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Review

Biological Invasions in Fresh Waters: *Micropterus salmoides*, an American Fish Conquering the World

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Abstract: Biological invasions in fresh waters cause biodiversity loss and impairment of ecosystem functioning. Many freshwater invasive species are fish, including the largemouth bass *Micropterus salmoides*, which is considered one of the 100 worst invasive species in the world. Fast individual growth rates, high dispersal ability, ecological tolerance, and trophic plasticity are among the characteristics contributing to its success. The negative impact of *M. salmoides* on littoral fish communities is believed to be mitigated by habitat structural complexity resulting from aquatic vegetation and coarse woody debris, while the main limits on its spread seem to be strong water flows and high turbidity, which impairs visual predation. Together with the human overexploitation of its potential fish antagonists, habitat alteration could result in *M. salmoides* having seriously detrimental effects on native biodiversity. The purpose of this study is to critically review the life history and ecology of *M. salmoides*, its impact on ecosystems outside North America, and the effects of anthropogenic activities on its spread. This will highlight environmental factors that favor or limit its invasive success, helping to identify management measures that might mitigate its negative effects on freshwater biodiversity.

Keywords: biological invasions; invasive species; native species; fish; freshwater ecosystems; habitat management and conservation

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1. Introduction

Biological invasions represent a pervasive global problem that threatens indigenous biodiversity. They have been a matter of public concern and a subject of study for ecologists since the last century [1,2], providing useful case studies with which to refine ecological theory and study novel species' interactions and communities [3]. There are many reasons and mechanisms behind the introduction of novel species, their establishment, and their invasiveness [4]. Their success depends on a range of ecological factors, including habitat conditions, the presence of competitive native fauna, and the invasive skills of the introduced species. Managing invasions and forecasting the success of species introduction, whether intentional or unintentional, require knowledge of the main ecological forcing factors that can favor or impede the reproductive success of an invader.

Globally, fresh waters are among the ecosystems that are most frequently affected by biological invasions [2,4,5], which can have major consequences for native communities [6,7]. Despite this, they have historically been overlooked, compared to terrestrial and marine ecosystems, although a Web of Science keyword literature search showed that since 2003, studies of freshwater invasions have increased faster than those of other habitats (Figure 1a, line blue). Compared to other ecosystems, however, the percentage of research articles on biological invasions of fresh waters is still low (less than 4%).

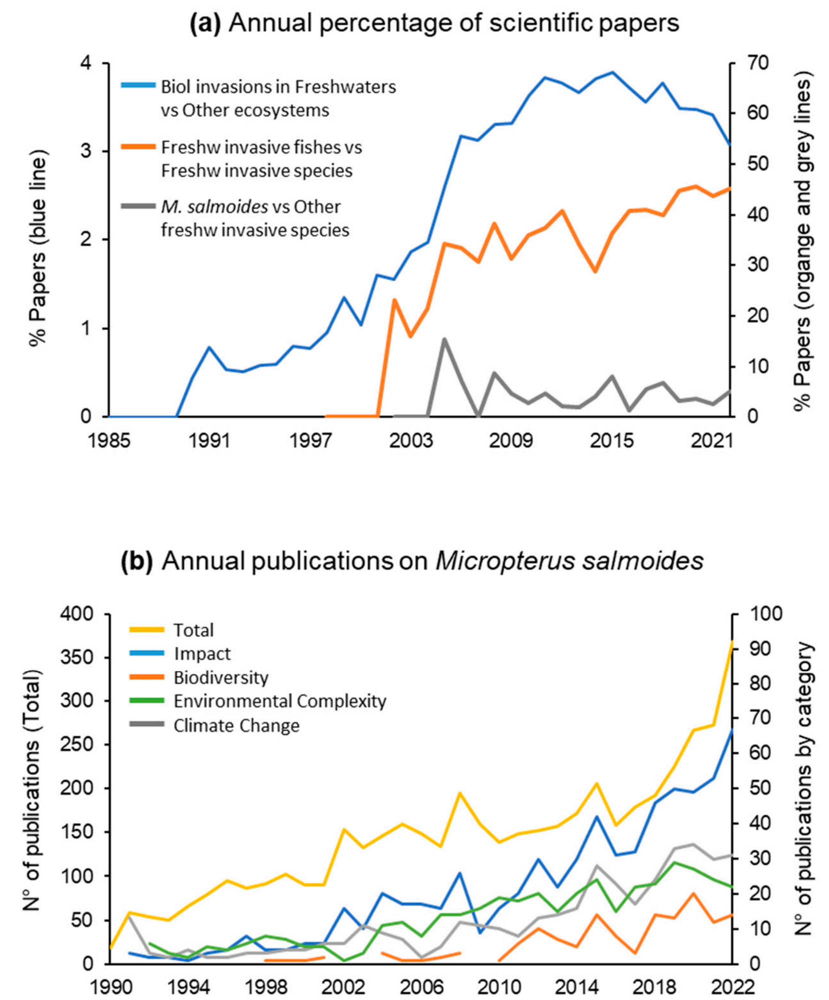

Figure 1. Search performed in the Web of Science topic field, considering: (**a**) only scientific papers, for which the blue line = (biological invasion* OR alien OR invasive) AND (freshwater* OR lake* OR river* OR pond* OR inland water*)/(biological invasion* OR alien OR invasive"), the orange line = (freshwater invasive species AND fish*)/(freshwater invasive species), and the grey line = (freshwater invasive species AND fish*) AND (*Micropterus salmoides* OR *M. salmoides* OR largemouth bass OR black bass)/(freshwater invasive species AND fish*); (**b**) all document types for (*Micropterus salmoides* OR *M. salmoides* OR largemouth bass OR black bass) = yellow line, subsequently refined for impact* = blue line, biodiversity = orange line, (Climat* OR warm*) = grey line, (habitat compl* OR env* compl*) = green line.

Given the importance of freshwater ecosystems for human societies and the value of the biodiversity that they host, invasion control and management have become mandatory. Many freshwater invasive species are fish [4], and this is reflected in the published literature (Figure 1, orange line). The present review focuses on a highly invasive freshwater fish, the centrarchid *Micropterus salmoides*, which is rapidly spreading in many continents (Figure 2). Scientific interest in *M. salmoides* has accounted for up to 15.4% of papers on freshwater invasive species over the last few years (Figure 1a, grey line).

Since 1990, the number of studies of this species has increased rapidly (Figure 1b, yellow line), especially studies regarding its impact (Figure 1b, blue line). The growing interest in *M. salmoides* is linked to central topics in the study of invasion ecology, including biodiversity (Figure 1b, orange line), environmental integrity and complexity (Figure 1b, green line), and climate change (Figure 1b, grey line), which are all considered in this review.

Figure 2. Specimens of *Micropterus salmoides* caught in Lake Albano (central Italy) in Spring 2019 by hook-and-line with artificial lures. The unit of measurement is cm.

Micropterus salmoides is native to North America. The two subspecies, the Northern largemouth bass *M. salmoides salmoides* (Lacépède 1802) and the Florida largemouth bass *M. salmoides floridanus* (Lesueur, 1822), are often considered different species [8]. They are known to hybridize [9] in northern Florida, where they often exhibit intermediate characteristics [10,11], and in Texas, Nevada, Arizona and California, with the rapid introgression of Florida bass genes [12]. The two subspecies are also known to hybridize in ecosystems where both have been introduced [8,13–15].

The more common Northern largemouth bass originates from eastern North America (Figure 3), but for various reasons, it has been introduced in more than 50 countries around the world, mainly for angling purposes [16,17]. Following its introduction, this species has become invasive in many European [17–20], Asian [21], and African [13,22] countries, as well as South America and other parts of North America [17,23–25].

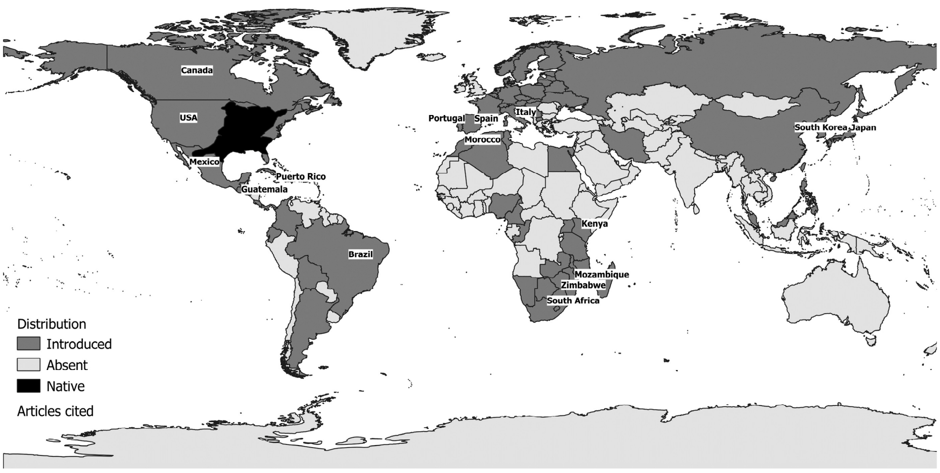

Figure 3. Distribution of *Micropterus salmoides* according to GISD [26]. Native distribution according to Brown et al. [9]. The labels indicate the names of the countries of origin of the literature describing *M. salmoides* as an invasive species cited in this review.

The introduction of largemouth bass has negative effects on native fish fauna [26], and this species is listed among the world's "100 worst invasive species" [27]. The detrimental effects of *M. salmoides* on host ecosystems result from its predation and competition with respect to native fauna [19,28,29]. These negative consequences are strongly dependent on the nature of the environment and the biological characteristics of other species [4]. However, results from the literature are not always consistent. In addition, because *M. salmoides* is one of the most sought-after species for sport fishing and has nutritional value for fish farming, the costs and benefits of its introduction and spread have generated much controversy [25,30–32].

The purpose of this paper is to critically review the life history and ecology of *M. salmoides* and its impact on ecosystems outside North America. This paper highlights the environmental factors that can favor or limit its invasive success, helping to identify management measures that can mitigate its negative effects on freshwater biodiversity.

2. Ecological and Life-History Traits of *M. salmoides*

2.1. *M. salmoides Traits in Native and Invaded Ecosystems*

According to the literature, the largemouth bass displays wide environmental tolerances that allow it to survive in a variety of native and invaded ecosystems, as summarized in Table 1.

Table 1. *Micropterus salmoides* life-history characteristics in native and invaded ecosystems; y: years, NR: data not reported; * the criteria for measuring fish length varied between studies.

Characteristics	Description
Scientific name	*Micropterus salmoides salmoides* (Lacépède 1802)
Common names	Largemouth bass, Northern largemouth bass, Black bass
Native range	North America (St. Lawrence Lowlands, Great Lakes, Mississippi River basin, Quebec to Minnesota, South Carolina, Florida, part of New Mexico)
Non-native range	>50 countries around the world
Habitat	Predominantly warm [33–38], eutrophic [21,39–42], and lentic [9,37,43–45] waters. Submerged plants [9,19,21,33,45–61], woody debris, or underwater structures [48,62–66].
Age of sexual maturity	3–5 y in Canada [33], 2–3 y in Italy [67], 1.3–2.3 y in South Africa [68] 2.0–2.4 y [69], 1 y in Zimbabwe [70], 0.9 y in Mozambique [22].
Maximum life span	15 y in Canada [33], 14 y in South Africa [68], 9 y in Zimbabwe [70], 8 y in South Korea [69], 7 y in Italy [67], 5 y in Mozambique [22].
Mean length (min–max) *	38.4 cm (10.2–54.4) in Canada [33]; NR (6.1–46.5) in Kenya [71]; NR (2.7–59.5) in South Africa [68]; 32.5 cm (22.0–53.7) in Zimbabwe [70]; 24.4 cm (10.0–47.8) in South Korea [69]; NR (21.0–46.6) in Brazil [72]; NR (up to 43.0 cm) in Japan [73]; 25.0 cm (13.8–42.9) in Italy [19,74].

M. salmoides prefers salinities below 5‰, although it is sometimes found in brackish waters [75,76], and pH values of 6.5 to 8.5 [9]. It can tolerate low dissolved O_2 concentrations, but it avoids values below 1.5 mg/L. It spends part of its life cycle at depths of 1 m to 15 m, but it reproduces in shallower waters [9,33] and is able to explore deeper waters where visibility and light intensity are not so low as to limit its foraging ability [77].

The largemouth bass tolerates a very wide range of temperatures, from 0.1 to 39 °C [76–79], although temperature is an important variable in models aiming to predict *M. salmoides* distribution [38,80,81]. Optimal individual growth is generally achieved at temperatures of 24–30 °C [82], and the optimal temperature for reproductive activity is 20–21 °C [9]. This might explain the large variety of spawning periods, as well as the variable age and length at sexual maturity worldwide [9,22,67,69,74] (Table 1). In Canada, male bass achieve sexual maturity at the age of 3 or 4 years, and females at 4 or 5 years [33]. This happens earlier (about 1–2 years) in countries at lower latitudes outside *M. salmoides*'s native range, probably because the higher temperatures in these areas favor individual growth for most of the year [69,70,74]. This is supported by the von Bertalanffy growth model, which highlights a correlation between individual growth and latitude [83].

The role of temperature in speeding up *M. salmoides*'s individual growth rates has also been highlighted by comparisons of native and introduced ranges [36], as well as by studies of lakes heated by power plant effluent and similar non-heated lakes [77]. In spite of the varied growth rates, the mean length achieved by *M. salmoides* adults ranges between 20 and 38 cm in Canada [33], which is similar to values seen outside its native range in other continents [15,67,69,70], although lengths of more than 95 cm have been recorded [10,84] (Table 1). *M. salmoides* can live up to 15 years in the northern part of its native range [65,85]. Outside its native range, a population living up to 14 years was recorded in a South African reservoir [68], but elsewhere its longevity does not usually exceed 9 years [36,67,69,70].

As with other species, *M. salmoides*'s growth rate, maximum length, and lifespan depend not only on temperature, but also on population density, competition, habitat quality, and food availability [34,86–88].

2.2. Traits Conferring Success on M. salmoides

In addition to longevity (Table 1), high fecundity, which counterbalances the typically low genetic diversity of newly introduced populations [15,89,90], is among the life-history traits of *M. salmoides* shared by other successful invasive fish species [91–93]. The female simultaneously produces from 4000 to 14,000 adhesive demersal eggs per kg of its own weight [9,33].

The great reproductive potential of this species, along with parental care, might be key to establishing populations and rapidly colonizing new environments. The male usually builds a nest in undisturbed vegetated sites (Table 1) or close to fallen trees and other forms of coverage, where it protects the eggs and the fry after female spawning [9]. Woody debris is also a good substrate for egg attachment, and it provides protection from predation in this phase ([63,64,66], and references therein). Intensive parental care and precocious spawning may also benefit *M. salmoides* in biodiverse environments, where fish eggs are more exposed to predation [94].

Large size and opportunistic feeding strategies are other successful traits of this species [19,44]. Big adult individuals are not likely to become the prey of native predators, thanks to their large body size, while they are able to include in their diet food sources that belong to a range of food chains and trophic levels [19,95]. In addition, young specimens feed on various families of aquatic insects and crustaceans before undergoing an ontogenetic shift to piscivory [9], a key factor affecting their probability of survival [96]. The length at which the smaller individuals begin eating fish varies widely (from about 20 mm to 200 mm) and depends on the abundance and size of the available prey [21,33,46,73]. If fish availability is very low, *M. salmoides* might continue feeding on aquatic insects or crustaceans as its main prey throughout its life [62,65,97,98]. Cannibalism by bass is also common when prey availability is very low and where warmer temperatures favor early spawning and high individual and population growth [9,22,33,96,97,99]. Under stressful conditions, feeding opportunistically on young conspecifics, which are abundant and high-energy food sources, may allow largemouth bass to control population density, reduce competition, and increase invasion success [33,73,99,100]. The large range of resources it can exploit allows the bass to sustain populations in most ecosystems with suitable abiotic conditions, a trait common to other successfully introduced piscivores [101].

The wide environmental tolerance range and high trophic plasticity (Table 1) have enabled the species to establish itself in many countries (Table 2), where it generally exhibits Fulton's body condition factor (Bennet, 1971; cited in [76]), which denotes an averagely fat or very fat fish [22,70,71,74,98]. In some areas, *M. salmoides* may account for a large proportion of the fish biomass [102–104].

Table 2. Native and invasive *Micropterus salmoides* environments, taken from the literature cited in this review.

Micropterus salmoides **Environments from the Cited Literature**
Lakes and reservoirs
North America: Lake Opinicon-St. Lawrence [33,56], Ottawa system, Lake Simcoe-Great Lakes system [33], Ontario [33,95,105,106], Laurentian Great Lakes [79,107], Wisconsin (Paul Lake, Peter Lake [96,97,108], West Long Lake, Tuesday Lake [108], Trilby Lake [109], Lake Mason [110], McDermott and Sandy Beach [111], Little Rock Lake [62–65], Camp Lake [63], Lake Mendota [87], Bay Lake, Indian Lake, Alequash Lake, Little John Lake, Brandy Lake, Johnson Lake [66] and many others: [85,112–114]), Indiana (numerous lakes [88]), South Carolina (Par Pond [82]), Illinois (natural lakes: Forbes Lake, Lake Shelbyville, Lake Paradise, Pierce Lake, Lake Mingo, Lake Charleston; power plant cooling lakes: Clinton Lake, Newton Lake, Lake Coffeen [77] and others [115]), Michigan (Paul Lake [99], Big Crooked Lake and Camp Lake [55]), Minnesota [116], Mississippi [117], Nebraska (West Long Lake [118]), Texas (Balancing reservoir [42,119], Lake Conroe [46]), Virginia (Lake Chesdin and Lake Charles [120]), Ohio (Acton Lake, Burr Oak Lake, Pleasant Hill Lake [34], Knox Lake [109] and Ross Lake [52]), Oklahoma (Boomer Lake, Sooner Lake and Guthrie Lake [121], as well as lakes near Stillwater [47] and several reservoirs [12]), Puerto Rico (Carite Reservoir [122])
Central and South America: Guatemala (Lake Atitlán [123]), Brazil (Passauna, Piraquara, Capivari and Vossoroca reservoirs [23]).
Africa: Kenya (Lake Naivasha [36,71], Lake Baringo [71]), Mozambique (Lake Chicamba [22]), and Zimbabwe (Lake Manyame [70]).
Asia: Japan (Lake Biwa [51,124], Lake Izunuma [41,73], Lake Izunuma-Uchinuma [125,126], Lake Kawahara Oike [21], Lake Kizaki [127], Lake Hataya Ohnuma [128]), Miharu Dam Reservoir [37]), South Korea (Goe-San Lake [69], Masan, Gucheon and Yeongdeok reservoirs [103], and Nakdong River basin reservoirs [60]).
Europe: Italy (Lake Bracciano [19,74,129,130], Lake Candia [39], Lake Trasimeno [67,98,131], Lake Mergozzo, Lake Maggiore, Lake Iseo, Lake Idro, Lake Garda [104]); and Spain and Portugal (several reservoirs [38,43], including Póvoa e Meadas, Monte Novo and Morgavel [132]).
Ponds
North America: (Moe Pond [40] and other ponds [133] in New York State, the Eagle Mountain Fish Hatchery [134] and U.S. Army Corps of Engineers Aquatic Ecosystem Research Facility [58] in Texas, and ponds near Stillwater in Oklahoma [47].
Asia: Japan (farm ponds in Saitama Prefecture [135], farm ponds in Hyogo Prefecture [136], farm ponds in Iwate Prefecture [48,124,137–139], ponds in Shiga Prefecture [140], and Mizoro-ga-ike Pond in Kyoto [102].
Europe: Italy (several permanent ponds in Cornocchia and Montagnola senese, Tuscany [141]).
Rivers
North America: California (Sacramento-San Joaquin Delta [49]), Florida (Hillsborough River [142]), Georgia (Chattahoochee River [50]), Oklahoma (Brier Creek [143], Maries River [144]), Missouri (Loose Creek [144]), Virginia and Maryland (Lower Potomac River [145]), Indiana (Blue River [146]), and Wisconsin (Big Spring Creek [110]).
Africa: South Africa (Assegaaibos River, Amandel River [147], Berg River [147,148], Tyume River [28], Kubusi River [100]), Zimbabwe (Manyame River and other streams around Harare [13]), Blindekloof stream in the Swartkops River system [29], Olifants–Doorn River basin [149], and several other catchment areas [94].
Asia: China (Songhua-Liaohe Rivers, Haihe River, Huaihe River, Yellow River, Yangtze River, Pearl River, the Southeast, Southwest and Continental Basins [150]), Japan (Ezura River [151]), South Korea (various large South Korean rivers and their tributaries and small streams including Geum River [80,152–155], Han River [80,152,154,155], Nakdong River [60,80,152,154–156], and Yeongsan River [80,152,155]).
Europe: Italy (several rivers in Sardinia [157]), Spain and Portugal (Bullaque River [44], River Jándula [18], Guadiana basin [35,158,159], the Raia tributary of the River Sorraia [45], Júcar River basin [160], and Degebe River basin [161]).
Brackish waters
North America: California [75].
Europe: Spain (Lake Caicedo Yuso-Arreo [20]).

3. Influences on Freshwater Biodiversity

The main negative influences of *M. salmoides* on biodiversity result from predation and competition. This factor was reviewed by Brown et al. [9], with a focus on North America, and by Takamura [14], whose study was limited to Japan, but many cases have also been reported from other countries. Pereira and Vitule [31] recently performed a systematic review of the literature on this topic, highlighting patterns that were apparent from indexed publications. Another negative consequence of the introduction of an invasive species is the co-introduction of its parasites, which, if not highly specific, can also infect local species [9,162].

3.1. Negative Associations with Native Fish Species: Predation and Competition

While predator–prey relationships may be difficult to observe directly in the field [65,97,163], they are more easily recognized by gut and stable isotope analyses [19,100,152,164] and references therein. Direct observation of predation of native fish might be difficult in some cases, due to the rapid eradication or drop in abundance of prey, with the consequent reduction in fish diversity. This especially concerns native cyprinids, as appears to have been the case in South African rivers [29,149], the upper Manyame catchment area in Zimbabwe [13], large river systems in South Korea [154], Japanese farm ponds [139], and Spanish rivers and lakes [158].

Sometimes, the negative correlation between abundance of *M. salmoides* and other fish has been attributed to similar food preference, as in the case of native carnivorous Korean fish [127,145,154]. This may even be the cause of species extinction, as in the case of the waterbird *Podilymbus gigas*, the Atitlán grebe [123].

The largemouth bass can have substantial diet overlap with top predators, such as *Esox lucius*, *Perca fluviatilis*, and *Gobiomorus dormitor*. Often it can also feed on smaller individuals of these species, thereby having a dual detrimental effect by both predation and competition, depending on their size [19,95,98,122]. Bass-related predation and competition also threaten the anabantid *Sandelia bainsii*, an endangered endemic South African fish species. It has been suggested that the two species' diet similarity is due to the scarcity of prey, including the anabantid fish itself, determined by predation pressure by the bass [28]. Indeed, experimental comparisons showed that the bass has greater prey consumption and a greater increase in feeding rate with prey density (i.e., functional responses, FRs) than native fish, including South African anabantid species, thanks to its shorter handling time [165]. In other cases, the reduced prey availability caused by bass predation induces native species to change their diets, as suggested for the declining cyprinid *Opsariichthys uncirostris* in Lake Biwa in Japan [124].

3.2. Non-Lethal Effects of Predation by Bass

Micropterus salmoides can affect the fitness of other fish either by feeding on them directly (consumptive effects) or by prompting certain behaviors (non-consumptive or non-lethal effects), including defensive responses to minimize the risk of predation [52,130]. The outcome can be decreased movement, feeding, and growth on the part of prey individuals [166], as well as changes in habitat use. For example, the non-lethal effect of the largemouth bass on the centrarchid bluegill *Lepomis macrochirus* is to force the smaller-size classes to use only areas with complex structures, thereby increasing their competition for food, resulting in lower individual growth rates than those of the larger classes [167]. The cyprinid *Campostoma anomalum* does not feed on algae attached to pebbles in the proximity of *M. salmoides*, while they do graze on pebbles further away, favoring habitat segregation between the two species [143]. Non-consumptive effects on crayfish have also been reported: these include the alteration of movement patterns [146] and foraging activity [168].

While decreasing the predation risk from largemouth bass, these prey-avoidance behaviors can increase overall predation risk from co-occurring predators with different foraging behaviors. For example, more bluegills were captured in experimental treatments with both *M. salmoides* (a cruising predator with an opportunistic ambush strategy) and *Esox masquinongy* (an obligate ambush predator) than were expected in the presence of a single predator [169]. Indeed, different predator foraging behaviors require different responses from the prey that generally cannot be implemented at the same time [169,170].

3.3. Community-Wide Effects of *M. salmoides*

The introduction of invasive species, which often differ functionally from the components of the invaded community, can have effects that propagate along the food web [7,19,130] and can be either positive or negative, depending on the community structure and the trophic level. In Japanese farm ponds, it has been demonstrated that *M. salmoides* has a direct negative influence on the abundance of fish, shrimps, odonata, and exotic crayfish, and an indirect positive effect on macrophytes consumed by crayfish [135]. Positive cascade effects on benthic organisms due to native fish depletion by bass piscivory have also been suggested by Natsumeda et al. [136].

By inducing cascading effects on lower trophic levels, the largemouth bass can also affect the dynamics and composition of the planktonic food web [40,42,57,87,128,171]. Given its negative effects on zooplanktivorous fish, *M. salmoides* has been used for biomanipulation aimed at controlling phytoplankton density [57,87]. However, biomanipulation efforts have not always led to an improvement in water quality [119,172], and the bass has sometimes been found in eutrophic water bodies [39,41]. This has been attributed to the low vulnerability of the target prey fish to *M. salmoides* [134,172], low water temperatures limiting *M. salmoides*'s activity, and the establishment of an inedible phytoplankton community such as blue-green algae [57,87,119].

3.4. Factors Influencing Bass Predation Efficiency: Prey Naivety and Body Shape and the Predator–Prey Size Ratio

Fish living in predator-free habitats do not exhibit defensive responses to predation, since, when not necessary, these responses entail a waste of energy and a consequent decrease in fitness, and they can, therefore, be lost through selection [173]. Some species might have the ability to learn by experience to recognize predator cues, and thus might acquire defensive behaviors in a short time [174–176]. The naivety of some fish to predator archetypes they have never been exposed to has been proposed as an explanation of their vulnerability to predation: they might lack the ability to recognize non-native predator cues and, thus, to adopt appropriate responses for reducing predation risk [29,177,178]. Naivety is also suggested as one possible reason why the largemouth bass concentrates its predation on native species rather than non-native species, such as the bluegill [21,151]. The co-introduction of largemouth bass and bluegill can lead to a community dominated by these fish, as observed in Iberian aquatic ecosystems [18,20,45,159] and Italian lakes [19]. It has also been suggested that body shape makes the bluegill less appealing than long fusiform prey for *M. salmoides* [151]. Indeed, the bass is a gape-limited predator and seems to consume fish with a fusiform body (e.g., the fathead minnow *Pimephales promelas*) more easily than those with a wider or deeper body (e.g., the centrarchid *Lepomis* spp.; [62,179]). The latter, in turn, might be preferred to those with spines (e.g., the yellow perch *Perca flavescens* or the channel catfish *Ictalurus punctatus* [120,163,180]). Deep and wide body shapes and fin spines increase handling time and the risk of predator injury, inducing the predator to focus its predatory pressure on other types of prey [100,133,134,181]. The role of the soft and spiny dorsal fins of *Lepomis* spp. is not yet clear. In addition, it has been demonstrated experimentally that acceleration, which allows the prey to escape attack, can reduce prey vulnerability to bass predation more than spines [179].

The bass-to-prey length ratio is another factor influencing the predator–prey relationship. The preferred size of the prey item is between 22 and 29% of *M. salmoides*'s length, depending on prey shape, although it can ingest much bigger fish [182,183]. The preferred sizes were found to differ little from those predicted by optimal foraging, although in natural environments they encompassed a wider range, probably due to prey availability [97,182,184]. Size-selective predation influences fish community structure [40,57,73,159], with the depletion of fish size classes vulnerable to predation by bass [40,73,103,134], as well as interactions between crayfish species [185].

4. Influence of Environmental Variables on the Occurrence and Interactions of *M. salmoides*

4.1. Habitat Structural Complexity: The Effect of Vegetation and Coarse Woody Habitats

The interactions of the largemouth bass with other organisms are influenced by habitat structural complexity. Coarse woody habitats (CWH) and aquatic vegetation play an important role by providing shelter to prey species, thus favoring their abundance and diversity [65,138], and by influencing *M. salmoides*'s behavior. Indeed, bass are able to opportunistically change their predation strategy in response to habitat complexity [52,61,63]: beyond a certain level of vegetation density or CWH debris abundance, the bass switch their strategy from cruising to ambushing.

Differences in bass diets have been found in environments with different types of aquatic vegetation cover [19,48]. In the presence of both vegetation and open waters, largemouth bass forage almost exclusively on open-water fish species [49]. Dense vegetation reduces (a) predator–prey visual contact, (b) attacks per prey via active search, and (c) captures per attack [52], thus increasing the handling time (for chasing and catching prey) and reducing predator–prey encounter rates. This decreases the maximum number of prey a predator can catch per unit of time [53–55].

In experimental systems, vegetation was found to be effective at reducing predation by the largemouth bass on centrarchids (*Lepomis* spp. and juveniles of the largemouth bass itself), the cyprinid *Squalius alburnoides* [35,49,52], and the guppy *Poecilia reticulata* [53,54]. Furthermore, using artificial vegetation, Gotceitas and Colgan [56] found a density threshold above which the success of bass foraging on juvenile *L. macrochirus* was reduced and suggested a non-linear relationship between habitat complexity and prey habitat choice.

The largemouth bass can have greater attack rates in a diverse macrophyte assemblage than in a monotypic canopy, since the former leaves more gaps that allow the bass to access prey than the latter [55]. This suggests that the optimal habitat for bass is a mix of open or semi-open areas and areas with moderately dense vegetation, which results in both high prey abundance and successful predation ([55,57], and references therein]), as well as higher individual growth and fecundity [50]. In enclosures with *Myriophyllum spicatum*, the largemouth bass consumed mainly fish, while in enclosures with *Potamogeton nodosus*, it fed mainly on invertebrates, despite similar macrophyte densities and prey items [58]. It has also been observed that in areas characterized by dense macrophytes, hypoxic conditions might enhance the refuge effect for prey species that are more tolerant of low oxygen concentrations than bass [51], further reducing *M. salmoides*'s predation success and population growth [59].

The detrimental effect of vegetation does not appear to be a feature of the relationship between *M. salmoides* juveniles and invertebrate/insect prey [47,60]. Younger individuals were observed in densely vegetated areas, and their diet mostly consisted of macroinvertebrates. By providing habitat and food resources for invertebrates, aquatic vegetation boosts their abundance and diversity, making them alternative prey for adult bass, which may adopt a more generalist diet, reducing predatory pressure on fish [19].

4.2. Effect of Turbidity on Predation by Sight

Bass occurrence and foraging ability can be limited not only by vegetation in shallow waters and low light intensity in deep waters, but also by loss of transparency due to suspended particles, which reduce visibility. Turbidity has been suggested as an explanation for the largemouth bass's failure to establish itself in some ecosystems in South Africa [94]. Using bentonite clay, it has been experimentally demonstrated that turbidity lowers the encounter rate between prey and predator by reducing visibility [186], thus lowering the feeding rate [49] and affecting prey selection as the bass switch to slower prey or to prey that use clear-water habitats. High turbidity levels might not allow *M. salmoides* to catch its daily food ration [115,121].

However, although sight plays a key role in the success of largemouth bass predation, laboratory studies have shown high success, albeit with greater catch effort, when *M. salmoides* attacked prey blindly [142,187]. Indeed, the prey movements in the water could be also detected by the lateral line organ [142], which ensures the success of *M. salmoides* attacks even in dark conditions. In these cases, the largemouth bass usually changes its predation strategy by swimming more slowly and opening its mouth more quickly and widely near prey [142,187].

4.3. Anthropogenic Alteration of Freshwater Systems

The effects of largemouth bass introduction are often exacerbated by other anthropogenic alterations to freshwater ecosystems (e.g., flow regulation, pollution, water extraction, and introduction of other exotic species). All these drivers can threaten local species if they are endemic or have a restricted distribution range [148,160,188,189].

In South Korea and southern Africa, the introduction and spread of *M. salmoides* and other invasive species have been linked to anthropogenic alterations to rivers, including the construction of impoundments and large dams, where exotic species recovered better than the native fauna [94,156]. In many other ecosystems, *M. salmoides* occurrence was greater in (or restricted to) sites influenced by dams [13,37,190]. Indeed, largemouth bass do not tolerate high flow conditions [75], as they are easily flushed out, or the intermittent conditions that are typical of Mediterranean streams [45]. The regulation of river flow can, thus, facilitate invasion by this species. Reservoirs provide lentic and stable conditions [43–45] and are characterized by simple communities and "vacant niches" [117,191,192], especially shortly after an inundation. Reservoirs and impoundments favor the establishment and spread of exotic fish species and can provide propagules of invasive species to nearby water bodies, acting as stepping stones [193]. They might also serve as bases for the recolonization of parts of the river from which bass have been displaced [75] and as nursery sites, producing juveniles that are able to populate downstream sections [18].

4.4. The Influence of Climate Change

Climate change influences an ecosystem's vulnerability to invasion by non-native fish species, as it can change the distribution ranges of many species, including *M. salmoides*, prompting them to spread northward and colonize new environments [105,106], thereby threatening native species [95,106] or changing their distribution [80]. Adults of *M. salmoides* do not seem to be particularly constrained by low winter temperatures, tolerating long periods in cold and ice-covered waters [78,79,194]. However, *M. salmoides* displays lower growth and feeding rates at temperatures lower than 10 °C [9,33], and severe temperatures can limit its recruitment. Indeed, under long-lasting cold conditions, 0-year-old largemouth bass often fail to gain sufficient size and energy reserves to survive until the next favorable season [9,109]. In addition, ice coverage of water bodies can reduce oxygen levels in waters and, thus, promote winterkill, further reducing bass survival [9,33]. A warmer climate in the northernmost areas of *M. salmoides*'s current range could remove these limitations. In addition, the global increase in annual mean temperature appears to be the main factor in predicting the spread of bass toward higher altitudes, with an average movement of about 9 m per decade [155].

Climate change might also influence the spawning periods, growth rates, diets, behavior, and distribution of invasive fish, including the largemouth bass [77,155,195], with negative consequences for native species [147,196].

The effects of temperature on *M. salmoides*'s foraging rates [86,197] are highlighted by several bioenergetic models, which estimate the fish energy budget and its variation [108,198]. Using this approach, Rice et al. [82] showed that seasonal temperature variation has an indirect effect on bass body condition, as it influences prey density and, thus, feeding rates. Based on bioenergetics and field studies, the lower increase in *M. salmoides*'s per capita prey demand with temperature and its higher capacity to tolerate prey decline could explain its increasing densities with respect to the congeneric *M. dolomieu* [144].

Altered foraging activity and individual growth rates are likely to influence the interaction of the largemouth bass with other piscivores: in a simulation of climate change scenarios for 2040 and 2060, the bioenergetic model showed increased impact on prey species and potential changes to the fish assemblage [118]. A comparison of 359 lakes in Wisconsin suggested that the negative effect of climate warming on the recruitment of other piscivores (e.g., the walleye *Sander vitreus*) was amplified where bass densities were high [112].

Climate change is also expected to favor flow regime alterations due to changes in rainfall patterns, increased evaporation rates, and reduced runoff, which, combined with changing thermal regimes, water chemistry, and DO dynamics, will stress local communities, leading to changes in the interactions between bass and native biota. These effects can be exacerbated by human activities. Indeed, climate change, along with water extraction and the construction and use of dams, is expected to increase the frequency of severity of drought events and the intermittence of freshwater ecosystems [86,161]. Habitat fragmentation could favor the development of pools in which organisms undergo severe stress related to extreme temperature variation, low resource availability, and strong biotic interactions [161]. This could increase the spread of highly tolerant top-predator species such as *Micropterus salmoides*, further stressing and threatening the persistence of native communities [86,153,161]. In contrast, as a limnophylic species that needs protected nursery and wintering habitats, bass will struggle to colonize intermittent streams, as they are able to survive only in the dry-season pools of downstream reaches [35,161].

Climate change could also influence bass abundance in large and deep lakes, where rising temperatures will generate a larger total volume of thermally suitable habitat for this invasive species than small and shallow lakes [199]. Furthermore, climate change is expected to have negative effects on the vegetated littoral belt and its associated species richness, exacerbated by human activities [62,156]. All this can result in both direct and indirect benefits for warmer and opportunistic species such as *M. salmoides*, with strongly negative effects not only on native fauna, but also on the functioning of the entire ecosystem.

5. Socio-Economic Implications of Bass Introductions

Although economic losses due to fish invasions are difficult to quantify, due to the scarcity of data, based on an estimate of only 27 species, Haubrock et al. [32] reported that fish invasions potentially caused losses of at least USD 37.08 billion from the 1960s to 2017. Socio-economic pressure for the introduction of *M. salmoides* for sport fishing purposes may overcome conservation concerns related to bass invasion. In some cases, the introduction of non-native species has been promoted by administrations in order to meet societal demand for angling opportunities, where these were previously absent or where native stocks were reduced.

Elvira and Almodóvar [200] reviewed introductions of invasive fish, including *M. salmoides*, in Spain during the 20th century. Most species were imported from neighboring countries and intentionally transferred. Notably, the introduction of predatory fish led to a cascade of further intentional introductions, since the depletion of native prey by the non-natives necessitated the introduction of other prey to support the predators targeted by anglers.

While the impact of *M. salmoides* on biodiversity has been broadly described, the evaluation of economic gains and losses resulting from its introduction is extremely complicated, and the outcome is closely related to the characteristics of the invaded habitat. A further serious shortcoming arises from the fact that the two factors are often evaluated separately [130,201,202], reducing the power to distinguish between the positive, negative, and neutral effect of its introduction. The introduction of *M. salmoides* in artificial systems for aquaculture purposes or in small sport fishing ponds can be considered a source of net economic gain. Even in larger reservoirs, revenues can be substantial. For example, Chen et al. [201] estimated that trophy largemouth bass fishing in Lake Fork, Texas, produced USD 27.5 million in annual income and created 163 new jobs (cited in [86]).

In some countries, such as China and Portugal, largemouth bass have been one of the most frequently farmed freshwater species for food, due to its rapid growth, flesh palatability, and ability to satisfy market demand [132,203–205]. More than 700,000 tons of bass were produced in China in 2021 alone. These have stimulated the procurement and production of both natural and artificial feeds to further increase flesh quality and optimize fish farming yields [132,203,204]. However, any unintentional spillover of individuals from artificially managed systems into natural habitats may extend the area of impact (and associated economic losses) far beyond the small areas of intentional introduction [6,200]. Hunt et al. [107] reported that *M. salmoides*'s introduction in the Laurentian Great Lakes (Canada) reduced the economic value attributed by recreational anglers to fishing activities due to the transition from walleye (*Sander vitreus*) to bass (*Micropterus* spp.). In this case, the estimated economic loss to anglers was based on increased travel costs to reach better-stocked lakes, further highlighting the difficulty of measuring economic losses associated with bass introduction.

In an Italian temperate lake (Lake Bracciano), Costantini et al. [19] reported that the two native species most affected by *M. salmoides* were the percid *Perca fluviatilis* and the forage fish *Atherina boyeri*, both of which were of higher commercial value than the bass according to the local fish market. Professional fishers reported a decrease in the two fish stocks following bass introduction into the lake [19,130]. Calizza et al. [130] estimated a potential loss of EUR 1720.5 $\pm$ 53.7 per 100 m of shoreline per year on the northern side of the lake and EUR 362.1 $\pm$ 25.5 per 100 m of shoreline per year on the southern side of the lake. This difference has been attributed to differences in aquatic vegetation coverage and, thus, biodiversity: the higher the coverage, the greater the complexity of the food web and the lower the economic losses [19,129,130,206].

In addition to competing with other fish such as *Esox lucius*, a native predator of higher commercial value [19,98], the bass has been reported to negatively affect amphibian species of conservation interest [131,207], representing an indirect source of economic loss. Indeed, some of the species affected by bass (e.g., the Italian crested newt *Triturus carnifex*; [131,141]) are not only important for nature tourism, but are also the subject of funded conservation and research programs, as they are particularly vulnerable to changes in both aquatic and terrestrial habitats [208].

Currently, the worldwide estimate of economic losses caused by the presence of largemouth bass is around USD 5.29 million [5,32]. Since not all countries have produced reports of economic damage linked to the presence of this invasive species, the figure could be even greater [5,32].

6. Management Options

In light of the above observations on the ecology and impacts of bass introduction, and given the opportunistic behavior of bass, multiple measures to mitigate its effects on native freshwater biodiversity are necessary. First, preserving the integrity and complexity of freshwater ecosystems seems to be crucial in defending them against the detrimental effects of *M. salmoides* invasion. The structural complexity of vegetation can reduce *M. salmoides*'s visual contact with its prey and, hence, its foraging success. At the same time, structurally complex vegetation can support high species richness and more complex food webs. It also provides refuge for fish juveniles, increasing their recruitment [19,60,138]. This is of particular importance, as highly biodiverse communities have the greatest ability to limit the bass by means of antagonist fish [19,130,172]. Unfortunately, native fish communities in lakes are threatened by structural habitat loss, mostly due to drought-driven lake-level decline, lakeshore residential development, and land-use change causing water pollution [116,129,148,160,188,189]. These three causal factors represent widespread anthropogenic problems that need to be properly addressed by means of suitable policies in order to preserve ecosystems and native communities and contain the spread of bass.

For rivers, anthropogenic and climate-induced habitat loss and fragmentation have a greater impact on native fish than on the largemouth bass, which is highly tolerant of many abiotic factors, with the exception of current speed. Thus, proper management measures aimed at preserving or restoring the river ecosystem's integrity, natural flow regime, and water levels can help control the bass population [209]. Removal of disused dams, for example, could help to counteract drought-driven effects and restore habitat complexity and water flow. In other cases, management measures aimed at preventing or reducing water-quality impairment due to nutrient and pollutant loads could serve to minimize potential eutrophication processes [210]. In any case, restoring the optimal growth conditions for native fauna, including the availability and quality of food sources, could promote the biotic resistance of native communities, generating a self-sufficient food web able to resist the invader [19,130,210]. However, ad hoc experiments on other invasive species have shown that flow restoration can have little effect on native fish abundance if the invasive fish populations are not simultaneously removed or controlled [211].

Concerning bass-density control, preserving native antagonist fish is a more sustainable solution than introducing other antagonist species, whose long-term effects are unknown. Habitat loss can have negative effects on native biodiversity, including bass antagonists, and these negative effects are amplified by overfishing. Bass antagonists are often fish of great economic interest (e.g., *Perca fluviatilis*, *Perca flavescens*, *Sander vitreus*, and *Esox lucius*) that are overexploited by professional fishers [110,113,130,212]. Thus, an effective approach for the proper management of *M. salmoides* requires calibrating the fishing effort directed at its antagonists, while abandoning—at least for bass—the practice of catch-and-release that is often associated with recreational angling [114,209]. In a framework of sustainable fishing, in order to compensate for the massive reduction in the catch of target species without affecting profits, Kolding and Van Zwieten suggested fishing for other large species and/or catching the more numerous and abundant smaller species and/or sizes [213]. This would help maintain other fish species, including effective largemouth bass antagonists. However, if antagonist populations are already compromised or extinct, supporting their recovery or reintroduction, as well as monitoring, might be necessary.

According to the guiding principles on invasive species adopted by the Convention on Biological Diversity, when the prevention of alien species introduction fails, control and/or eradication are possible strategies. Constant and selective bass removal through fishing, mainly of those individuals that are most reproductive and vulnerable to angling, may help reduce or eradicate this highly invasive species, depending on the size of the invaded water bodies [214]. Eradication and control directed at *M. salmoides* have proven to be successful strategies in ponds and small lakes [102,125,215]. During the breeding season, adults, eggs, and larvae are distributed in restricted spawning areas, and this allows easier capture of fish than would be the case if they were found throughout the habitat. In these conditions, artificial spawning beds and semicircular dipping nets above the spawning site could successfully be used [125]. A recent study also highlighted the role of male pheromones in capturing mature females during the spawning season [126].

None of these methods is easy to apply in large freshwater bodies. Partial removal may be ineffective, leading to population recovery [20]. Furthermore, other alien fish have sometimes been found to invade and proliferate in the bass-eradicated ponds. In the case of co-occurring alien species, the best management practice is to eradicate or reduce the density of these species before or together with the eradication of *M. salmoides* [135]. Therefore, continuous monitoring and adaptive management after eradication to ensure successful restoration of the native biota must be planned [137]. Similar to what has been tried on tilapia, brook trout, and lampreys [4,216], inducing nest failure as a control mechanism is also a viable control option. Combining fishing and aquaculture with target-specific biological measures, such as the release of sterile males or Trojan Y carriers (which make male individuals phenotypically female), could be effective to control invasive species and balance the costs and benefits of rearing bass.

Given the growing interest in this species for aquaculture purposes, the implementation of well-isolated farming systems with minimal risk of escape might be sustainable [4,150,217]. Indeed, farming largemouth bass can lead to environmental impacts on nearby water bodies and further favor the spread of this species [150,217], possibly due to the discharge of high-temperature fish-farming wastewaters, along with feed and/or drugs, into nearby freshwater bodies [30,217]. The use of intelligent feeding strategies coupled with microalgae, which can reduce the nutrient load, could mitigate the negative effects on receiving and nearby water bodies [217]. Monitoring systems in the surrounding water bodies aimed at identifying the dispersal of potentially invasive individuals should also be encouraged [150].

The possible effects of climate change must be taken into account in planning management activities. Overall, the spread of invasive species and their negative effects on native fauna are expected to increase under current global warming scenarios [155]. However, the magnitude of these effects could vary between ecosystems and species. The resist-accept-direct (RAD) framework, encompassing management options that range from resisting change to directing the trajectory of change, can help decision makers achieve effective management in a context of ecosystem transformation [111,209,212,218]. Resistance to change includes all possible efforts aimed at preserving or restoring aquatic ecosystems, including the improvement of habitats, the restocking of native communities, and the reduction of their overexploitation.

Potential measures to counteract the effects of climate change include the reduction of water temperatures by restoring riparian areas, the regulation of inlet and outlet water flows, and the reduction of anthropogenic impacts in both the freshwater body and the surrounding area ([111,209,212,218], and references therein]). As well as generating non-optimal abiotic conditions for *M. salmoides*, these measures, especially in moderately sized freshwater bodies, can improve the persistence of the local community by increasing its ability to resist the invader.

7. Conclusions

Life-history traits have been shown to be good predictors of freshwater fish invasions and native species extinctions, with rapidly spreading non-native fish species occupying "vacant niche positions in the life-history space" due to either the "niche opportunities" provided by anthropogenic environmental conditions or a low overlap with native fish. Life-history traits common to successful invasive fish species include large size, longevity, and high fecundity [91–93]. In addition to these traits, fast individual growth, high dispersal ability, tolerance of a wide range of environmental conditions, and trophic plasticity are among the characteristics of *M. salmoides* that have enabled it to successfully invade freshwater ecosystems all over the world. Once a habitat has been invaded, largemouth bass can interact both directly and indirectly with native fauna on several trophic levels. These interactions have cascading effects, mostly negative, on the entire community (Figure 4) and might lead to the imperilment of native species with a narrow distributional range, threatening their conservation, and to economic loss for commercial fishers when the native fish are of economic interest. If not properly managed, *M. salmoides* can spread further in the countries where it has been introduced, often taking advantage of the scarcity of local predators.

Structurally complex habitats can provide shelter and preserve fish species from predation by *M. salmoides* and, thus, they help maintain fish diversity in invaded environments, also preserving bass antagonists. Unfortunately, climate change and human pressures threaten these habitats. The increased individual growth rate of the largemouth bass, in combination with the overexploitation of potential antagonist species, could allow the bass to rapidly escape its critical size as prey, thus favoring its piscivory and invasiveness, with serious detrimental effects on both native biodiversity and fishing for economically valuable species. Measures to prevent the lowering of water levels, habitat fragmentation and degradation, nutrient loading from human activities in surrounding areas, and the overexploitation of local fish communities can help maintain or restore healthy antagonist species populations in cases where bass eradication is inapplicable. Management strategies that consider both recreational and commercial fishing will be crucial to containing the spread of this non-native species [219], reducing the negative effects on aquatic biodiversity and species of conservation interest and mitigating possible socio-economic conflicts between the two fishing sectors.

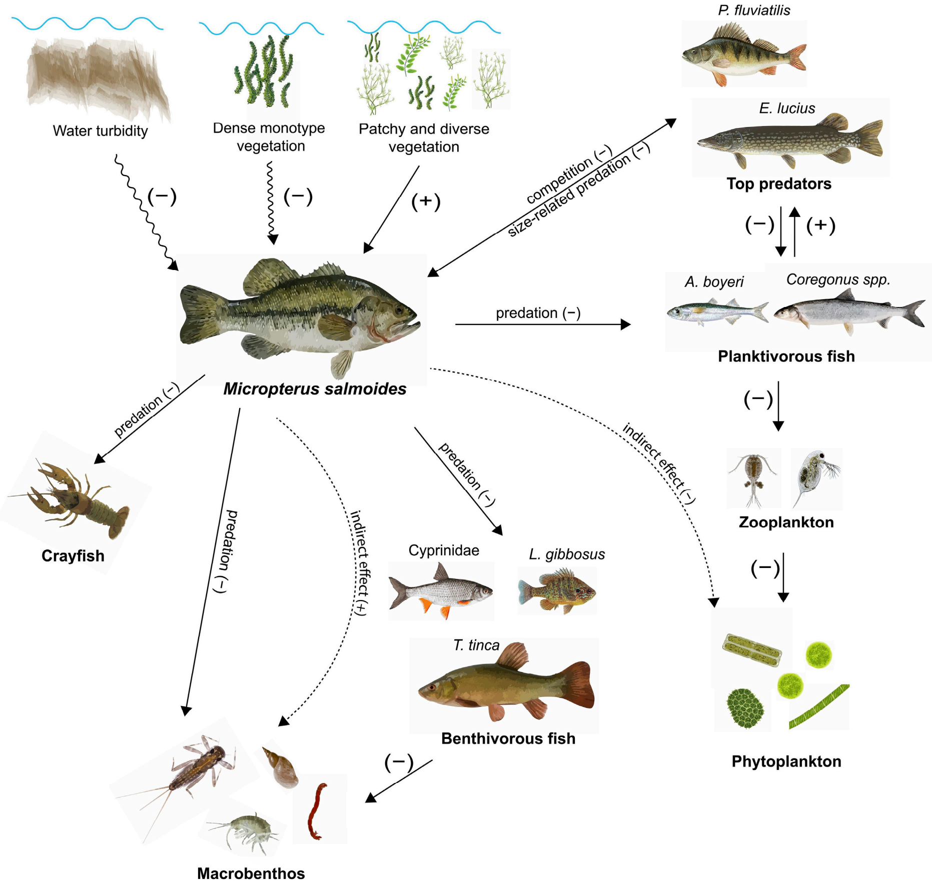

Figure 4. Direct and indirect effects of *Micropterus salmoides* on aquatic communities, and the influence of water turbidity, dense monotype vegetation, and patchy and diverse vegetation on largemouth bass feeding activity.

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