



Introduction to the Biology and Control of Invasive Fishes and a Special Issue on This Topic

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Abstract: Across the globe, dozens of species of invasive fish are now found in fresh as well as marine waters, where they alter habitats, compete with native fish for food, and prey on native fishes, exerting both indirect and direct effects on ecosystems and economies. While efforts to understand and control these species are growing, most are still in their infancy; however, a few examples stand out. This special issue is comprised of 11 notable articles on freshwater invasive fish and is the first to address this topic. This introductory article serves as an introduction to these articles which focus on 5 topics on invasive freshwater fish: (1) the damage they cause (one article); (2) techniques to ascertain their presence (one article); (3) techniques to restrict their movement (one article); (4) strategies to control them (three articles); and (5) lessons learned from ongoing management efforts (five articles). This introduction notes that successful management efforts share a few approaches: (1) they develop and use a deep understanding of local species and their abundance as well as distribution; (2) they focus on reducing reproductive success; (3) they use multiple complimentary control strategies; and (4) they use a long-term approach.

Keywords: integrated pest management; aquatic invasive species; sea lamprey; lake trout; northern pike; common carp; bigheaded carp; eDNA; suppression; eradication



Citation: Sorensen, P.W. Introduction to the Biology and Control of Invasive Fishes and a Special Issue on This Topic. Fishes 2021, 6, 69. https:// doi.org/10.3390/fishes6040069

Received: 21 November 2021 Accepted: 24 November 2021 Published: 30 November 2021

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1. Introduction

Rapid increases in human population size and activity over the past century have resulted in an increasing number of species being transported between locations and developing self-sustaining populations that many consider to be invasive from an ecological perspective [1]. Notably, many of these newly self-sustaining populations are now also causing notable ecological and/or economic problems, leading governmental entities to legally recognize them as "invasive species" and deserving of management efforts [2]. Damage caused by aquatic invasive species (AIS), including fish, is often highly problematic because of the high level of interconnectedness of waters. Although both marine and fresh waters are affected by AIS, fresh waters are especially impacted, perhaps because they tend to be smaller, more isolated, as well as evolutionarily younger than marine waters and so have less well-developed ecosystems that less able to fend off invaders. Although many millions (likely hundreds) of US dollars are presently spent each year trying to understand and control invasive fish [1], the topic as a whole remains poorly understood and has not yet been reviewed.

This volume reflects an effort to remediate this deficiency. Work on this volume started in 2018 when the author was invited by the publisher to pursue a volume on invasive fishes and subsequently invited dozens of invasive fish biologists to contribute on any subtopic within this field of their choosing. While many were interested, ultimately 11 groups wrote articles, all of which were then peer-reviewed and published. All happen to be on freshwater fish and most focus on management, a previously poorly reviewed area. This brief article provides an introduction to these 11 articles which I have grouped into five categories: (1) Damage caused by invasive fish (n = 1); (2) Techniques to assess the

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presence and distribution of invasive fish (n = 1); (3) Techniques to control the abundance of invasive fish (n = 1); (4) Strategies to control invasive fish (a strategy uses multiple techniques to exert a specific effect such as suppression of reproductive success) (n = 3), and (5) Lessons learned from extant invasive fish control programs (n = 5). In each instance, I provide a brief overview of the sub-discipline (category) and then review some of the high points of each article in it and its contributions. A few references are included for context although it is beyond the scope of this paper/special issue to provide a comprehensive review. Common points made by these articles are highlighted to assist readers interested in specific themes. I conclude with a brief summary and a call for future study.

1.1. Damage Caused by Invasive Fish

Invasive fish are often a concern because they alter local ecosystem structure, usually in ways that also negatively impact economic activity. Frequently, preservation of bio-diversity (species loss) is a special concern. Invasive fish are usually perceived as "damaging" in several ways that are both interesting and important to understand, especially because invasive species managers often require economic information to justify their efforts. Effects of invasive fishes can be indirect and/ or direct. Important indirect effects include altering an ecosystem structure (for example, the common carp, Cyprinus carpio, uproot benthic plants, leading to changes in water clarity/chemistry (see [3])), and/or consuming prey at the base of foodwebs (for example bigheaded carp, Hypthophthalmichthys sp., feed on plankton, reducing food availability for gamefishes (see [4])). Direct effects can include aggressive interactions with other species to acquire reproductive territories (lowering reproductive success), consuming or parasitizing native fishes (directly reducing abundance; for example, the sea lamprey, *Petromyzon marinus* preys on lake tout, *Salvelinus namaycush* (see [5]), hybridizing with native fishes (leading to the disappearance of some species), and/or exhibiting behaviors that reduce the value and appeal of sport fishing (for example bigheaded carps jump, reducing the appeal of sport fishing(see [4])). Unfortunately, I am unaware of a comprehensive review of the effects of invasive fish on aquatic ecosystems. In this volume, Newman and colleagues [6] contribute to this field by describing an important experiment in which an invader, the Eurasian ruffe, Gymnocephalus cernua, was placed together with a species native to North America, the yellow perch (Perca flavescens), in large outdoor mesocosms and found a reduction of the growth rates of perch, which appeared unable to shift their dietary preferences. The latter may be a novel finding.

1.2. Techniques to Assess the Presence and Distribution of Invasive Fish

To control a population of invasive fish, managers need to know where members of that population are found and preferably their abundance. More sophisticated control strategies (for example efforts to reduce reproductive success in the common carp (see [7]), also require information on life history stage and reproductive condition. Traditionally, this information has been obtained by various types of netting, electrofishing, and trapping surveys (see [3]). However, these techniques can be of very limited value in deeper waters where fish can often avoid gear, in remote large waters that might be difficult and expensive to reach, or in flowing water that may wash nets away. Also, nets usually only work well for large individuals. Clearly, new sampling techniques and strategies are needed. One recent development has been to measure environmental DNA (eDNA), or DNA released to the water by organisms where it can be sampled and measured using highly sensitive molecular tools (PCR). Sometimes this technique can be conducted together with sex pheromone measurements to acquire more information on reproductive state [8]. eDNA has many distinct advantages (ex. easy to collect, extreme sensitivity, etc.) and some disadvantages (ex. dilution, false positives from dead fish, etc.), but is being actively explored as a means to compliment traditional sampling. There are several reviews of this rapidly developing topic [9]. In this volume, Hayer and colleagues [10] describe how eDNA presence in river waters shows a positive relationship to the presence of invasive grass carp, Ctenopharyngodon idella, in North America, especially when these fish

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are spawning. Because, grass carp, like many invasive fishes, are very difficult to sample, this is an important observation, especially if eDNA concentration could be directly linked to reproductive state.

1.3. Techniques to Control the Abundance of Invasive Fish

The origins of invasive fish control are seemingly found in the responses of the American and Canadian governments to the parasitic sea lamprey, Petromyzon marinus, which invaded the Laurentian Great Lakes in the early 1900s and caused a collapse in their fisheries. Efforts initially focused on blocking adult sea lamprey from migrating to their fluvial spawning habitat and adult removal, but soon shifted to chemicals (abiotic) approaches. Eventually, after testing thousands of chemicals, 4-nitro-3-(trifluoromethyl)phenol (TFM) was identified as a compound with unusual potency and specificity (although it does kill other ancient fishes and insects) that will kill most larval lamprey. While TFM presently serves as the primary technique of sea lamprey control, it is now complimented by several other techniques including blocking migratory adults as part of an integrated pest control program (see [5]). Mimicking sea lamprey control, many other invasive fish programs have also attempted to identify a variety of biotic and abiotic techniques to control their target species and assemble them into strategies, and then combine them for use in control programs. Although no program has seemingly been as successful as the sea lamprey control in the Great Lakes, at least on such a large scale, many have developed a variety of effective biotic and abiotic control techniques that have achieved notable levels of success, some of which are described herein. A third approach, genetic engineering/manipulation of populations, is also now being examined but not reviewed. Genetic engineering approaches are still in their infancy and generally attempt to manipulate gender and face challenges with societal acceptance. Biotic control techniques include new techniques to locate/attract and remove adults (ex., "Judas fish" [3,7]); techniques to remove/kill eggs/young using native microbes, etc. [11]; enhanced/targeted fishing [4]; introduction of new predators or management of extant ones, especially predators for vulnerable young [3]; and introduction of novel pathogens [12]. Important abiotic approaches include the strategic use/development of new piscicides (fish poisons) [13], and the development of physical techniques to selectively block movement/migration of invasive fish into new areas where they might breed successfully [14,15]. It has been a major challenge to develop techniques that are simultaneously effective and highly specific, and also acceptable to the public. Although the topic of invasive fish control has never been comprehensively reviewed, it appears that no technique (even TFM) has been developed that meets all desired criteria.

This special issue includes an article by Suski [14] that describes how carbon dioxide, a natural gas that many fishes find inherently repulsive, might be used to control the movement of invasive fishes, especially bigheaded carps that must migrate upstream to reproduce. Suski [14] reviews how and why even small amounts of CO_2 might be introduced into the riverine lock systems to deter carp from entering them. Although the actions of CO_2 are not highly specific, this approach has the advantage that it is not difficult/expensive, only small amounts are needed, and it could be paired with other sensory cues such as sound/air that can be more specific. CO_2 is currently being tested, along with various acoustic and electrical stimuli [16], including multimodal deterrent systems such as ensonified bubble curtains [17].

1.4. Strategies (and Associated Techniques) to Control Invasive Fish

Early in the development of the first invasive fish control programs, including the one for the sea lamprey, it became apparent that techniques were most likely to be effective if targeted to specific life history stages and used in combination with other techniques; in other words, they were part of a strategy. Control programs (see below) now generally employ multiple strategies. Strategies can revolve around either optimizing specific techniques (e.g., blocking adults using different types of barriers using several sensory fields), and/or using multiple techniques to complement each other to achieve a specific goal

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(e.g., stopping the successful reproduction by blocking adults while also removing young [3]). Three articles in this issue describe three new, promising strategic approaches to control invasive fishes. All strategies emphasize the value of targeted approaches that also use local understanding of species and their ecosystems, and include multiple "integrated" techniques.

McColl and Sunarto [12] review the status of a pathogen-based research program that could be used to control common carp in Australia. They describe how cyprinid herpesvirus 3 (CyHV-3; also known as the koi herpesvirus) is highly specific and could be introduced cheaply and easily to kill very large numbers of adult and juvenile common carp across this huge continent. In addition, they describe how numeric models have shown that pathogen release must be extremely strategic, because common carp will eventually develop immunity and their larvae will not be affected. Further, plans must be in place to address large adult die-offs. Fascinating analogies are drawn to a virus-based rabbit control program, and it is emphasized that complimentary control techniques (e.g., fishing-out) will be needed while local conditions must be carefully factored in if this strategy is ever to be employed.

In a study addressing bigheaded carps, Zielinski and Sorensen [15] focus on how the upstream of movement (i.e., invasion) of bigheaded carp through locks and dams in the Upper Mississippi River could be arrested. They show how the velocity of water passing through the locks and dams, which already divide this river into a series of pools, could be exploited to arrest carp movement upstream at a few specific locations (i.e., local conditions are very important) by adjusting dam spillway gate openings to increase water velocities and reduce carp passage. Perhaps most importantly, Zielinski and Sorensen describe a strategy in which, in addition to adjusting lock and dam spillway gate openings, carp removal would also be conducted at key locations while deterrents such as CO2 and sound could be added to their locks to affect a nearly complete (99%) block at low cost, even in the event of flooding. Zielinski and Sorensen [15] model over 100 scenarios in the Upper Mississippi River to show how this integrated multi-component control scheme could be immediately implemented at low cost at several key sites (pairs of locks and dams that rarely experience "open-river" conditions) without necessarily substantially affecting native fish populations in the river as a whole because particular species and locations can be targeted. Like McColl and Sunarto [13], real biological data are used, meaning that this strategy could be implemented and at low cost. In both cases, few alternatives are presently available to control carps in these vast regions.

Finally, Bouska and colleagues [4] examine the possibility of controlling bigheaded carps in the Illinois River (a tributary of the Mississippi River) by using different types of removal fisheries. This is an important question for many of the invasive species that are edible, because politicians usually wonder if control could be self-funded and/or possibly lead to pressures to maintain an otherwise undesirable fishery. Specifically, Bouska et al. [4] describe how a decade-long contracted harvest program has successfully led to reduced bigheaded carp densities in the upper stretches of the Illinois River, seemingly preventing them from invading the Laurentian Great Lakes, but at great expense. They then describe a previously unpublished study which examined two alternatives ways of removing adult bighead carp with commercial fisheries in this river: (1) one in which a few fishers were offered a "fisher-side" incentive program, in which they were financially rewarded to catch carp for direct consumption if they shared data; (2) another in which many fishers were offered a "market-side" incentive program, which used set-quotas and guaranteed prices set by the industry to provide fish for fertilizer markets. Interestingly, while the market-side program was successful, the fisher-side program was not, suggesting that if demand (and prices) for bigheaded carp could be controlled and maintained, market-side fisheries could become a good alternative and supplement to contract fishing. This study also points out that all fishing favors large fish, but that control requires all size classes of fish to be caught, and so additional complimentary approaches (e.g., deterrent systems in locks and dams) are still required to affect full control if removal fishing is to be used effectively for bigheaded carps in rivers over the long-term.

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1.5. Lessons Learned from Invasive Fish Control Programs

Numerous management programs currently attempt to control invasive fishes across the globe. A few of these are reporting success and producing important lessons. This special issue includes five articles which describe success stories from both the southern and northern hemispheres. It is the first such synthesis of management information that I know of. Experiences controlling the common carp, a salmonid, an esocid (northern pike), and sea lamprey are documented. All programs employ multiple techniques optimized to local conditions and use a detailed understanding of invasive fish abundance and distribution generated by some type of numeric model. Interestingly, while all are costly, none rely on expensive state-of-the-art techniques, and all include some type of sustainable adult removal. One example [7] describes eradication. I briefly introduce these studies and their lessons below.

An article by Young and colleagues [5] describe the history of the sea lamprey control in Lake Champlain, a large lake that is just east of, but not directly connected to the Laurentian Great Lakes, whose sea lamprey program (http://www.glfc.org, assessed on 27 November 2021) uses a strategic combination of the larval toxin, TFM (see above), and barriers to block adults to reduce lamprey populations by ~90%. Young and colleagues [5] describe how their multi-agency team instituted a very similar management program in Lake Champlain, but have not observed a similar level of success. Surprising local differences emerged between the two programs; in particular, a few spawning rivers were found to have disproportionate importance in Lake Champlain, and the larvae there appear to survive the TFM treatment better than in the Great Lakes. A system of temporary (and unique) lamprey barriers has thus been implemented to supplement TFM, which is also used more liberally. This activity has required extensive new monitoring and research, along with a more highly coordinated program of control. However, indications that local fishes including lake trout may now be recovering as lamprey numbers also appear to finally be dropping. Comparisons with the Great Lakes' sea lamprey program are very interesting, as they emphasize the importance of adaptive management and an understanding of local conditions to invasive fish control.

A somewhat similar story is described in a large, high-altitude and isolated lake, Yellowstone Lake [11], where lake trout were first observed in the early 1990s after apparently being introduced from the Great Lakes (where they have been decimated by the sea lamprey). Exotic lake trout now prey on the local endemic trout in Yellowstone Lake, the cutthroat (Oncorhynchus clarkii bouvieri) and are seriously threatening its survival and biodiversity. Koel and colleagues [11] describe how initial large-scale removal of lake trout by the local agency had little benefit, but how population modeling recommended by an outside review, eventually led to a much more targeted and larger-scale netting effort focused on lake trout spawning beds which is now showing success. Most importantly, they describe how this removal program is now supplemented by a complementary (integrated) program that kills larval lake trout on their benthic spawning beds by sinking the carcasses of extirpated lake trout there, inducing anoxic conditions. Further, private foundation and local angler groups are now assisting with intensive monitoring, and long-term support and planning is now in place. Remarkably, the population of cutthroat trout population is now starting to recover. Integrated sets of strategies with a focus on eliminating reproductive success and which use deep local knowledge have clearly been enabling in this example.

Dunker and colleagues [13] describe an invasive species program designed to protect and preserve migratory Pacific salmonids, *Oncorhynchus* spp., in a large area of southern Alaska which was invaded by northern pike, *Esox lucius*, an apex predator, several decades ago. This esocid (which came from northern Alaska) now preys on native salmon species which it has extirpated from dozens of lakes and greatly reduced in many more. Given the vast size of the area and the limited resources to manage it, the challenge is enormous. Once again, a suite of integrated and targeted approaches has been implemented to consider local conditions carefully and include: (1) population suppression in larger open systems using

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targeted netting; (2) eradication using rotenone (a natural fish poison) in other systems; and (3) prevention using angler awareness (as in Yellowstone Lake). Restocking native fish has complimented this long-term multi-faceted effort that is now paying hard-won dividends.

Finally, two studies at opposite ends of the world report success controlling the common carp, a species from Eurasia. Yick and colleagues [7] report eradicating this species in a large high-altitude Tasmanian (Australian) lake after a 12-year removal program accompanied (and now followed by) an equally long period of monitoring. The primary goal has been the preservation of biodiversity via eradication in this unique and ecologically-delicate lake. Success was realized using a series of innovative approaches which included containing fish in the lakes; removal of adults using both electrofishing and large-scale seining using radio-tagged "radio-transmitter" or "Judas" fish (tagged fish that lead biologists to other carp so they can be removed); and finally reducing their reproductive success by keeping carp out of known shoreline spawning grounds using kilometer-long fences, and when eggs have been detected, killing them. This might be the only known example of invasive fish eradication that has not used poisons. In another story about common carp and the importance of understanding local ecosystems, Sorensen and Bajer [3] report similar, albeit slightly less dramatic success at controlling and reducing populations of common carp in two chains of Midwestern (USA) lakes. The goal here was to improve water quality, and although success relied on many of the same elements used in Tasmania, some differed because of differences in local ecosystems. Notably, control has been realized using a strategic combination of three approaches: (1) removing aggregating over-wintering adults using large nets and Judas fish; (2) blocking adult migration into spawning areas located in adjoining outlying lakes using simple barriers; and (3) suppressing reproductive success (the production of young) by enhancing the numbers of a native micro-predator, the bluegill sunfish, Lepomis macrochirus, which was found capable of consuming very large numbers of carp eggs and larvae. Tasmania does not have similar populations of micro-predators which have reduced the cost of control and made it sustainable without the need for eradication in the Midwest. This study and its control program spanned two decades and involved long-term commitment/ discovery. Importantly, common carp densities have been reduced to levels that are no longer deemed highly environmentally damaging (allowing for treatments to improve water quality) and sustainably controlled by native fish. This example may be the first to control an invasive fish using native predators. Together, these two studies of common carp control show how strategies that include reducing reproductive success (the production of young), adult removal, and blocking movement of adults to key local areas, have been highly effective at controlling a long-lived invasive fish in two different areas of the world with very different ecosystems. Understanding local ecology has in both cases also been key to their success.

2. Summary and Future Study

Great progress is being made understanding how and why fish are invasive in freshwaters and some management programs are registering success, using strategic suites of well-established techniques. However, there is still room for improvement and in particular, a need for new techniques including genetic control, sensory deterrents, and eDNA, especially if these techniques are to be integrated into control plans. Nevertheless, based on the five programs reviewed in this issue, it appears that in order to succeed, control plans need to develop a deep local knowledge and focus on both reducing reproductive success and adult removal in targeted manners supported by numeric models. Long-term financial and administrative support is essential. Although this special issue summarizes some of this progress and many important lessons in science and invasive freshwater fish control, there is still a strong need to review, synthesize, and publish data on other control techniques, strategies and programs we could not cover. Marine fishes in particular need to be considered. I hope that this special issue sparks such efforts and thank its contributors for their many valuable insights and contributions.

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Funding: This research received no external funding.

Conflicts of Interest: The author declares no conflict of interest.

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