricted for an extended period, then more or less abruptly begins to spread rapidly (Crooks, 2011). A well-known marine example is the hybrid cordgrass *Spartina anglica* C.E. Hubbard, 1978 (Thompson, 1991); zebra and quagga mussels underwent a lag of about 30 years before becoming extensive invaders in the Laurentian Great Lakes (Crooks, 2011). In some instances the reasons for the lag and the timing of its end are evident (e.g., a chromosomal doubling for *S. anglica*); often they involve a change in the biotic or physical environment (Crooks, 2011). In other cases they remain mysterious, but the presence of the phenomenon for many invasions cannot be doubted. This means that the status of some fraction of existing, currently innocuous non-native populations may change abruptly—an "invasion debt" exists (Essl et al., 2011), and if populations can be eradicated, the debt would be lessened. A second relevant point is that some invasions that have appeared to be innocuous in fact were consequential well before their impacts were understood. The invasion of New England by the European periwinkle *Littorina littorea* L., 1758, which changed many coastal areas completely by consuming massive amounts of algae and marsh grasses and bulldozing sediment (Bertness, 1984), is an example. Davis et al. (2011) argue that, in the absence of evidence of an important impact, there is no good reason to attempt to eliminate or control an invasion. However, the above two considerations suggest that, if there is a good chance of eradicating a recent, restricted invasion with an existing technology, as may well be the case in a pond or small lake, one should perhaps make the attempt even in the absence of a detailed study of its likely impacts and potential methods of control (Simberloff 2009). The previously described eradications of *M. sallei* and *C. taxifolia* soon after discovery surely prevented subsequent major ecological impacts.

For longstanding invasions, the calculus is more complicated (Simberloff et al., 2013; Simberloff, 2014). It is possible that the invader is enmeshed in interactions with native species in the invaded community such that eradication or even a greatly reduced population would have inimical impacts. Further, for an invasion that occurred long ago, the damage caused may have been completed and eradication would not redress it (e.g., if a native species has been eliminated). It is also likely that a long-established non-native species that is a prominent member of the current biological community will have human advocates who have learned to use it for various purposes (food, sport, building material, etc.) and may not even realize it was introduced. Finally, the likelihood of achieving eradication is surely much lower for a widespread, longstanding invasion, at least in the absence of new technologies.

If the do-nothing option is rejected, eradication and maintenance management projects for freshwater invasions have racked up numerous successes, generally through incremental improvement of various venerable technologies—chemicals, biological control, physical or mechanical methods, drainage, and the like. Successful eradication projects discussed in the text are listed in Table 2. Importantly, at least as many projects—in fact, probably more—fail as succeed, and these failures include cases in which the same species is targeted by the same method, such as particular invasive plant species treated with a particular herbicide, or electrofishing of a particular fish species. This fact reflects a major feature of invasions generally—their trajectories, fates, and impacts are highly context-dependent (Queirós et al., 2011; Pyšek & Chytrý, 2014). Context-dependency does not mean that an attempt to eradicate or control is reduced to hoping for success in the face of some fixed and often high probability of failure. One aspect of the history of management of aquatic invasions is increasing understanding of the particular circumstances and features of an invasion that would suggest a particular goal (eradication or maintenance management) and a particular method (e.g., a piscicide rather than netting).

An important feature of most maintenance management approaches is that management actions must continue indefinitely and be regularly or at least intermittently applied. Aside from the case of classical biological control, this requirement incurs an ongoing cost and often ongoing monitoring for long-term success—simply greatly reducing a target population once does not suffice. Thus, many maintenance management projects declared "successful" arouse a degree of skepticism because the maintenance has not persisted for long (e.g., Rytwinski et al., 2019). When classical biological control works, the interaction between the target and control agent maintains populations of both at an acceptably low level, and no further human effort is needed. A similar requirement—albeit not a perpetual one—pertains to

Table 2 Successful eradications described in text

Species	Location	Entity	Method	References
Myocastor coypus	England	Government agency	Trapping	Gosling (1989)
				Gosling & Baker (1989)
Myocastor coypus	California	?	?	Carter & Leonard (2002)
Myocastor coypus	Indiana	?	?	Carter & Leonard (2002)
Neovison vison	Outer Hebrides	European Union government agencies (Scotland)	Trapping	Roy (2011)
		Regional NGO		Roy et al. (2015)
	Hiiumaa Is. (Estonia)	Government agency	Trapping	Maran (2003)
Ondatra zibethicus	Great Britain	Government agency	Trapping	Sheail (1988)
				Gosling & Baker (1989)
	Ireland	Government agency	Trapping	Fairley (1982)
Pseudorasbora parva	England	Government agency	Trapping	Davison et al. (2017)
		Academic scientists	Biological control	
Salvelinus fontinalis	California	Academic scientists	Gill-netting	Knapp et al. (2007)
Oncorhynchus mykiss aguabonita				
× *O. mykiss* hybrids				
Gyrodactylus salaris	Norway	Government agency	Rotenone	Sandodden et al. (2018)
Pacifastacus leniusculus	Norway	Government agency	Pyrethroids	Sandodden & Johnson (2010)
				Sandodden (2019)
	Scotland	Government agency	Pyrethroids	Ballantyne et al. (2019)
		NGO		
Cherax tenuimanus	New Zealand	?	Pond drainage	Gould (2005)
				Duggan & Collier (2018)
Sinodiaptomus valkanovi	Bulgaria	?	Pond destruction	Duggan & Collier (2018)
Boeckella symmetrica	New Zealand	?	Quarry infilling	Branford & Duggan (2017)
Myriophyllum spicatum	Washington State	Government agency	Water body drainage	Thurston County Department of Water and Waste Management (1995)
Nymphoides geminata	New Zealand	Government agency	Polyethylene covering	Clayton (1996)
Nymphoides peltata	New Zealand	Government agency	?	Champion & Clayton (2003)
Lagarosiphon major	New Zealand	Government agency	Hand-weeding suction pump	Clayton (1996)
				Bickel (2012)
				De Winton et al. (2013)
				Champion & Wells (2014)
Egeria densa	New Zealand	Government agency	Biological control	Rowe & Champion (1994)
				Champion & Wells (2014)
Ceratophyllum demersum	New Zealand	Government agency	Biological control	De Winton et al. (2013)

Table 2 continued

Species	Location	Entity	Method	References
				Champion & Wells (2014)
Menyanthes trifoliata	New Zealand	Government agency	?	Champion & Clayton (2003)
Hydrilla verticillata	California	Government agency	Herbicide	Kratville (2013)
				Anonymous (2017)
	New Zealand	Government agency	Biological control	Hofstra et al. (2018)
Potamogeton perfoliatus	New Zealand	Government agency	?	Champion & Clayton (2003)
Alternanthera philoxeroides	Australia	Government agency	Herbicide	Gunasekera & Bonila (2001)
				Schooler (2012)
Pistia stratiotes	New Zealand	Government agency	?	Champion & Clayton (2003)
Zizania palustris	New Zealand	Government agency	?	Champion & Clayton (2003)
Ludwigia grandiflora	Europe	?	Hand-weeding	Hussner et al. (2017)
Terabrasabella heterouncinata	California	Government agency	Hand-picking	Culver & Kuris (2000)
		Commercial enterprise		
		Academic scientists		
Ascophyllum nodosum	California	Volunteers mobilized by government agencies	Hand-picking	Miller et al. (2004)
Mytilopsis sallei	Australia	Government agencies	Chemicals	Bax et al. (2002)
Caulerpa taxifolia	California	Government agencies	Chemicals	Anderson (2005)
				Muñoz (2016)
		NGOs		
	South Australia	Government agency	Replacing salt water with fresh water	Walters (2009)
Undaria pinnatifida	New Zealand	Government agency	Heat treatment	Wotton et al. (2004)
Perna perna	New Zealand	Government agency	Dredging	Hopkins et al. (2011)

"Entity" is the entity responsible for the eradication. In several cases, either the entity or method cannot be determined from published sources; such cases are denoted by "?"

eradication projects: commitment of resources must be maintained even when the target population has been reduced so greatly that individuals may be difficult to find and treat (Myers et al., 2000).

The record for marine maintenance management and eradication shows many fewer successes, and those few are limited to invasions restricted to small areas, generally because they were detected early. The vast extent of the great majority of marine habitats means that existing methods of management, except possibly for biological control, would become impractical for a widely dispersed invasive population. In principle, a biological agent might be able to disperse throughout the range of a widely dispersed invader. However, in comparison to the extensive record of biological control projects in terrestrial and freshwater habitats, very few such efforts have even been proposed for marine invaders (Lafferty & Kuris, 1996; Secord, 2003). Perhaps the most interesting indication that classical biological control might be fruitful in a marine setting is the striking decline of the invasive ctenophore, *Mnemiopsis leidyi* A. Agassiz, 1865, in the Black Sea, apparently largely due to the unplanned introduction of another ctenophore, *Beroe ovata* Bruguière, 1789, that preys on it (Secord, 2003). This event occurred as a different biological control agent for *M. leidyi* was under active consideration.

The various genetically based control methods under development for terrestrial invasions may prove useful for freshwater invaders and even for short-lived, sexually reproducing marine invaders that have not spread widely, although the same constraints that may hinder terrestrial applications apply also to aquatic ones. Gene drives in principle work only on sexually reproducing organisms, and the rate at which they could possibly achieve population reduction is limited by the length of the life cycle of the target species, so they are most likely to be useful, at least in the immediate future, for species that reach sexual maturity relatively quickly. Also, natural selection will counteract the effects of a gene drive that reduces fitness, so the best likelihood of success will be with a small target population that lacks much genetic variation on which natural selection can act before the population goes extinct.

Finally, in both freshwater and marine environments, even aside from the fact that long-established invaders are likely to be less tractable targets for maintenance management and eradication, the possibility of unintended consequences, especially of an irrevocable action like eradication, should be strongly considered. Even the most thoughtful assessment of possible outcomes of removing a long-embedded population will have a substantial probability of failing to account for non-target impacts because of the myriad and complex ways in which any species is likely to interact with other members of a biotic community (Simberloff, 2014). The same context-dependency that complicates predictions of the outcome of various management activities bedevils attempts to minimize the likelihood of unintended consequences, and it thus behooves managers to act with great caution in considering campaigns to eliminate a longstanding, prominent, non-native member of an ecological community.

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