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Review

Invasive smallmouth bass (*Micropterus dolomieu*): history, impacts, and control

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Abstract

In this review, we (i) describe smallmouth bass (*Micropterus dolomieu* Lacepède, 1802) invasions past, present, and future; (ii) summarize the impact that this species can have on native communities; and (iii) describe and discuss various options for control. *M. dolomieu* are invasive throughout much of the United States, southern portions of Canada, and in countries in Europe, Asia, and Africa. Historically, this species spread via stocking programs intended to improve sport fisheries. Currently, their spread is facilitated by anglers and global climate change. Models predict that *M. dolomieu* will continue to spread with consequences for native prey fish, sport fish, and food webs through predation, competition, and hybridization. Effective control methods are necessary to mitigate these impacts. Options for *M. dolomieu* control include biological control, chemical control, environmental manipulation, and physical removal. However, our review of the literature suggests that only a handful of the possible control options have been explored (usually in isolation and with limited success), and that there is a clear need for focused research and informed management. For example, our elasticity analysis of published *M. dolomieu* matrix population models suggests that *M. dolomieu* control will be most effective when it targets eggs, larvae, and juveniles. We recommend targeting these life stages by using nest failure as part of an adaptive and integrated pest management approaches that incorporate existing and emerging technologies. However, we also emphasize that *M. dolomieu* control, where necessary and possible, is more likely to take the form of suppression rather than permanent eradication. Therefore, we also recommend efforts to prevent *M. dolomieu* (re)introduction.

Key words: largemouth bass; black bass; invasive species; fisheries management; integrated pest management; climate change

Introduction

The smallmouth bass (*Micropterus dolomieu* Lacepède, 1802) is a cool-warm water centrarchid (Brown et al. 2009; Shuter et al. 1980, 1989) and a popular sport fish among anglers. *M. dolomieu* are littoral predators, generally consuming small prey fish and crayfish (Vander Zanden et al. 1999). During the spring, male *M. dolomieu* build and guard nests in the shallows of lakes and streams (Ridgway et al. 1991). *M. dolomieu* are native to freshwater systems in 23 states in the east-central United States (Rahel 2000; Fuller and Cannister 2011) and the southern portions of two Canadian provinces (Scott and Crossman 1973).

Outside of its native range, *M. dolomieu* is an invasive species for which there is currently no effective means of control. *M. dolomieu* are invasive across much of the United States, southern portions of Canada, and in 9 other countries throughout the world (Fuller and Cannister 2011; Lyons 2011; Iguchi et al. 2004a). As with many invasive fishes, the spread of *M. dolomieu* beyond its native range has been facilitated by intentional and accidental stocking and climate-mediated habitat expansion (Jackson 2002; Rahel and Olden 2008). Invasive *M. dolomieu* reduce native small-bodied fish abundance and diversity through predation, outcompete other piscivorous game fish, and indirectly change planktonic and benthic communities (Jackson 2002). To date, most attempts to control invasive *M. dolomieu* have either produced undesirable results (e.g., Zipkin et al. 2008) or proven prohibitively labor-intensive (e.g., Tyus and Saunders 2000).

Here, we review the literature on invasive *M. dolomieu* and consider various options for control or eradication. Where *M. dolomieu* literature is lacking, we draw from the literature on invasive largemouth bass *(Micropterus salmoides* Lacepède, 1802), a sister species with a similar life history. First, we summarize the history of *M. dolomieu* invasions and review research that predicts *M. dolomieu* spread with climate change. We then summarize the impacts that invasive *M. dolomieu* have on native species and food webs. Finally, we outline various options for controlling or eradicating invasive species and describe their relevance to *M. dolomieu* in light of life history and previous control attempts.

Smallmouth bass invasions: Past, present, and future

Movement of *M. dolomieu* beyond their native range began primarily through intentional stocking by fisheries managers during the 19th century. The prevailing attitude in fisheries and wildlife management during this period was that nature should be controlled and improved upon. Additionally, recreational fishing was just beginning to come into its own during this era. Books aimed at outdoorsmen promoted bass fishing (e.g. Henshall 1889 and 1903) which was becoming a popular sport. Consequently, managers believed that introducing *M. dolomieu* would prove beneficial. The building enthusiasm for bass fishing led to a wealth of research on bass spawning and rearing (Bower 1897; Cushman 1917; Lydell 1902; Ripple 1908) allowing hatcheries to produce *M. dolomieu* for stocking throughout North America. For example, *M. dolomieu* were introduced to California in 1874 to improve sport fisheries (Moyle 1976). Similarly, from 1868 to 1881 the Maine Commissioners of Fisheries not only authorized *M. dolomieu* introductions in 51 water bodies, but also encouraged indiscriminate introduction by the public (Warner 2005). In the early 20th century, managers introduced *M. dolomieu* into lakes in Ontario, Alberta and Manitoba, and even into a national park in Saskatchewan (Rawson 1945). Unfortunately, fisheries managers in the 19th and early 20th century knew little about both the importance of native fishes and the threats that non-native fishes such as *M. dolomieu* could pose to biodiversity. Indeed, non-native fishes were often introduced to control certain “undesirable” native species and enrich biodiversity (Hey 1926; Moyle 1976). Some jurisdictions even enacted laws to protect these non-natives (Cambray 2003; Hey 1926). Enthusiasm for non-native stocking was eventually tempered by changing attitudes and a better understanding of the impacts of non-native fishes. Stocking non-native fish to provide angling opportunities lost momentum after a final surge in the 1950s (Crossman 1991) and by the 1980s most authorized introductions were into systems that had already been invaded (e.g. Rahel 2004; Carey et al. 2011).

Intentional and unintentional introductions by anglers have been and continue to be major drivers behind the spread of *M. dolomieu* (Jackson 2002). Unintentional introductions of non-native fishes commonly result from bait bucket transfers (Litvak and Madrak 1993). The most comprehensive analysis to date (Drake 2011) suggests that bait bucket transfers in Ontario are responsible for as many as 20 introduction events of *M. dolomieu* per system per year into waterbodies outside of their current range. Intentional introductions occur because *M. dolomieu* are a popular sport fish. Bass are responsible for millions of angler fishing days per year in the Pacific Northwest (Carey et al. 2011), and 77.8% of competitive fishing events in North America’s inland waters (Schramm et al. 1991). Both casual and competitive angling are important sources of revenue and development for many communities (Chen et al. 2003). Bass fishing has such a positive image that the negative effects of bass introduction usually go ignored. As early as the late 19th century, citizens recognized that introduced *M. dolomieu* alter fish assemblages (Warner 2005), but the general public has remained apathetic towards the spread of *M. dolomieu* (Jackson 2002). Anglers continue to intentionally introduce *M. dolomieu* to create more fishing opportunities for bass, without knowing or acknowledging the potential impacts.

Recently, the spread and establishment of *M. dolomieu* has also been facilitated by global climate change. The establishment of *M. dolomieu* is dependent on temperature because their range is limited by the severity of overwintering stress in coldwater lakes (Shuter et al. 1980; Shuter et al. 1989; Jackson et al. 2001). Suitable habitat for *M. dolomieu* is expanding because of warming of lakes and streams attributed to global climate change. Climate change can also facilitate the spread of *M. dolomieu* to uninvaded systems through flooding associated with an increase in extreme weather events (Rahel and Olden 2008).

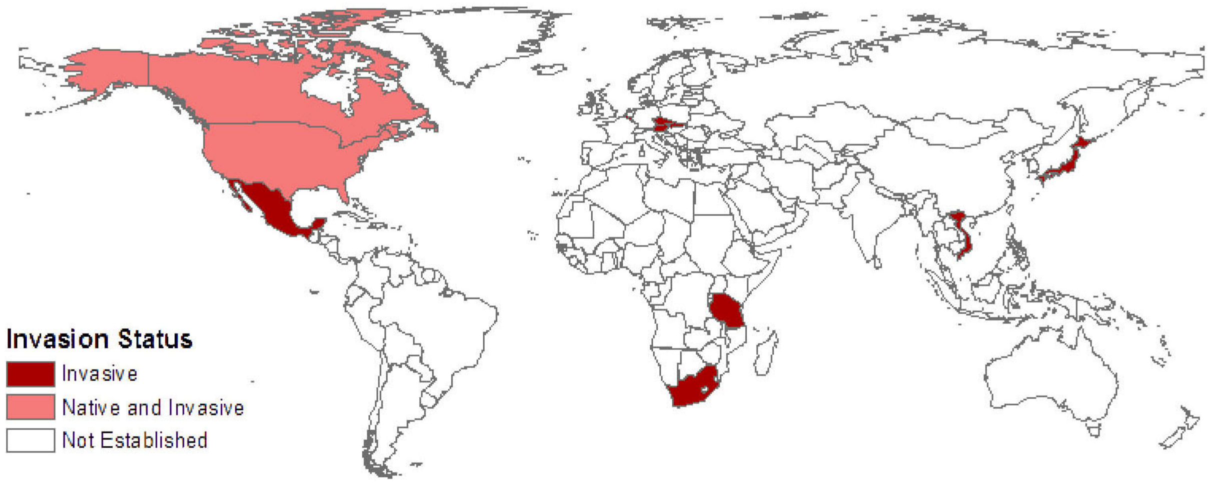

Figure 1. The invasion status of smallmouth bass worldwide. Data are from Table 1, where "introduced" has been interpreted to mean that an invasive population has established. See Fuller and Cannister 2011 and Brown et al. 2009 for details on native and invasive ranges within the United States and Canada, respectively.

Flooding has contributed to the spread of at least two other species: bighead carp (*Hypophthalmichthys nobilis* Richardson, 1845) and silver carp (*Hypophthalmichthys molitrix* Valencienne, 1844) (Kolar et al. 2005). *M. dolomieu* are now spreading northward into Canada, where they pose a serious threat to native species (Dextrase and Mandrak 2006). At current temperatures, 6% of Ontario lakes are predicted to be at high risk for *M. dolomieu* introduction, establishment, and subsequent impacts on native fauna (Vander Zanden et al. 2004); with climate change this number could increase to 20% by the year 2100 (Sharma et al. 2009b). A conservative estimate is that at least 50% of Canada will become thermally suitable *M. dolomieu* habitat, including some arctic locations (Sharma et al. 2007). Combining these predicted changes in habitat suitability with predictions of where introductions will occur suggests that Manitoba and Ontario are the provinces at greatest risk for *M. dolomieu* invasion (Chu et al. 2005). Similar increases in thermal habitat are expected at northern latitudes throughout the world. For example, although cold temperatures prevented the establishment of *M. dolomieu* introduced to Sweden in the 1960s (Curry-Lindahl 1966, Kullander et al. 2012), they may be able to establish there under a warmer climate.

As a result of introductions and habitat expansion, *M. dolomieu* are currently invasive throughout much of the United States, southern portions of Canada, Mexico, and 8 countries on three other continents (Figure 1, Table 1). Forty-two states (including Hawaii) and most Canadian provinces bordering the United States have *M. dolomieu* in areas where they are considered non-native (Fuller and Cannister 2011; Lyons 2011). *M. dolomieu* have also established viable populations in Europe, Africa, and most notably in Japan where habitat suitability models suggest that most waterbodies in the country are at risk of *M. dolomieu* invasion (Iguchi et al. 2004b).

Impacts of invasive smallmouth bass

Invasive *M. dolomieu* can disrupt the native ecology of the systems to which they have been introduced. Bass are voracious predators that can decrease the abundance of, change the habitat used by, and even extirpate small prey fish such as brook stickleback (*Culaea inconstans* Kirtland, 1840), fathead minnow (*Pimephales promelas* Rafinesque, 1820), pearl dace (*Margariscus margarita* Cope, 1867), finescale dace (*Phoxinus neogaeus* Cope, 1867) and northern redbelly dace (*Phoxinus eos* Cope, 1861) (MacRae and Jackson 2001; Trumpickas et al. 2011). In streams, prey fish alter their behavior to avoid invasive *M. dolomieu* by moving from pools to riffles and areas with more structural complexity

Table 1. Known smallmouth bass introductions by country. Data compiled from sources listed as well as FishBase and the FAO Fisheries and Aquaculture Department. Table does not include Belize because this record is believed to be in error (Peter Esselman, pers. comm.).

Country	Status	Year introduced	Introduced from (country)	Method of introduction	Sources
Austria	introduced	unknown	unknown	unknown	Welcomme 1988
Belgium	introduced	1873	USA	angling/sport	Welcomme 1988
Canada	native and introduced	unknown	USA, Canada	angling/sport	Scott and Crossman 1973
Czech Republic	introduced	1889	unknown	unknown	Hanel 2003
Denmark	not established	1958	Canada	unknown	Ostergaard pers. comm.
Fiji	not established	1962	unknown	angling/sport	Andrews 1985
Finland	not established	1893-1963	Sweden, Germany, Canada, Sweden, Germany, Canada	angling/sport, aquaculture	FAO 1997
France	not established	unknown	North America	unknown	Allardi and Keith 1991
Germany	not established	1880	USA	angling/sport	Welcomme 1988
Guam	not established	1962	unknown	unknown	Welcomme 1988
Japan	introduced	unknown	unknown	unknown	Masuda et al. 1984
Mauritius	introduced	unknown	unknown	unknown	Fricke 1999
Mexico	introduced	1975	USA	aquaculture	Welcomme 1988
Netherlands	not established	1984	USA	unknown	Welcomme 1988
Norway	not established	1887-1895	Germany	fill ecological niche	Welcomme 1988
Slovakia	introduced	unknown	unknown	unknown	Welcomme 1988
South Africa	introduced	1937	USA	angling/sport	Welcomme 1988
Swaziland	not established	1938	South Africa	angling/sport	Welcomme 1988
Sweden	not established	1890	USA, Germany	angling/sport	Welcomme 1988
Tanzania	introduced	unknown	unknown	unknown	Fermon 1997
United Kingdom	not established	1878-1890	USA	angling/sport	Welcomme 1988
United States	native and introduced	unknown	USA	angling/sport	Page and Burr 1991
Vietnam	introduced	unknown	South Africa	unknown	Kuronuma 1961
Zimbabwe	not established	1942	South Africa	angling/sport	Welcomme 1988

(Schlosser 1987). Shifting habitat use from pools to shallower areas could expose these fish to predation from terrestrial predators and result in higher energy expenditures during foraging. Invasive *M. dolomieu* pose a serious predatory threat to small native fish in the Yampa River, Colorado, a regional hotspot of native fish diversity (Johnson et al. 2008). The rate of piscivory by *M. dolomieu* is estimated to be ten times that of two other invasive piscivores in this system. In New Mexico, predation by invasive *M. dolomieu* is depleting populations of the threatened bigscale logperch (*Percina macrolepida* Stevenson, 1971) (Archdeacon and Davenport 2010). The spread of *M. dolomieu* into Ontario alone is expected to extirpate more than 25,000 cyprinid populations (Jackson and Mandrak 2002). The loss of such species can lead to both a loss of diversity within invaded waters and a homogenization of fish fauna among invaded waters (MacRae and Jackson 2001; Jackson 2002).

Invasive *M. dolomieu* can also impact top predators, many of which are also prized sport fish. These impacts occur primarily through competition for prey and predation on juveniles. Salmon and trout are particularly sensitive to *M. dolomieu* invasion (Sharma et al. 2009a). Stable isotope studies suggest that *M. dolomieu* predation alters food webs by forcing piscivorous lake trout (*Salvelinus namaycush* Walbaum in Artedi, 1792) to prey on zooplankton, a low-quality food source (Vander Zanden et al. 1999; Morbey et al. 2007). However, the presence of pelagic prey fish can buffer *S. namaycush* from the effects of competition with *M. dolomieu* by providing an alternative high - quality food source (Vander Zanden et al. 2004). In the event of a shift to sub-optimal prey, *S. namaycush* growth and reproduction could be limited. For example, in the 1960s *M. dolomieu* were introduced into Utah's Flaming Gorge Reservoir to control the native Utah chub (*Gila atraria* Girard, 1856),

Table 2. Invasive fish control methods, examples of their use for smallmouth bass control, the bass life stage they target, and their pros and cons. This table draws from and builds upon a review by Halfyard (2010). For "Target", 1=eggs, 2=fry, 3=juveniles, 4=adults.

Method	Description	Example(s)	Target	Pros	Cons
Biological control (pathogens)	Introduction of a parasite or disease that targets bass	Davis (1937,1942)*, McCormick and Stokes (1982)*, Grizzle et al. 2003*	1-4	inexpensive (application), not labor-intensive, effective in all waterbodies and habitats	expensive (development), unconventional, controversial, risk to non-target species, resistance
Biological control (predators)	Introduction of organisms that prey on young bass	Iguchi and Yodo (2004)*	1,2	inexpensive, not labor-intensive, effective in all waterbodies and habitats	controversial, unexpected ecological effects
Biological control (sterilization)	Limit reproductive success (e.g. sterile males)	Dey et al. (2010)*	1,4	species-specific, effective in all waterbodies and habitats	expensive, labor-intensive, unconventional
Chemical	Use of piscicides to kill bass	Smith (1941), Ward (2005)	1-4	not labor-intensive, effective in all waterbodies and habitats	unconventional, controversial, expensive, affects non-target species, destructive
Environmental manipulation (water level)	Complete or partial dewatering to affect survival/reproduction	Kleinschmidt (2008), Mukai et al. 2011*, Kitazima and Mori 2011*	1-4	effective, inexpensive, not labor-intensive	affects non-target species, controversial, limited applicability
Environmental manipulation (winterkill)	Encouragement of a low-oxygen environment that cannot support bass	Smale and Rabeni 1995*, Verrill and Berry 1995*, Shroyer 2007*	3,4	effective, inexpensive, not labor-intensive	unconventional, affects non-target species, limited applicability
Removal (angling)	Use of angling to remove bass	Boucher (2006)	3,4	conventional, uncontroversial, species- and size-selective, applicable to all depths	labor-intensive, inefficient, impractical in large waterbodies
Removal (electrofishing)	Use of electrofishing gear to remove bass	Rinne (2001), Weidel et al. (2007), Boucher (2006, 2005), Burdick (2008), Hawkins et al. (2008)	3, 4	conventional, uncontroversial, effecitve in small waterbodies	labor-intensive, inefficient, affects non-target species, ineffective in deep/complex habitat or large waterbodies, overcompensation
Removal (explosives)	Use of explosives to kill bass	Munther (1970)*, Metzger and Shafland 1986*	2-4	cheap and effective in small waterbodies and in all habitats	unconventional, controversial, affects non-target species, destructive, dangerous, ineffective in large waterbodies
Removal (netting)	Use of nets and traps to remove bass	Boucher (2006), Gomez and Wilkinson (2008)	3,4	conventional, uncontroversial, species- and size-selective, applicable to all depths	labor-intensive, ineffective, affects non-target species

*Study contains proof of concept of the applicability of the control method to smallmouth bass, but does not attempt smallmouth bass control.

which was competing with salmonid sport fish (Teuscher and Luecke 1996). However, decades after introduction, competition with *M. dolomieu* for food appears to be inhibiting the growth of young *S. namaycush* in the reservoir (Yule and Luecke 1993). In Canada, climate change models predict that by 2100, 11% of *S. namaycush* populations will be negatively impacted by competition with *M. dolomieu* (Sharma et al. 2009b).

Invasive *M. dolomieu* also impact sport fish by preying directly on juveniles. For example, predation by *M. dolomieu* is putting some threatened and endangered species of Pacific salmon (*Oncorhynchus* spp. Suckley, 1861) at greater risk of extinction (Reiman et al. 1991; Carey et al. 2011). In the Pacific Northwest, invasive *M. dolomieu* consume an average of about 20% of outmigrating juvenile salmon in streams; in some cases that figure can approach 40% (Sanderson et al. 2009). *M. dolomieu* also consume young walleye (*Sander vitreus* Mitchill, 1818) (Liao et al. 2004), but the extent to which this predation affects *S. vitreus* populations is unclear. On one hand, the native range of *S. vitreus* includes the native range of *M. dolomieu* and these species appear capable of coexisting in both native (e.g., Johnson and Hale 1977; Kempinger and Carline 1977) and non-native

(Galster et al. 2012) *M. dolomieu* lakes. On the other hand, population abundances can be inversely related, likely due to multiple factors including predation (Fayram et al. 2005; Johnson and Hale 1977) and preferences for different conditions (Inskip and Magnuson 1983; Robillard and Fox 2006).

Invasive *M. dolomieu* can also hybridize with native bass. Hybridization can result in genetic introgression and the displacement, decline or extirpation of native species. *M. dolomieu* are known to hybridize with *M. salmoides*, spotted bass (*Micropterus punctulatus* Rafinesque, 1819), and Guadalupe bass (*Micropterus treculii* Vaillant and Bocourt, 1874) (Whitmore 1983; Whitmore and Hellier 1988). Hybridization with *M. treculii* is of particular concern because this species is endemic to the Edwards Plateau of south central Texas (Edwards 1980).

Fish are not the only taxa affected by invasive *M. dolomieu*; mammals, birds, amphibians, reptiles, and invertebrates can be impacted as well. *M. dolomieu* will consume almost any prey small enough to ingest including crayfish, rats, mice, young waterfowl, frogs, snakes, and salamanders (Sanderson et al. 2009). Frog species can be impacted by predation from *M. dolomieu*, although the severity could depend on the presence of other invasive species and the life stage of the frog (Kiesecker and Blaustein 1998). Any organism that depends on the prey of *M. dolomieu* can also be impacted. In an extreme case, competition with invasive *M. dolomieu* and *M. salmoides* for food contributed to the extinction of an endemic Guatemalan waterbird, the Atitlán grebe (*Podilymbus gigas* Griscom, 1929) (Hunter 1988). In ponds invaded by *M. salmoides*, the loss of prey fish and crayfish populations can lead to a reduction in top-down control of benthic invertebrates and macrophytes (Maezono and Miyashita 2003; Maezono et al. 2005).

Controlling invasive smallmouth bass

M. dolomieu control is essential for mitigating, minimizing and perhaps even eliminating the impacts of *M. dolomieu* on native species and food webs. However, there has been little documented work on *M. dolomieu* control to date, and many potential control options remain untested. Here we describe and discuss various control options as they relate to *M. dolomieu*. This section draws from and builds upon a recent review by Halfyard (2010). We summarize control options in Table 2.

Removal

Removal refers to the physical capture and removal of fish from a system, typically via electrofishing, netting, explosives, or angling. These methods are labor-intensive and rarely result in successful control. However, in certain systems they may be an effective component of an integrated management plan.

Electrofishing

Electrofishing is a common, uncontroversial removal method in fisheries management that has been applied to invasive *M. dolomieu* with limited success. Electrofishing programs in small reaches of the Colorado and Yampa Rivers decreased *M. dolomieu* abundance, but only temporarily due to immigration (Burdick 2008; Hawkins et al. 2008). Other attempts to control invasive *M. dolomieu* via electrofishing have ultimately failed because of increased recruitment following treatment (Boucher 2005 and 2006; Weidel et al. 2007; Hawkins et al. 2008). In one striking example, the mass removal of 47,474 *M. dolomieu* over a 6-year period from an Adirondack lake in New York initially reduced *M. dolomieu* abundance by 90%, but ultimately resulted in increased abundance (Weidel et al. 2007; Zipkin et al. 2008). This unexpected increase was attributed to decreased intraspecific competition that led to accelerated maturation of juveniles and, ultimately, improved recruitment (Ridgway et al. 2002; Zipkin et al. 2008). This phenomenon is known as the hydra effect or overcompensation (Abrams 2009; Strevens and Bonsall 2011; Zipkin et al. 2008). Because electrofishing gear tends to remove more adults than juveniles (Moore et al. 1986; Kulp and Moore 2000; Earle and Lajeunesse 2007), this method can lead to overcompensation. Therefore, a control plan that involves electrofishing should include one or more methods that reduce the abundance of young *M. dolomieu*. Electrofishing is only likely to be effective in shallow, isolated streams and ponds absent of complex habitat. This method is labor-intensive, inefficient, non-species-specific, and requires repeated, long-term application.

Netting

Netting is another common fisheries management tool but is generally ineffective at controlling invasive *M. dolomieu*. For example, a springtime attempt to net invasive *M. dolomieu* in a 70 ha pond captured only 7 individuals in 2,103 trap net hours (0.003 fish/hour), as compared to 200 *M. dolomieu* captured in 8.62 hours of electrofishing effort (23.2 fish/hour; Boucher 2006). In another attempt, less than 1% of the 3083 fish captured in gill nets were *M. dolomieu* (Gomez and Wilkinson 2008). These results might reflect the relative abundance of *M. dolomieu* in the system, the low vulnerability of centrarchids to passive netting (Hayes et al. 1996), or seasonal variation in catchability (i.e., *M. dolomieu* are most trappable in mid-summer, Wright 2000). In general, nets are much less effective at catching *M. dolomieu* than electrofishing (Bacula et al. 2011 and references therein). Therefore, although netting is a familiar, available, and uncontroversial control option that can be both size- and species-selective and deployed at most depths, the inability of nets to catch large numbers of *M. dolomieu*, even when effort is high, is a significant shortcoming that precludes the use of nets for control, even in combination with other methods. However, netting may be the only option in systems that are not conducive to electrofishing. For example, invasive young-of-the-year *M. dolomieu* in Lake Opeongo, a low-conductivity lake in Algonquin Park, Canada, are routinely (and effectively) sampled using minnow traps (e.g. Dunlop et al. 2005a, 2005b).

Explosives

Explosives have been proposed for invasive fish control (Lee 2001). Although there are no known applications to *M. dolomieu* control, the use of detonation cord to sample *M. dolomieu* in deep reaches of the Middle Snake River, Idaho (Munther 1970) suggests that at least some degree of removal is possible. Detonation cord tends to kill most fish within 9 meters of the blast (Metzger and Shafland 1986). In general, explosives are effective at killing adult and larval fish with swim bladders, but not fish eggs (Baxter II et al. 1982; Metzger and Shafland 1986; Bayley and Austen 1988; Keevin et al. 2002; Settle et al. 2002; Faulkner et al. 2008).

Explosives are an effective and relatively cheap method for killing fish in almost any habitat, but there are a number of issues that are likely to limit their use in *M. dolomieu* control. Explosives are difficult to obtain, highly controversial, and dangerous to both human and environmental health. They are not selective for fish species, and can destroy habitat and leave behind toxic chemical residues (Hayes et al. 1996; Lotufo and Lydy 2005). Explosives may also be inappropriate for large waterbodies because of scale. Several authors recommend explosives only when there are no other options for sampling or control (e.g., Bayley and Austen 1988; Hayes et al. 1996).

Angling

Removal by angling is another control option that is unlikely to be effective. In the only documented attempt, anglers removed *M. dolomieu* from a 70 ha pond in Maine at a rate of 0.31 fish/hour as compared to 23.2 fish/hour for electrofishing (Boucher 2006). The author did not believe that angling was an appropriate control measure for that system. In another program, nearly 300 angler hours over two years resulted in the removal of just 150 *M. dolomieu* (Gomez and Wilkinson 2008). Even though angling for *M. dolomieu* control has not been successful, increased fishing pressure either from liberalized regulations or intensive effort has been advocated for the control of other invasive fishes (Wydoski and Wiley 1999; Beamesderfer et al. 1996; Moore et al. 2005). Because angling is an inefficient removal method, it is probably most effective in small systems and/or when fishing pressure is high.

Options for enhancing removal

The efficacy of a particular removal method can be enhanced through techniques that improve catchability. Here we describe two such techniques: pheromone-baited traps and “Judas fish”. Pheromone-baited traps use species-specific chemical attractants to improve trap efficiency (Sorensen and Stacey 2004). Although we are unaware of examples involving *M. dolomieu*, these traps have been used successfully for other invasive fish such as sea lamprey (*Petromyzon marinus* Linnaeus, 1758) and common carp (*Cyprinus carpio* Linnaeus, 1758) (Wagner et al. 2006; Sorensen and Stacey 2004). Therefore, we recommend exploring pheromone traps as an option for *M. dolomieu* control. Another technique that can improve catchability is the addition of “Judas fish” to the system (Bajer et al. 2011). The Judas technique was first developed in Hawaii, where it was used to locate non-native feral goats (Taylor and Katahira 1988). A Judas fish is a conspecific that has been implanted with a radio tag and then tracked to an aggregation of fish. These fish can then be more effectively targeted for removal. The Judas fish technique should be evaluated for its potential to locate aggregations of *M. dolomieu* (e.g., during spawning or winter shoaling), particularly in large systems.

Chemical

The addition of chemical piscicides to a system is perhaps the most common method of fish control (Wydoski and Wiley 1999; Meronek et al. 1996). Piscicides such as rotenone and antimycin-A are effective at killing a large proportion of fish in the system with minimal effort (Lennon et al. 1971, Baker et al. 2008). Both rotenone and a newly-developed piscicide, Supaverm®, can effectively kill invasive *M. dolomieu* (Smith 1941; Ward 2005). Rotenone eliminated *M. dolomieu* from Potter's Lake, New Brunswick (46 ha), and Supaverm® holds promise as a more selective option that tends to spare native minnows. Overall, and given adequate funding, chemical control can be a quick and effective option for *M. dolomieu* control in many systems. However, most piscicides are lethal to all fish in the system (Finlayson 2001; Dawson and Kolar 2003) and can also affect amphibians, aquatic invertebrates, and zooplankton (Smith 1940; Brown and Ball 1943; Morrison 1979; Finlayson et al. 2000; Arnekleiv et al. 2001; Ling 2001; Dinger and Marks 2007). Additionally, stakeholders may be opposed to this option on ethical grounds or due to its non-target effects and high cost. Managers should also be aware that piscicides are not always 100% effective at extirpating invasive fishes. Chemical eradication is, on average, only 35% effective 10 years after treatment (Wydoski and Wiley 1999). For chemical treatment to be effective, managers must acknowledge and manage for public opposition, non-target effects, and the potential need for additional control measures.

Biological control

Biological control (biocontrol) refers to the introduction or enhancement of an invasive species' predators or pathogens, or the sterilization of the invasive species. Although these methods tend to be controversial and are largely untested for *M. dolomieu*, there is evidence to suggest that they can be effective. To this end, we encourage research into the efficacy of biocontrol methods as they apply to invasive *M. dolomieu*.

Predation

Predation is the most common and effective method of biological control, through either the introduction of new predators or the enhancement of existing ones (Wydoski and Wiley 1999). This type of control would be most effective for small non-game fish or young sport fish (e.g., *M. dolomieu* eggs, fry, and juveniles) given their vulnerability to predation. The impact of this kind of biocontrol on *M. dolomieu* may be limited by the tendency of nesting males to aggressively guard eggs and larvae from predators during the spawning season (Ridgway et al. 1991). However, nest guarding may not be a limiting factor in all cases. For example, native Japanese dace (*Tribolodon hakonensis* Günther, 1877) are extremely effective nest predators, consuming on average 92.4% of invasive *M. dolomieu* eggs, even while males guard their nests (Iguchi and Yodo 2004). In this case and others, removing the guarding male would enhance nest predation. Nest predators such as crayfish, yellow perch (*Perca flavescens* Mitchill, 1814), sunfish (*Lepomis* spp. Rafinesque, 1819), and the introduced round goby (*Neogobius melanostomus* Pallas, 1814) can consume an entire nest of unprotected eggs in as little as 17 minutes (Kieffer et al. 1995; Steinhart et al. 2004).

Although invasive species are unlikely to be appropriate predators to introduce for biocontrol, management plans that enhance native predators or introduce otherwise benign predators could be useful. Once an appropriate predator is identified, this type of control is usually inexpensive, requires minimal effort, and can be effective in a variety of habitats. Predatory biocontrol is nonetheless risky and controversial (Hoddle 2004). Before introducing a predator species (or enhancing natural predators), it is important to consider the vulnerability of the target species, the potential for non-target effects, and the likelihood that introduced predators will survive, establish, and spread (Wydoski and Wiley 1999). Managers should carefully weigh the pros and cons of this untested method and researchers should consider its study, as it appears to be a promising option for *M. dolomieu* control.

Pathogens and parasites

The introduction or enhancement of novel or existing pathogens or parasites is another biocontrol option for invasive fish. We find one promising example in Australia, where research is underway to use koi herpes virus to control common carp (McColl et al. 2007). Although we are unaware of attempts to use pathogens or parasites to control invasive *M. dolomieu*, there are at least two *M. dolomieu*-specific parasites that hold promise. The first parasite is a protozoan that attaches itself to *M. dolomieu* gills and can cause mortality (Davis 1937, 1942). The second parasite is a tapeworm (*Proteocephalus ambloplitis* Leidy) that limits *M. dolomieu* fecundity by preferentially infesting its oocytes (McCormick and Stokes 1982). With proper testing and development, these parasites could be used as biocontrol agents for invasive *M. dolomieu*. Similarly, the pathogen known as the largemouth bass virus (Family Iridoviridae; genus unknown) causes a disease that is specific to *M. salmoides* (Grizzle et al. 2003) but could potentially be genetically engineered to target *M. dolomieu*. Testing and developing *M. dolomieu*-specific pathogens and parasites is likely to be both expensive and time-consuming. Once developed, however, these agents could be used simply and cheaply in almost any system. Nonetheless, development and application should be undertaken with caution to avoid effects on non-target species, the development of resistance, and public controversy (Wydoski and Wiley 1999).

Sterilization

Sterilization is a form of biocontrol that involves the release of sterile conspecifics or the alteration of individual physiology to limit reproductive success. Sterilization is not currently available as a control technique for invasive *M. dolomieu*, but the idea merits further research. One promising option is to use pheromones to effectively sterilize *M. dolomieu* by altering their behavior. Treatment with pheromones can reduce a male bass's ability to guard his nest, causing increased nest failure (Dey et al. 2010). Another option is the release of sterile males, which has been used successfully for sea lamprey (Twohey et al. 2003). Recombinant gene therapy could be used to develop sterile *M. dolomieu*, but this technology is largely untested (Thresher 2008). Other sterilization techniques such as irradiation and chemically-induced sterilization should be researched for *M. dolomieu*. Sterilization is species-specific and applicable to all types of habitats, but it can be expensive to develop, controversial, and labor-intensive to implement.

Environmental manipulation

Environmental manipulation seeks to control invasive fishes via changes to their physical environment. Here we focus on manipulation of water levels and dissolved oxygen concentration.

Water level manipulation

Draining, or dewatering, a system is considered to be the most effective way to guarantee complete removal of fish (Finlayson et al. 2002; Ling 2001; McClay 2000). However, this approach affects non-target species and organisms and is impractical in many places due to logistics or public opposition. Partial dewatering may be a more feasible option, especially in managed reservoirs, rivers, and streams in which it is easy to manipulate water levels. Partial dewatering can cause behavioral changes in *M. dolomieu* and increase predation on juveniles (Rogers and Bergersen 1995; Heman et al. 1969). Because *M. dolomieu* spawn in shallow water (Ridgway et al. 1991), partial dewatering can also be used to limit the availability of spawning habitat or kill incubating eggs. The only example of water level manipulation specifically targeted at controlling invasive *M. dolomieu* induced discharge pulses in a stream during the spawning season (Kleinschmidt 2008). These pulses evacuated all fry from 43% of the study nests and removed some of the fry from another 21%. While the author believes that this reduction in *M. dolomieu* young could improve trout habitat, the long-term impacts of this treatment have not been determined as of 2013. Water level management is probably an inexpensive and effective option for *M. dolomieu* control in certain systems. However, this method cannot be applied everywhere, has the potential for non-target effects, and could be controversial given conflicting water uses (agriculture, industry, residential, recreational, hydroelectric power, navigation, etc.).

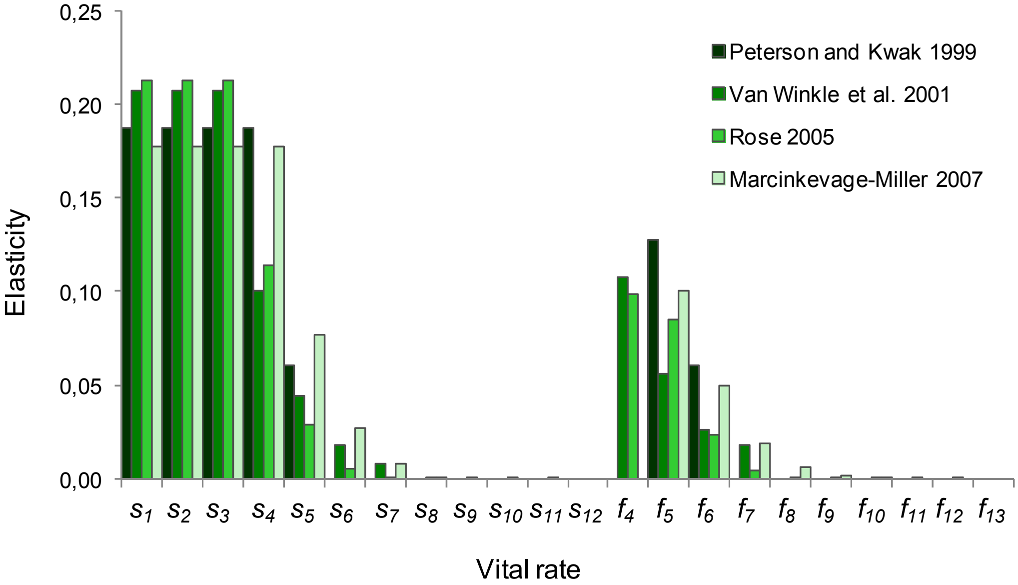

Figure 2. Elasticities of the annual survival probability (s_i) and fertility (f_i) at age i for four smallmouth bass matrix population models.

Dissolved oxygen concentration

It may be possible to control *M. dolomieu* by reducing the wintertime concentration of dissolved oxygen (DO) below the lethal threshold of ~1.2 mg/L (Smale and Rabeni 1995). One can induce lethal concentrations of DO in winter (producing a winterkill event) by partially drawing down water or causing disturbances (e.g., artificial mixing of the water column) that stir up anoxic water and sediments containing oxygen-consuming bacteria (Verrill and Berry 1995; Shroyer 2007). Winterkill has been used successfully for other invasive fishes (Verrill and Berry 1995; Shroyer 2007), but not for *M. dolomieu*. The applicability of this option is likely limited to shallow, eutrophic lakes and ponds, where it could be effective and inexpensive. However, inducing low DO is likely to kill non-target organisms and could be controversial.

Targeting specific life stages

Directed research is a necessary first step in the development of *M. dolomieu* control methods that are both efficient and effective (Buhle et al. 2005; Eiswerth and Johnson 2002). First and foremost, research should help to focus management effort by identifying those aspects of the *M. dolomieu* life cycle that contribute most to population growth rate. To this end, we conducted an elasticity analysis of four published matrix population models of *M. dolomieu* from lakes and rivers in Canada and the United States (Peterson and Kwak 1999; Van Winkle et al. 2001; Rose 2005; Marcinkevage-Miller 2007). Elasticity is a measure of the sensitivity of population growth rate to systematic and proportional changes to age-specific parameters for survival and fertility. Our results suggest that population growth rate is most sensitive to survival in the first 1–4 years of life (Figure 2). Therefore, from a biological perspective, targeting *M. dolomieu* eggs, larvae, and juveniles is the most efficient approach to controlling invasive *M. dolomieu*. Additionally, targeting these early life stages alone or in concert with management of adult *M. dolomieu* could potentially prevent overcompensation.

Options for targeting *M. dolomieu* eggs and larvae outnumber options for targeting *M. dolomieu* juveniles, and would be far more effective due to the relatively narrow habitat requirements for nesting and incubation. Whereas juveniles can be removed via electrofishing, angling, and perhaps minnow traps, options for targeting eggs and larvae include the physical removal of eggs from nests, the chemical treatment of nests, nest predator management, sterilization, explosives (larvae only), water level management during nest guarding, and the removal of nest-guarding males. Although angling is itself an inefficient removal method (Boucher 2006; Gomez and Wilkinson 2008), angling may be an effective means of inducing nest failure. Generally, the aggression of nest-guarding males makes them easy to angle during spawning season (Ridgway et al. 1991). Both field and modeling studies involving *M. dolomieu* suggest that even short handling times during catch-and-release angling can increase the risk of nest predation (Ridgway and Shuter 1997; Suski et al. 2003; Steinhart et al. 2005), and that released bass can be too exhausted to adequately defend their nests (Kieffer et al. 1995; Hinch and Collins 1991; Hanson et al. 2008).

Conclusion

Human introductions and global climate change are facilitating the spread of *M. dolomieu* beyond their native range in Canada and the United States, and into other countries around the world. Invasive *M. dolomieu* can impact native food webs through predation, competition, and hybridization, and can even extirpate native fishes. These impacts are well documented and fairly well understood, but our ability to control invasive *M. dolomieu* is severely limited. Although numerous options for *M. dolomieu* control exist, few have been tested or developed and even fewer have been successful.

To improve *M. dolomieu* control, we recommend integrated pest management plans that include several nest failure strategies, perhaps in combination with other options (e.g., adult removal). For example, using catch-and-keep angling to remove nest-guarding males while simultaneously enhancing native nest predators is probably more effective at inducing nest failure than either of these options alone. Additionally, because a small subset of spawning males (~5%) can produce over half of a population's young of year (Gross and Kapuscinski 1997), we recommend using genetic techniques to identify and subsequently target the most productive males. We also recommend research to develop control methods that are not yet available for *M. dolomieu* (e.g., pathogens, parasites, pheromone traps). Of course, the combination of control options to use in an invaded system also depends on environmental constraints (e.g., lentic vs. lotic, depth, structural complexity, substrate type, ecology), logistic constraints (e.g., budget, timeline, available infrastructure/equipment), and social factors (e.g., acceptability, political climate). *M. dolomieu* control may be unnecessary or impossible in some systems. For those systems in which control is an option, it is important to learn from previous attempts (*M. dolomieu* or other species) and practice adaptive management (Pine et al. 2009; Zipkin et al. 2009).

It is also important to maintain realistic expectations: *M. dolomieu* extirpation is unlikely except for in small and/or isolated systems, and *M. dolomieu* suppression will require multiple applications, probably in perpetuity (even rotenone can be <100% effective; Wydoski and Wiley 1999). For these reasons, in addition to sound research and management, we stress the importance of preventing *M. dolomieu* (re)introductions, for example through bait regulations and public awareness campaigns. Creative, comprehensive solutions need to be developed and implemented to minimize further spread of invasive *M. dolomieu* and mitigate their impacts on native ecosystems.

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