NON-NATIVE BLACK BASS: POTENTIAL CONFLICTS IN FISHERIES MANAGEMENT

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Abstract: Black bass (*Micropterus* spp.) are among the most highly sought after recreational fishes around the world, which has resulted in widespread introductions outside of their indigenous ranges. Non-native black bass can, simultaneously, imperil native biodiversity and bring economic benefits to local economies, thus highlighting the paradox of stocking sport fishes. In an effort to disentangle these fundamentally incompatible forces, I systematically reviewed the ecological and economic impacts of non-native black bass, which has not been updated in over 30 years. Considering the constant flux of human-mediated dispersal events, the distribution of the two most stocked species of non-native black bass, Largemouth (*M. salmoides*) and Smallmouth Bass (*M. dolomieu*), were reevaluated. Further, I administered a novel broad scale survey of U.S. fisheries biologists assessing current perceptions surrounding the ecological and economic impacts of non-native black bass. My updated distribution represents data from the most recently available sources and has filled a knowledge gap concerning the current range of these species. The establishment success rate between Largemouth Bass (76%) and Smallmouth Bass (22%) differed widely, suggesting that ecological and biological factors influence their distribution. The case studies highlighted within show a global reevaluation of socio-economic values and conservation priorities in relation to the level of risk associated with non-native species. My survey results indicate that non-native black bass are considered economically beneficial in both anthropogenic and natural waters. Contrastingly, non-native black bass were perceived to have significantly more negative ecological impacts in natural waters than in anthropogenic waters. Largemouth Bass, Smallmouth Bass, and Florida Bass (*M. floridanus)* were perceived to provide the most economic benefits, while Alabama Bass (*M. henshalli)*, Smallmouth Bass, and Spotted Bass (*M. punctulatus)* were perceived to cause the most ecological imperilment. My findings suggest that habitat may be an important factor to partitioning the conflicting ecological-economic dynamic of non-native black bass. Implications of this study suggest that challenges remain for managers attempting to balance the paradoxical nature of non-native black bass as both a desired sport fish and as a potentially harmful invader.

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CHAPTER I

CURRENT STATUS OF NON-NATIVE BLACK BASS: A GLOBAL OVERVIEW

Introduction

With 21.3% of North American, 24% of European, and 21% of east African freshwater fishes at risk of extinction, freshwater fauna remains disproportionately imperiled compared to all other biota (Ricciardi & Rasmussen, 1999; Darwall et al., 2009). However, at the same time, freshwater fishes have been widely distributed, with over 624 species introduced worldwide (Gozlan, 2008). Thus, freshwater fishes are simultaneously one of the most introduced aquatic species, as well as, one of the most threatened (Gozlan, 2008). One of the main reasons for the introduction of these fishes is recreational angling, through legal and illegal transfers (Gozlan, 2008; Johnson et al., 2009), which has led to the homogenization of freshwater fish diversity (Rahel, 2000).

Black basses, a collective term for species in the genus *Micropterus*, are piscivorous, freshwater, game fishes native to North America (Jenkins & Burkhead, 1994; MacCrimmon & Robbins, 1975; Scott & Crossman, 1973), and are emblematic of the results of human-mediated dispersal. Two of these species, Largemouth Bass *Micropterus salmoides* (LMB) and Smallmouth Bass *Micropterus dolomieu* (SMB), are among the most highly sought after game fish species around the world (Long et al., 2015), and as such, have been widely stocked outside of their native range (Welcomme, 1988). Largemouth Bass, for example, is native to only 3 countries, but have since been introduced to over 70 countries mainly to provide sport fishing opportunities (Robbins & MacCrimmon, 1974; Welcomme, 1988). Similarly, SMB have a native range in 23 states within the U.S., and now have established populations in 47 states, again mainly to provide recreational fishing opportunities (Fuller et al., 2019a; Robbins & MacCrimmon, 1974). Thus, LMB and SMB are model species to describe current perceptions on the ecological and economic impacts surrounding non-native fishes.

As top-level predators and highly competitive species, black bass alter predator-prey dynamics, reduce native species richness, modify nutrient cycling, and alter habitat structure in their introduced range (Jackson, 2002; Loppnow et al., 2013). Ultimately, aquatic communities can become more homogenous when non-native black bass are present (Jackson, 2002). Due to these attributes, LMB are regarded as one of the "100 World's Worst Invasive Alien Species", which is considered as a representative for the *Micropterus* genus, for their role in global biodiversity loss (Global Invasive Species Database [GISD], 2018). Among the major threats to freshwater biodiversity, invasive species are credited with considerable loss of native species richness (Dudgeon et al., 2006). For example, LMB have led to the decline and listing of 29 species, namely fishes, through predation and competition, which has led to their designation as "invasive" in 12 countries (CAB International, 2018).

However, stocked populations of LMB and SMB have economic incentives in terms of sport fishing tournaments, tourism, job creation, economic output, and angler license sales both in the U.S. and abroad, which are all factors for which they were originally introduced. In the U.S., freshwater fishing contributes $41.9 billion to the economy and sustains over 525,000 jobs annually (Southwick Associates, 2018a). Further, in 2016, there were 9.6 million black bass anglers fishing over 117 million days in the U.S., making these anglers the primary group in both fish preference type and participation (U.S. Fish and Wildlife Service [USFWS] & U.S. Census Bureau, 2016). Worldwide, there are over 118 million recreational anglers across industrialized countries in Europe, North America, and Oceania (Arlinghaus et al., 2015) with the global recreational fishing industry valued at $116 billion annually (Reid et al., 2013).

Although economic values for introduced black bass have not yet been quantified globally, other indicators can act as estimates for economic impacts. For example, several world-class sport fisheries have been created around non-native black bass in Japan, Korea, Italy, Australia, and South Africa, which has led to the creation of the Black Bass World Championship fishing tournament (USFWS, n.d.). Moreover, black bass are an economically beneficial aquaculture resource in Cameroon, Costa Rica, Dominican Republic, Argentina, Poland, Yugoslavia, and Taiwan (CAB International, 2018). Finally, economic benefits from recreational black bass fisheries are reported in Zimbabwe, Namibia, and Mozambique (Ellender et al., 2014).

Thus, non-native black bass regulated for recreational sport fishing create an enigma of competing impacts as their economic incentives and their potential ecological damages are fundamentally conflicting forces. As introductions of freshwater fishes continue worldwide due to demands for food security and recreation (Gozlan et al., 2010) and as invasive species threaten freshwater ecosystems and biodiversity globally (Cambray, 2003), the spread of non-native black bass is concerning. With such a high angler preference of black bass, there is still considerable effort to stock and manage black bass for angler satisfaction, further perpetuating this issue.

A worldwide assessment of these paradoxical impacts, which has not been updated for over 30 years (Robbins & MacCrimmon, 1974; Welcomme 1988), is an essential step to synthesize our current understanding of non-native black bass. Since some non-native populations of black bass have been targeted for control and eradication (e.g., Spotted Bass *Micropterus punctulatus* eradication in South Africa (van der Walt et al., 2019)), case studies of these instances will provide greater insight into how these fishes impact regional economies and biodiversity. Furthermore, comparing these case studies across continents will allow for the perception of non-native black basses to be revealed on a global scale. Thus, simultaneously examining the ecological and economic impacts of non-native black bass is imperative to gain a discerning comprehension of the current social perceptions surrounding these species.

The objectives of this study are twofold: (1) assess the worldwide distribution of LMB and SMB, and (2) compare the ecological and economic impacts of LMB and SMB across their introduced range. A systematic review of the current literature was conducted to provide an updated distribution list and to detail how current impacts of non-native black bass are perceived globally.

Methods

To assess the worldwide distribution of LMB and SMB, searches of published literature were carried out using Google Scholar, Web of Science, Scopus, Eschmeyer's Catalog of Fishes, and the Oklahoma State University Library catalog. Keywords including: scientific names, common names, Centrarchidae, freshwater fishes, checklist, alien, distribution, and status, and combinations thereof with the country name, were all used to find publications. Sources were reviewed from the period 1989-2019 to update the previous assessment completed in 1988 and to verify current distribution status. Peer-reviewed papers assessing freshwater fish populations and management, presented valid topics where distribution data could be obtained.

For each species, the first record of their historical introduction into specific countries was determined by consulting Robbins and MacCrimmon (1974), Scott and Crossman (1973), and Welcomme (1988). Previous global distribution lists of Froese and Pauly (2019b), CAB International (2019), and Global Invasive Species Database (2019) were then used as a baseline regarding the presence/absence of each species' current range. A list of countries was obtained from the U.S. Department of State (www.state.gov) to standardize disputed boundaries, territories, and present statehood.

Where primary literature could not be found to verify the current distribution of a specific country, secondary literature, such as regional freshwater fish checklists, citing original sources were used. In lieu of secondary sources, online searches were conducted for technical reports (e.g., Food and Agriculture Organization of the United Nations [FAO] country profiles on fisheries). For countries that proved to be data deficient, historical distribution sources were then used based on precedent set by other publications and databases (e.g. Froese & Pauly, 2019b; Loppnow et al., 2013). To supplement data on the updated distribution lists, museum collection records were obtained from FishNet2 (www.fishnet2.net) and Global Biodiversity Information Facility (GBIF) (www.gbif.org). These databases consolidated LMB and SMB species occurrence records from over 50 partner museum institutions for FishNet2 (2013) and over 80 contributors for GBIF (2019).

The establishment of each species was then reported as “Yes” or “No” based on distribution criteria discussed in relative publications. A status designated as “Uncertain” was given when conflicting accounts of establishment were discussed between publications, or when publications determined establishment to be uncertain. The status of “Probably Not” was given when publications surveyed fish distributions for the majority, but not all, of a country. Finally, establishment status determined to be “Questionable” are cases when the authors thought diffusion through connected waterways were probable, while a status of “Unknown” was given when neither historical nor current references confirming establishment could be found.

The updated LMB and SMB distributions completed within this study were then compared to FishBase to detect differences. Since its inception in 1990, FishBase has developed a global database on fish biodiversity, science, and distribution (Froese, 1992). After decades of operation, FishBase has become the premier database on fishes and has established its significance among researchers. As such, other databases describing LMB and SMB distributions (e.g. CAB International and GISD) regularly cite FishBase for records of occurrence. Using the distribution data for these two species that was available on FishBase (Froese & Pauly, 2019b; 2019c, downloaded March 14, 2019), error matrices were then constructed to assess the accuracy of online databases.

Using ArcGIS (Esri, version 10.5.1), maps were created to visualize the historical introduction, current distribution, reason for introduction, and spatial introduction patterns for LMB and SMB. Case studies of LMB and SMB were chosen based on their geographic distribution to represent three continents and for their ability to illustrate the paradox of non-native black bass: Colorado (Unites States), Japan, and South Africa. A systematic and extensive review of literature for the history of their introduction, management regimes, and current perceptions was conducted to provide a thorough depiction of their present status.

Results

In my study, 84 papers and 38 books were included for documentation of LMB and SMB distribution. I found that LMB have been introduced into 80 countries and 11 territories (91 total regions), which included an additional 12 countries and 7 territories than historically reported (Robbins & MacCrimmon, 1974; Welcomme, 1988) (Table 1). Upon initial LMB introduction, 72 regions (79%) experienced successful establishment (Figure 1). The majority (46%) of LMB introductions were due to sport, while 23% were due to aquaculture and an additional 6% were due to both sport and aquaculture (Figure 2). Largemouth Bass originating from the U.S. in their native range, were introduced to 32 other regions (35%), while LMB originating from Germany were subsequently spread to 13 countries (14%), and LMB originating from France were subsequently spread to 7 countries (8%) (Figure 3). Currently, LMB are established in 54 countries and 7 territories (61 total regions), which makes for a success rate of 67% since reports of initial introduction (Figure 4, Table 1). In addition, 10 regions have “uncertain” establishment given conflicting documentation, while 3 countries have “unknown” establishment due to lack of data.

Smallmouth Bass have been introduced into 35 countries and 2 territories (37 total regions), which included an additional 3 countries than historically reported by Robbins and MacCrimmon (1974) and Welcomme (1988) (Table 2). Upon initial introduction, 13 regions (35%) experienced successful establishment, while 18 regions (49%) had failed establishment (Figure 5). The majority of SMB introductions (51%) were due to unknown reasons, while 35% were due to sport (Figure 6). Smallmouth Bass originating from their native range in the U.S., were introduced to 13 other regions (35%), while another 32% were subsequent introductions from Germany (Figure 7). Currently, SMB are established in only 8 countries, which makes for a success rate of 22% since initial introductions were reported (Figure 8, Table 2). This includes Tanzania, where historically SMB were specifically not introduced in order to preserve the native fishery. Additionally, 4 countries have "uncertain" establishment due to conflicting documentation, 2 countries are "probably not" established due to incomplete field sampling, 1 country and 1 territory have "unknown" establishment due to lack of data, and 2 countries have "questionable" establishment due to possible diffusion through connected water bodies.

In comparison to FishBase which lists 64 regions where LMB are present, my updated LMB distribution has 3 fewer regions where LMB are currently established. While FishBase reports 79 regions with historical introductions of LMB, my study found 91 regions with historical LMB introductions. A further breakdown of the discrepancies found between my study and FishBase are as follows: 5 countries and 2 territories were newly added to "currently established"; 2 countries (Brazil and Costa Rica) and 1 territory (Taiwan) changed from "absent" to "currently established"; 2 countries and 1 territory were newly added to historical introductions; 3 countries and 1 territory were no longer considered "established"; 1 country changed from "questionable" to not established"; 8 countries changed in status from "present" to "uncertain"; and 2 countries changed in status from "absent" to "uncertain" (Table 1). In total, FishBase had a 24% error rate when compared to my updated LMB distribution (Table 3).

In terms of SMB, FishBase lists 14 regions where SMB are present, while my updated SMB distribution has 6 fewer regions where SMB are currently established. While FishBase reports 27 regions with historical introductions of SMB, my study found 37 regions with historical SMB introductions. A further breakdown of the discrepancies found between my study and FishBase are as follows: 1 country (Lesotho) was newly added to "currently established"; 8 countries were added to historical introductions; 3 countries were no longer considered "established"; 1 country (Vietnam) changed in status from "present" to "probably not" established; 2 countries changed in status from "present" to "uncertain"; 1 country (Germany) changed in status from "absent" to "uncertain"; 1 country (South Korea) was newly added to "uncertain" establishment; 2 countries are newly added to "questionable" establishment; and 2 countries are newly added to "unknown" establishment (Table 2). In total, FishBase had a 28% error rate when compared to my updated SMB distribution (Table 4).

The following case studies were chosen to illustrate the paradox of non-native black bass in that both economic profit and ecological degradation occurs following their introduction. Further, examples from Colorado (U.S.), Japan, and South Africa will provide greater insight into how these fish currently impact local economies and biodiversity across three continents. By examining the conflicting impacts of non-native black bass on a world-wide scale, a global perspective of non-native black bass emerges.

Case Studies: Introduction, Impacts, and Management of Non-Native Black Bass

United States - Colorado. The Upper Colorado River Basin (UCR) spans five states within the Intermountain West. Native fish that evolved within the Colorado River basin are highly adapted for extreme variation in flow, turbidity, and temperature of water (Behnke & Benson, 1983). There are thirteen indigenous fish species that are endemic to this region. In particular, the Colorado Pikeminnow *Ptychocheilus lucius*, Humpback Chub *Gila cypha*, Razorback Sucker *Xyrauchen texanus*, and Bonytail Chub *Gila elegans* are species of concern and are specialized to live in this watershed (USFWS, 1987).

Early European settlers in the UCR considered the native fish communities useless and were nostalgic for the game species that were common in the eastern United States (Hawkins & Nesler, 1991). To add value to their local fishery and to supplement native fauna, stocking of non-native sport fish began in the 1880s (Behnke & Benson, 1983). Due to this mentality, 67 species of non-native fish were introduced for recreational purposes, and now more than 50 non-native fish currently inhabit the UCR (Upper Colorado River Endangered Fish Recovery Program [UCREFRP] & San Juan River Basin Recovery Implementation Program [SJRBRIP], 2018). These non-native fish became readily established and increased in abundance to the point where they are now widespread and outnumber indigenous fish (Hawkins & Nesler, 1991). To date, the Colorado River Basin continues to be one of the top five watersheds most affected by non-native fishes in the U.S. (Tyus & Saunders, 2000).

Smallmouth Bass were introduced to Colorado in 1912 (Robbins & MacCrimmon, 1974), and were stocked in Elkhead Reservoir (northwest CO) by

Colorado Parks and Wildlife (CPW) in 1978 (Breton et al., 2014). Draw-downs of this reservoir in 1992 and 2005 allowed SMB to escape downstream and become established in the UCR basin (Breton et al., 2014). This non-native predator preys directly on native fish and causes increased competition for resources within dietary and habitat overlaps (Hawkins & Nesler, 1991; Martinez et al., 2014). As such, SMB is one of the greatest predatory threats impeding the recovery of endangered fishes in the UCR (Martinez et al., 2014).

Current management actions to remove invasive SMB are extensive and began in 1988 with the implementation of the UCR Endangered Fish Recovery Program (UCREFRP & SJRBRIP, 2018). This program has determined that increased predation and competition from non-native fish, including SMB, to be the primary reason for the decline of endemic fishes (Hawkins & Nesler, 1991; Martinez et al., 2014). However, mechanical control efforts did not begin in earnest until about 2004 (Breton et al., 2014) when the abundance of SMB in the UCR increased drastically (Burdick, 2008). Several management strategies are utilized by the USFWS and CPW to promote the control and removal of non-native fishes in this river basin. These strategies include: electrofishing and netting for removal; sponsoring fishing tournaments targeting non-native SMB; implementing harvest incentive programs for invasive fish; enforcing “Must Kill” fishing regulations; planning fish kills using piscicides; and constructing reservoir control screens to limit downstream dispersal (UCREFRP & SJRBRIP, 2018).

In the UCR, electrofishing has been stated as being effective at reducing the abundance of invasive adult and sub-adult SMB (Breton et al., 2014). However, electrofishing alone has been inadequate at maintaining sustained SMB population declines (Breton et al., 2014). In fact, the UCR Endangered Fish Recovery Program has found that reproduction, recruitment, and movement of SMB following electrofishing can offset removal efforts by allowing populations to recover in certain river reaches (Breton et al., 2014). Further, in response to electrofishing, SMB may overcompensate for harvest by increasing the abundance of juvenile SMB, which leads to an increase in overall population abundance (Zipkin et al., 2008). Although removal efforts have generally caused SMB abundance to decline in the UCR, some SMB populations remain stable or are increasing (Breton et al., 2014).

Environmental and hydrological conditions experienced annually affect the reproduction and growth of immature SMB, which then contributes to the survival of SMB throughout the UCR (Brenton et al., 2014). For example, during poor growing seasons for SMB, as experienced in 2014 from prolonged, high spring discharges and cooler water temperatures, electrofishing catch rates of SMB declined to 0.17 fish/hour (<100mm total length) (Francis & Ryden, 2018). When favorable environmental conditions, such as elevated fall water temperatures occur, survival of SMB becomes facilitated by a longer growing season, which led to a 597% increase in adult SMB (>200mm total length) and 1,700% increase in juvenile and young-of-year SMB (<100mm total length) catch rates during 2018 compared to 2017 (Francis & Ryden, 2018). For example, the 2018 mean catch rate of SMB (< 100mm total length, 15.98 fish/hr) was significantly higher than the previous highest SMB mean catch rate experienced in 2010 (< 100mm total length, 5.82 fish/hr) (Francis & Ryden, 2018). Thus, this variation in SMB abundance experienced in the past 15 years throughout the UCR emphasizes the hardship of agencies working to eradicate invasive species once it has become widely established. Therefore, this highlights the necessity of prevention, early detection, and rapid response programs in dealing with invasive species.

Moreover, SMB remains popular among anglers in Colorado as it still has a high net economic value within the state (Loomis & Ng, 2012). This has led to angler opposition to SMB removal efforts since SMB are a popular sport fish among anglers (Martinez et al., 2014). It is unclear if SMB anglers are adhering to "Must Kill" policies to prevent the release of any SMB that is caught since they would be removing their preferred recreational fish species (Martinez et al., 2014). Due to this apparent conflict, there is no statewide management against SMB, which still maintain healthy populations in reservoirs where they were previously stocked (CPW, 2018). Further, Tyus and Saunders (2000) contend that non-native fish control measures in the UCR, including the removal or elimination of black bass, is unfavorable due to socio-political reasons.

As of 2011, out of 767,000 anglers in Colorado, there were 57,000 anglers (7%) specifically targeting black bass who fished for a total of 551,000 days (USFWS & U.S. Census Bureau, 2011). Black bass anglers contributed $45.4 million out of $649 million in total fishing expenditures to Colorado in 2011 (USFWS & U.S. Census Bureau, 2011). More recently, recreational fishing added $2.4 billon to the economy of Colorado and supported over 17,000 jobs in 2017 (Southwick Associates, 2018b).

However, these economic benefits must be evaluated against the costs to remove non-native fishes. Since the creation of the UCR Endangered Fish Recovery Program in 1988, a total of over $394 million has been spent on the project to date (UCREFRP & SJRBRIP, 2018). In 2018, 21% of a budget of over $7 million was spent on non-native fish management in the UCR (UCREFRP & SJRBRIP, 2018), which is greatly outweighed by the economic contribution of black bass anglers annually (USFWS & U.S. Census Bureau, 2011).

Japan. Since 1877, 103 species of freshwater fish have been introduced to Japan, and 23 of those have established populations in natural ecosystems (Yuma et al., 1998). These introductions were carried out for three reasons: to establish inland fisheries, augment protein sources for human consumption, and to increase fish stocks (Yuma et al., 1998). Largemouth Bass were first introduced to Japan in 1925 to create recreational fishing opportunities (Hossain et al., 2013; Robbins & MacCrimmon, 1974). In the 1960s, broad-scale introductions of LMB occurred and they are now ubiquitous throughout the nation (Yuma et al., 1998).

Established LMB populations have caused the local extinction of native fauna and the eradication of small-bodied fish species that did not coevolve with piscivorous fish (Tsunoda & Mitsuo, 2012). Maezono and Miyashita (2003) found that top-down LMB predation is linked to the decline in crustaceans, small-bodied fish, and aquatic insects which then cause a trophic cascade down to benthic invertebrates. This can lead to an irreversible change in aquatic community structure which, ultimately, will alter food web structure and biodiversity (Hossain et al., 2013; Maezono & Miyashita, 2003). Furthermore, once introduced, LMB can often reproduce and grow faster than native fauna, which allows them to become the dominant species in the system (Hossain et al., 2013). Overall, the presence of LMB indicates a decrease in species richness and abundance, an increase in local extirpations of native fauna, and alterations to food-web structure (Takamura, 2007). In the long term, these ecological impacts can lead to irreparable changes in ecosystem function.

Lake Biwa, one of the world's oldest lakes, illustrates its juxtaposition as a world-class LMB fishery and as a severely degraded natural ecosystem. In Japan, this lake is unique because it contains a high number of native freshwater fish species including 13 that are endemic to Lake Biwa and 58 that are indigenous to the region (Yuma et al., 1998). After the introduction of LMB into Lake Biwa, fisherman noticed a decline in catch-rate of commercially important fish populations of Ayu *Plecoglossus altivelis* (Yuma et al., 1998). Since Ayu constitutes 8% of the 39,000 ton inland fisheries catch, this has huge potential for economic ramifications (FAO, 2009). For example, in 2010, the inland fisheries catch of Ayu was valued at 10 billion yen which constituted 39% of total revenue from inland fisheries (Popescu & Ogushi, 2013). Furthermore, because Japan has few native piscivorous fish species, the introduction of LMB left many indigenous, commercially valuable fishes vulnerable to predation (Maezono & Miyashita, 2003). A recent study showed that significant declines in catch per unit effort of commercially important fishes were attributed to exotic piscivores (Matsuzaki & Kadoya, 2015).

After LMB had been implicated in the decline of 305 fisheries, laws were created in the 1990s to ban the release of LMB to protect collapsing inland fisheries (Washitani, 2004). For example, LMB reduced the annual catch of Bitterling (subfamily *Acheilognathinae)* from 5-11 tons down to 0.8 tons (Katano & Matsuzaki, 2012). Thus, the Japanese Ministry of the Environment legally declared LMB to be an invasive alien species in 2005 (Takamura, 2007). In response to this action, LMB are now regulated under Japan's Invasive Alien Species Act which prohibits the import, transport and raising of LMB, and LMB are regarded as "100 of Japan's Worst Alien Species" (National Institute for Environmental Studies, n.d.).

Management strategies to control invasive LMB populations include: using artificial spawning sites to reduce reproduction; netting for removal of adult LMB; completely drying water bodies where applicable; restoring habitats for native species; stocking native fishes; and patrolling to prevent smuggling of fishes (Katano & Matsuzuki, 2012; Nishizawa et al., 2006). To compensate for the loss of indigenous commercial fishes in Lake Biwa, the local government subsidized a program to buy back black bass from fisherman to incentivize alien fish removal (Nishizawa et al., 2006). New research to improve methods to remove and control non-native black bass are currently underway, with the ultimate goal of restoring Lake Biwa to its native fauna (Ide & Seki, 2010).

However, by the late 1990s, LMB became a popular sport fish and, despite efforts to eliminate invasive LMB, has become a lucrative fishery in Japan (Nakai, 1999). According to the Japan Sportfishing Foundation, there are 3 million black bass anglers in Japan who generate over $1 billion in economic value (Japan Sportfishing Foundation as cited in Ichiban Tackle, n.d.). With the rise in black bass popularity in Japan, several organizations were created to promote recreational black bass angling, tournaments, and tackle such as the World Bass Society, Japan Ladies Bass Association, Japan Game Fish Association, and Japan Lure Anglers Association. Finally, the Japanese Ministry of Agriculture, Food and Forestry has promoted the development of recreational fishing as a way to revitalize local economies (Ministry of Agriculture, Forestry, and Fisheries, 2009). Conversely, these economic incentives must be weighed against black bass removal costs in Lake Biwa. The annual budget for black bass eradication at the Shiga Prefecture Fisheries Experimental Station is around 229 million yen (approximately $1.94 million) (Nishizawa et al., 2006).

In 2009, an angler caught a LMB from Lake Biwa weighing in at 22 pounds 6 ounces which tied the existing world record set in 1932 (International Game Fish Association, 2015). This has spurred the interest of LMB anglers internationally because of the potential for other record-breaking LMB catches that could come from this lake (Quinn, 2014), but has also created increased controversy over black bass removal efforts. For example, illegal introductions of LMB have continued after its listing on the Invasive Alien Species Act in 2005 (Tsunoda et al., 2015). Additionally, black bass anglers strongly opposed a law to kill any alien species caught in Lake Biwa, as well as the legal designation of LMB under Japan's Invasive Alien Species Act, since they rightly saw it as a threat to their sport (Nishizawa et al., 2006). With the potential to produce another world-record sized LMB, Lake Biwa has established itself as an alluring destination for LMB anglers, which has become incentive enough to not eradicate this fish.

South Africa. The Cape Floristic Region (CFR), located in southwestern South Africa, is acclaimed as a global biodiversity hotspot containing high levels of endemic freshwater fish species (Marr et al., 2012). Currently, there are 17 recognized indigenous freshwater fish species within this region, of which, 10 are considered endangered and 3 are listed as vulnerable by the International Union for the Conservation of Nature (Weyl et al., 2014).

The biggest threat to survival of these endemic fish species are non-native fishes (Marr et al., 2012), of which SMB has caused the most ecological damage (Woodford et al., 2005). Non-native fishes have invaded over 90% of the CFR mainstream river habitat causing most native CFR fishes to experience constricted, genetically isolated, and fragmented ranges (Marr et al., 2012; Weyl et al., 2014).

Introductions of LMB and SMB into South Africa first occurred in 1928 and 1937 respectively, and government funded stocking programs and angler-mediated translocations have facilitated widespread distribution for recreational angling (Hargrove et al., 2017; Impson et al., 2013). As a result of growing awareness about ecological impacts caused by non-native fishes, stocking of non-native fishes stopped in the early 1990s and invasive species management became a priority in South Africa (McCafferty et al., 2012). Resultantly, the National Environmental Management: Biodiversity Act and the Alien and Invasive Species Regulations were created to legally declare invasive species a threat to biodiversity and to implement control measures (Weyl et al., 2014). Since many invasive species already had established populations, invasive game species, such as black bass, were to be regulated under the Invasive Species Management Program (Weyl et al., 2014).

CapeNature, a conservation agency in South Africa, has spearheaded SMB eradication efforts by prioritizing certain reaches of rivers that qualify for removal efforts because large-scale eradication is often unattainable (Marr et al., 2012). Specifically, the lower reach of the Rondegat River within the CFR was chosen for rehabilitation (Marr et al., 2012). Smallmouth Bass was a voracious predator on native fauna in this area, and subsequently, extirpated the Clanwilliam Redfin *Barbus calidus*, the Fiery Redfin

Pseudobarbus phlegethon, and the Clanwilliam Rock Catfish *Austroglanis gilli* (Weyl et al., 2013; Woodford et al., 2005). Furthermore, treatment of this segment would allow for the reintroduction of two native species previously extirpated by black bass: Clanwilliam Sawfin *Barbus serra* and Clanwilliam Sandfish *Labeo seeberi* (Marr et al., 2012).

Extirpation of SMB was carried out using the fish piscicide, rotenone, which removed over 470 individuals (Impson et al., 2013). Indigenous fishes that were previously absent prior to the SMB eradication, rapidly recolonized the treatment area, while the SMB population never recovered (Impson et al., 2013). This suggests that further eradication efforts will allow for range expansion and population increases of native fishes suppressed by invasive SMB (Impson et al., 2013). However, the continued success of these restoration efforts are contingent upon public acceptance, as anglers have been identified as a high-risk group who could reintroduce an eradicated invasive species (Marr et al., 2012).

Angling organizations, such as the South African Bass Anglers Association (SABAA), have become a contentious force in non-native fish policies (McCaffery et al., 2012). For example, CapeNature spent many years addressing the concerns of angler organizations during the initial stages of the Rondegat River SMB eradication project (Woodford et al., 2017). Furthermore, after initial opposition to the National Environmental Management: Biodiversity Act, SABAA supported these regulations since they saw little threat to their sport because many reservoirs already had established populations of black bass (Ellender et al., 2014). Similarly, due to lack of communication between CapeNature and stakeholders, black bass anglers originally challenged the SMB eradication project in the Rondegat River even though the targeted SMB population had no recreational value (Ellender et al., 2014). Moreover, it is recognized that non-native fish are the foundation of recreational angling in South Africa, and as such, rehabilitation projects must strive to find balance between conservation and invasive game species regulations (Marr et al., 2012).

Inland fisheries, which were mainly developed for recreational angling, are a beneficial resource in South Africa by providing food security, poverty reduction and regional economic development (Ellender et al., 2014; McCafferty et al., 2012). Participation in South African recreational angling is estimated to be more than 1.5 million people with over 20,000 anglers targeting black bass (Ellender et al., 2014; McCafferty et al., 2012). In 2007, the economic impact of recreational freshwater angling was estimated to be R9.4 billion (approximately $1.34 billion) (Leibold & van Zyl, 2007 as cited in Marr & Collier, 2012). Laying just downstream of the Rondegat River SMB eradication project, the Clanwilliam reservoir SMB fishery provides significant economic income to locals (Barrow, 2014). Black bass anglers funneled R2 million into the economy surrounding Clanwilliam reservoir with 62% of this money directly supporting workers employed in the food and accommodation industry (Barrow, 2014). Finally, black bass tournaments held in South Africa, such as the 13th Black Bass World Championship, and regional competitions, such as the SABAA Team Super Final and Bass Fishing South Africa Money Trail, undoubtedly bring money into local economies where events are held, in addition to cash prizes for competitors.

However, Weyl et al. (2015) cautions against the use of recreational fisheries in protected areas as this can compromise conservation objectives. Moreover, the economic profits of black bass must be compared against the cost of eradication. The total cost of the Rondegat River SMB eradication project was R3.3 million (approximately $290,000), and many more native fish recovery projects in the CFR have been proposed following this project (Impson et al., 2013; Weyl et al., 2014).

Discussion

Updating the distribution of LMB and SMB uncovered many status changes through the review of recent publications and has filled a knowledge gap about the dynamic distribution of these species. Given the constant flux of human-mediated introduction of fishes and population dynamics of species, the distributions of non-native fishes are constantly varying. Anglers are often a vector for non-native fish dispersal by facilitating illegal stocking of these two fishes (Johnson et al., 2009), thus exacerbating the inaccuracies regarding the true range of LMB and SMB. The updated distributions completed within my study provide more useful and comprehensive information because they are more accurate. Since distribution data can inform conservation networks and influence where invasive species management occurs, maintaining such databases is imperative for prevention and early detection programs.

Reviewing original sources proved to be essential in providing an accurate and modern establishment list. For example, Slovakia was listed in Froese and Pauly (2019c), CAB International (2019), Whitlock (2004), and Loppnow et al. (2013) as having established SMB populations based on the same source, Welcomme (1988). However, having reviewed Welcomme (1988), Slovakia was never listed as one of the countries where SMB was historically introduced and the current review could find no other evidence to support its occurrence there. Thus, this highlights the importance of researchers to have integrity and fastidiousness in their work when citing sources.

This study solely focused on two species of black bass, which makes it unique from the wealth of fisheries information contained in online databases such as FishBase. With the help of over 2,000 collaborators, FishBase has compiled biodiversity information on fishes for almost three decades. FishBase has become an irreplaceable encyclopedia on fisheries science, biology, and distribution with a variety of graphic and analytical tools, containing information on over 34,000 species (Froese & Pauly, 2019a). However, due to the scope and scale of this global information resource, some records within FishBase may not be regularly updated due to lack of funding (Froese & Pauly, 2019a). Further, as is only understandable in a database of this size, FishBase acknowledges that errors in their database or citations are inevitable, and thus, rely on users to point out discrepancies (Froese & Pauly, 2000). By only undertaking the task of reassessing the distribution of two species, my study had the time and resources to review, verify, and update the global distribution of LMB and SMB to confirm their present range.

Online distribution lists of fishes are beneficial because they provide wide-ranging information but, real-time updates are often difficult to achieve, as finding the time and funding to do so is challenging. Moreover, as databases like FishBase continue to add key information on species, emphasize different topics, and strive for future goals (Froese & Pauly, 2000), it would be hard to prioritize whether to concentrate efforts on reviewing existing information or adding new information. Finally, the historical establishment of LMB and SMB as compared to their current establishment, shows that not all populations remain viable and that new introductions are still occurring (e.g., LMB introduced into Réunion in 1994), but overall, these two species are not as widely established as they previously were. Thus, conducting regular systematic reviews of the distribution of non-native species is imperative to provide detailed and up to date information.

With this in mind, the following distribution list is certainly not absolute, but it does represent information from the most recently available sources. While some of the most reliable sources for obtaining distribution data come from taxonomic checklists based on specimen collections, these lists are still lacking for many countries, creating information gaps about the true distribution of non-native black bass. Furthermore, some sources had conflicting information on the establishment of these species, and this highlights the need for further field sampling. Moreover, given the scope of LMB and SMB distribution, some sources were only available in native languages, where translations service, such as Google Translate, were not always sufficient. Thus, the need to continually update and revise distribution lists as new publications become available is critical to maintaining this dataset.

Given that the establishment success rate between LMB (67%) and SMB (22%) differed widely, this suggests that some biological or ecological factors were involved in their success. For example, SMB prefer cool, flowing water, restricting their potential range to temperate world regions due to environmental and thermal constraints (Scott & Crossman, 1973). Contrastingly, LMB have a broader ecological and habitat tolerance, which has allowed them to be successful in a wider range of environmental conditions. For example, LMB can tolerate warmer water temperatures with slight turbidity (Scott & Crossman, 1973) allowing them to become established in many tropical regions and artificial water bodies (e.g., reservoirs) where SMB establishment had failed (Welcomme, 1988). Furthermore, LMB reach a larger maximum size than SMB, which make them prized among black bass anglers hoping to catch a record breaking LMB (Quinn, 2014). This in turn, increases the likelihood of repeated LMB introductions in attempts to establish a LMB population for trophy angling. However, both LMB and SMB have the life history traits and trophic generalism to become successfully established, while their intense fishing pressure allows for subsequent dispersal (Peoples & Midway, 2018). Thus, LMB and SMB display the invasibility characteristics necessary to bypass biogeographical, physiological, and biotic filters in their introduced range.

As depicted in the case studies, management of non-native black bass had a tendency to differ between natural and artificial systems. In natural waters, non-native black bass caused significant harm to the native biodiversity and were viewed as invasive species that were then removed. However, when contained within artificial water bodies (e.g., reservoirs), non-native black bass tended to be valued because they provided sport fishing opportunities and revenue to local economies. This difference in perspective is the crux of the ecological-economic dynamic, and habitat may be an important factor in partitioning these conflicting impacts (Chapter 2, 2019).

The environment which non-native black bass inhabit is crucial to understanding the perceived differences in ecological threat. Not only did the expansion of reservoirs allow for artificial lakes to be created where standing water did not previously occur, but a novel set of ecological parameters resulted from their construction (Wetzel, 1990). These highly altered environments contrast with natural lakes in respect to sediment loads, nutrient availability, temperature, water level fluctuations, and species diversity (Wetzel, 1990). Since anthropogenic waters are young, unstable systems, its biotic community has not become well developed, as opposed to natural waters that have had thousands of years to reach an ecological balance (Noble, 1986; Wetzel, 1990). Habitat modifications resulting from the dynamic nature of reservoirs largely displaced the native fauna, thus, creating concerns of aquatic “biological deserts” (Miranda, 1996). Thus, to enhance fish populations, initial stocking of reservoirs focused on species that were useful for sport fishing, namely LMB, both in the U.S. and South Africa (McCafferty et al., 2012; Noble, 1986; O’Brien, 1990)

Fisheries biologists appear to recognize a disparity in ecological harm caused by non-native black bass between natural and anthropogenic systems, with natural systems enduring more negative impacts than artificial ones (Chapter 2, 2019). In general, society fundamentally places higher value on natural ecosystems and their processes than those of artificial ones (Angermeier, 2000). This disagreement in values contributes to why degradation of natural ecosystems and of indigenous biodiversity is seen as an irreparable loss, and must instead be conserved (Angermeier, 2000). Thus, the impacts of invasive species in natural ecosystems are regarded more seriously, especially when the threats can be far-reaching. For example, the severity of impact caused by non-native black bass in natural ecosystems can range from local extirpations (e.g., South Africa case study) to global extinctions (e.g., Alaotra Grebe *Tachybaptus rufolavatus* (Birdlife International, 2016)). Due to these concerns, the New Zealand government declined to authorize the introduction of LMB because the harm to native fauna outweighed the potential benefits of a sport fishery (McDowall, 1968; Robbins & MacCrimmon, 1974).

Non-native fishes introduced for sport can cause a conflict of interest between angler satisfaction and conserving aquatic biodiversity. Similarly, agencies managing fisheries often have contradicting objectives (e.g., providing quality sport fishing opportunities with introduced species and protecting endemic species) (Hickley & Chare, 2004). For example, the USFWS is working to restore native fishes that are threatened by invasive SMB, while simultaneously stocking non-native LMB, a conspecific, as a compatible sportfish (UCREFRP & SJRBRIP, 2018). Furthermore, since conservation funds are often derived from angler license sales, anglers have become a key stakeholder group, upon which wildlife agencies are financially dependent (Jacobson et al., 2010). Thus, anglers have taken a central role in the stewardship of black bass conservation by influencing their policy and range expansion (Long et al., 2015). Therefore, it is understandable that policymakers may be swayed by the prospective income generated by non-native black bass. For example, in South Africa, both revenue from fishing licenses and taxes on fishing equipment, have been proposed as a way to fund inland fisheries management (Britz, 2015), and in the past, fishing licenses have funded stocking of non-native fishes (McCafferty et al., 2012).

Since humans favor species with direct economic value, society struggles with assigning an intrinsic, instrumental, or monetary value to biodiversity (Justus et al., 2009), which may contribute to why biodiversity is suffering. Globally, protection of biodiversity across land and water-scapes has been estimated to cost $290 billion annually (James et al., 2001), but only $21.5 billion is actually spent on conservation per year, thus highlighting the inadequacy of conservation funding world-wide

(Waldron et al., 2013). While the majority of conservation funds are spent in developed countries such as the U.S. (James et al., 2001), many countries remain severely underfunded, hindering their ability to reach conservation goals (Waldron et al., 2013). While South Africa previously had inadequate government funding for biodiversity management (Wynberg, 2002), $111 million is now spent annually on conservation efforts (Walden et al., 2013) and centers, such as the South African Institute for Aquatic Biodiversity, are dedicated to conservation research. Contrastingly, the Japanese government has been criticized for having biodiversity policies, but inadequate funding, staff, and resources to effectively implement wildlife conservation strategies (Knight, 2007; Knight, 2010).

However, for sportfish, direct expenditures can be calculated to provide an estimate of economic value. For example, revenue from angler license sales is spent on the game species they exploit (Geist et al., 2001). Yet, endemic non-game species conservation receives far less funding and is harder to quantify with regards to economic benefit. This economic discrepancy hints at a difference in our value system between non-native species and native biodiversity. In the United States, for example, fishing license sales in 2018 generated over $724 million (USFWS, 2018a), while the State Wildlife Grant program (funding specifically to conserve native, imperiled fishes and wildlife species) had just over $50 million (USFWS, 2018b). Thus, introduced LMB and SMB provide a direct utility to society that can be easily defined economically, which has resulted in their wide distribution and acceptance by many societies, often becoming integral parts of local economies around the world (Chen et al., 2003; Driscoll & Meyers, 2014; Ellender et al., 2014; Hargrove et al., 2015; Takamura, 2007; USFWS & U.S. Census Bureau, 2011).

Conclusion

This synthesis highlights the similarities experienced by countries across the world in terms of the ecological degradation and economic benefits resulting from introduced black bass. Despite this knowledge, we continue to struggle to decide between conserving biodiversity and relying upon income derived from invasive species. Since these impacts are intrinsically conflicting forces, non-native black bass continue to create a conundrum of social values with a tendency to evade consistent policies across its introduced range. By comparing the economic benefits and the ecological threats associated with non-native black bass, better fisheries management decisions can be made on society's behalf. The case studies I highlight in my review (U.S., Japan, and South Africa) show that the balance between socio-economic values and conservation priorities for non-native black bass are being reevaluated in terms of the level of risk associated with non-native species. However, whether these instances are outliers or harbingers of the future are yet unknown.

Tables

Table 1.1. Distribution table detailing Largemouth Bass (*M. salmoides)* introduction history and current establishment.

Country	Date of Introduction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established ?	Recent Source
Albania	Unknown	Unknown	Unknown	Yes	Dhora, 2010 as cited in Froese & Pauly, 2019b	Yes	Kottelat & Freyhof, 2007
Algeria	1970	France	Aquaculture	Yes	Welcomme, 1988	Yes	Zouakh & Meddour, 2017
Argentina	1959	USA	Aquaculture Sport	Artificial Reproduction	Welcomme, 1988	No[E]	Vigliano & Darrigran, 2002
Austria	1885	Germany	Fisheries	Yes	Robbins & MacCrimmon, 1974	Yes	Kottelat & Freyhof, 2007; Rabitsch et al., 2013
Azores†	1898	USA	Fisheries	Yes	Robbins & MacCrimmon, 1974	No	Ribeiro et al., 2009
Belarus	Unknown	Unknown	Unknown	Yes	Blanc et al., 1971	Yes	Elvira, 2001
Belgium	1877, 1885-90	USA, Germany	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Uncertain[E]	Elvira, 2001; Verreycken et al., 2007

Table 1.1. Distribution of Largemouth Bass (*M. salmoides)* continued.

Country	Date of Introduction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
Bolivia	Unknown	Unknown	Sport	Yes	Welcomme, 1988	Uncertain[E]	Welcomme, 1988; Carvajal-Vallejos et al., 2014
Bosnia and Herzegovina	1920	Adriatic Sea Drainage	Aquaculture	Yes	Welcomme, 1988	Yes[A]	Elvira, 2001; Kottelat & Freyhof, 2007; Tutman et al., 2017
Botswana	1937, 1938	South Africa, Swaziland	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Ellender et al., 2014; Hargrove et al., 2015
Brazil	1926	USA	Aquaculture	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes[N]	Schulz & Leal, 2005; Garcia et al., 2014; Bertaco et al., 2016
Cameroon	1956	France	Aquaculture	No	Welcomme, 1988		
Canada	Native and Introduced - 1900s	Columbia River, Washington, USA	Sport	Yes	Robbins & MacCrimmon, 1974; Scott & Crossman, 1973	Yes	Post et al., 2016

Table 1.1. Distribution of Largemouth Bass (*M. salmoides)* continued.

Country	Date of Intro-duction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established ?	Recent Source
China	1983; 1984	Hong Kong; USA	Aquaculture	Yes	Yan et al., 2001	Yes	Xu et al., 2006; Xu et al., 2012; Xiong et al., 2015
Colombia	1956	USA	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Jaramillo-Villa et al., 2010; Gutierrez et al., 2012
Congo	1955	France	Aquaculture	No	Welcomme, 1988		
Costa Rica	Unknown	Unknown	Aquaculture	Yes	Robbins & MacCrimmon, 1974	Yes[N]	Angulo et al., 2013
Croatia	1920	Adriatic Sea Drainage	Aquaculture	Yes	Welcomme, 1988	Yes[A]	Elvira, 2001; Kottelat & Freyhof, 2007; Dulčić et al., 2017
Cuba	1915, 1928	USA	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Welcomme, 1988; GBIF, 2019; FishNet2, 2013
Cyprus	1971	Canada	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Elvira, 2001

Table 1.1. Distribution of Largemouth Bass (*M. salmoides)* continued.

Country	Date of Intro-duction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established ?	Recent Source
Czech Republic	1885-90	Germany	Unknown	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Uncertain[E]	Elvira, 2001; Musil et al., 2010
Denmark	1901, 1906, 1907	Germany	Aquaculture, Sport	No	Welcomme, 1988	No	Elvira, 2001; Kottelat & Freyhof, 2007
Dominican Republic	1955	USA	Aquaculture, Fisheries	Artificial Reproduction	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Welcomme, 1988
Ecuador	1960	USA	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes[A]	Velez-Espino, 2005
Egypt	1949	Europe	Unknown	No	Welcomme, 1988		
El Salvador	1957	USA	Aquaculture	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	No[E]	McMahan et al., 2013
Estonia	Unknown	Unknown	Unknown	Yes	Blanc et al., 1971	Unknown	Elvira, 2001
Fiji	1962	Unknown	Sport	Artificial Reproduction	Welcomme, 1988	Yes	Boseto & Jenkins, 2006

Table 1.1. Distribution of Largemouth Bass (*M. salmoides)* continued.

Country	Date of Introduction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
Finland	1898	Germany	Stocking	No	Welcomme, 1988	No	Elvira, 2001; Kottelat & Freyhof, 2007
France	1877, 1930s	USA	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Elvira, 2001; Kottelat & Freyhof, 2007
French Polynesia†	1926	Unknown	Scientific Curiosity	Uncertain	Maciolek, 1984	No	Eldredge, 2000; Keith, 2002
Germany	1888, 1930	USA	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Uncertain[N]	Elvira, 2001; Kottelat & Freyhof, 2007; Wolter & Röhr, 2010; Rabitsch et al., 2013
Greece	Unknown	Unknown	Aquaculture	Questionable	Corsini-Foka & Economidis, 2007	Yes	Economou et al., 2007; Perdikaris et al., 2010
Guam†	1955, 1963, 1965, 1966	USA	Unknown	Artificial Reproduction	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Eldredge, 2000

Table 1.1. Distribution of Largemouth Bass (*M. salmoides)* continued.

Country	Date of Intro-duction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
Guatemala	1958	USA	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Welcomme, 1988; FishNet2, 2013; GBIF, 2019
Honduras	1954	USA	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Matamoros et al., 2009
Hong Kong†	1925-1949	USA	Unknown	Yes	Hay & Hodgkiss, 1981	Yes	GBIF, 2019
Hungary	1885-90, 1910, 1950s	Germany	Aquaculture	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Elvira, 2001
Iran	Unknown	Tigris-Euphrates basin & Namak Lake basin	Aquaculture	Yes	Coad, 1980	Uncertain[E]	Coad 1996a, 1996b; Coad 1998; Esmaeili et al., 2014; Esmaeili et al., 2017; Esmaeili et al., 2018

Table 1.1. Distribution of Largemouth Bass (*M. salmoides)* continued.

Country	Date of Intro-duction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
Italy	1886-97	Germany, USA	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Elvira, 2001; Bianco & Ketmaier, 2001; Kottelat & Freyhof, 2007
Japan	1925	USA	Sport	Yes	Robbins & MacCrimmon, 1974	Yes	Yuma et al., 1998; Iguchi et al., 2004
Kenya	1928, 1929	USA, Europe	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Seegers et al., 2003, Hickley et al., 2008
Kosovo	1914, 1920	Hungary?	Aquaculture, Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes[A]	Lenhardt et al., 2011
Latvia	Unknown	Unknown	Unknown	Yes	Blanc et al., 1971	Yes	Elvira, 2001
Lesotho	1937	South Africa, Swaziland	Sport, Aquaculture	Yes	Robbins & MacCrimmon, 1974; Welcomme; 1988	Yes	FAO, 2002

Table 1.1. Distribution of Largemouth Bass (*M. salmoides)* continued.

Country	Date of Intro-duction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
Lithuania	Unknown	Unknown	Unknown	Yes	Blanc et al., 1971	Yes	Elvira, 2001
Madagascar	1951	France	Sport	Yes	Welcomme, 1988	Yes	Schabetsberger et al., 2013; Fricke et al., 2018
Malawi	1937	Zimbabwe, Swaziland	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes, but not in Lake Malawi	Skelton, 1993; Weyl et al., 2010
Malaysia	1984	USA	Sport	Yes	Ang et al., 1989	Yes	Ang et al., 1989
Mallorca†	Unknown	Unknown	Unknown	Yes	Kottelat & Freyhof, 2007	Yes[A]	Kottelat & Freyhof, 2007; Hanel et al., 2011
Mauritius	1949	USA, South Africa	Sport	Yes	Robbins & MacCrimmon. 1974; Welcomme, 1988	No[E]	FAO, 1997; Fricke, 1999
Mexico	Native and Introduced – 1898	USA	Sport	Yes	Robbins & MacCrimmon, 1974	Yes	Miller et al., 2005; Alcocer & Bernal-Brooks, 2010

Table 1.1. Distribution of Largemouth Bass (*M. salmoides)* continued.

Country	Date of Intro-duction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
Montenegro	1920	Unknown	Aquaculture	Yes	Welcomme, 1988	Yes[A]	Elvira, 2001; Kottelat & Freyhof, 2007
Morocco	1934	France	Sport	Yes	Robbins & MacCrimmon, 1974	Yes	Clavero et al. 2015
Mozambique	1947	Swaziland	Sport	Unknown	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Weyl & Hecht, 1999; Scott et al., 2006
Namibia	1932	South Africa	Sport	Yes	FAO, 1997	Yes	Skelton, 1993; Okeyo, 2000; Scott et al., 2006
Netherlands	1883, 1984	Belgium	Diffusion through Meuse river	No	Robbins & MacCrimmon, 1974; Welcomme, 1988	Uncertain[N]	Elvira, 2001; Kottelat & Freyhof, 2007; Soes et al., 2011
New Caledonia†	1960	Unknown	Sport	Yes	Welcomme, 1988	Yes	Fricke et al., 2011

Table 1.1. Distribution of Largemouth Bass (*M. salmoides)* continued.

Country	Date of Introduction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
Nicaragua	1959-60	Unknown	Unknown	No	Robbins & MacCrimmon, 1974		
Nigeria	1976	USA	Unknown	Unknown	Welcomme, 1988	Unknown	
North Korea	1963	USA	To fill a vacant niche	Yes	Welcomme, 1988	Yes	Bartley, 2006 as cited in Froese & Pauly, 2019b
Norway	1887	Germany	Unknown	No	Robbins & MacCrimmon, 1974	No[Q]	Elvira, 2001; Kottelat & Freyhof, 2007

Table 1.1. Distribution of Largemouth Bass (*M. salmoides)* continued.

Country	Date of Intro-duction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established ?	Recent Source
Panama	1935, 1955	USA	Stocking	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Welcomme, 1988
Philippines	1907	USA	Aquaculture, Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988; Juliano et al., 1989	Uncertain[E]	Kottelat, 2013; Guerrero, 2014
Poland	1883, 1912	USA, Germany	Aquaculture	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Uncertain[E]	Elvira, 2001; Grabowska et al., 2010; Witkowski & Grabowska, 2012
Portugal	1952	France	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Elvira, 2001; Kottelat & Freyhof, 2007; Anastácio et al., 2018

Table 1.1. Distribution of Largemouth Bass (*M. salmoides)* continued.

Country	Date of Intro-duction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
Puerto Rico†	1915, 1946	USA	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Neal et al., 2009
Réunion†	1994	Unknown	Unknown	Yes	Phillipe, personal communication, 2006 as cited in GISD, 2019	No	Fricke et al., 2009
Romania	Unknown	Unknown	Sport	Yes	Froese and Pauly, 2019b	Yes	Froese and Pauly, 2019b
Russian Federation	1885-90	Germany	Fisheries	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Uncertain[E]	Elvira, 2001; Bogutskaya & Naseka, 2002; NOBANIS, 2006; Kottelat & Freyhof, 2007; Slynko et al., 2011

Table 1.1. Distribution of Largemouth Bass (*M. salmoides)* continued.

Country	Date of Intro-duction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established ?	Recent Source
Sardinia†	1962	North America	Unknown	Yes	Cottiglia, 1968 as cited in Orru et al., 2010	Yes[A]	Orru et al., 2010
Serbia	1984	Unknown	Aquaculture	Yes	Welcomme, 1988	Yes	Elvira 2001, Lenhardt et al. 2011
Slovakia	1885-90	Germany	Unknown	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Holcik, 1996; Elvira, 2001; Koščo et al., 2010
Slovenia	1920	Unknown	Aquaculture	Yes	Welcomme, 1988	Yes	Elvira, 2001; Povz & Sumer, 2005; Kottelat & Freyhof, 2007
South Africa	1928	Netherlands	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Skelton, 1993; Scott et al., 2006; Ellender & Weyl, 2014; Hargrove et al., 2017

Table 1.1. Distribution of Largemouth Bass (*M. salmoides)* continued.

Country	Date of Intro-duction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
South Korea	1963	USA	To fill a vacant niche	Yes	Welcomme, 1988	Yes	Jang et al., 2002; Jang et al., 2006; Zhang et al., 2013
Spain	1955-56	France	Aquaculture	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Elvira, 2001; Elvira & Almodovar, 2001; Kottelat & Freyhof, 2007; Comesana & Ayers, 2009
Swaziland	1933	Netherlands, South Africa	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Skelton, 1993; Breuil & Grima, 2014
Sweden	1885-90	Germany	Sport	No	Robbins & MacCrimmon, 1974	No	NOBANIS, 2005; Kottelat & Freyhof, 2007

Table 1.1. Distribution of Largemouth Bass (*M. salmoides)* continued.

Country	Date of Introduction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
Switzerland	1885-90	Germany	Sport	Yes	Robbins & MacCrimmon, 1974	Yes	Elvira, 2001; Kottelat & Freyhof, 2007
Taiwan†	late 1970s	North America	Aquaculture	Yes	Liao & Liu, 1989	Yes[N], in aquaculture	Liao & Liu, 1989
Tanzania	1956	Kenya	Sport	Yes	Robbins & MacCrimmon, 1974	Uncertain[E]	Fermon, 1996; Eccles, 1992 as cited in FAO, 1997
Tunisia	1966	Morocco	Sport	Unknown	Robbins & MacCrimmon, 1974	Yes	Doadrio, 1994; FAO, 1997
Uganda	1960	Kenya	Unknown	Unknown	Robbins & MacCrimmon, 1974; Welcomme, 1988	Unknown	
Ukraine	Unknown	Unknown	Unknown	Unknown	Blanc et al., 1971	Yes	Elvira, 2001

Table 1.1. Distribution of Largemouth Bass (*M. salmoides)* continued.

Country	Date of Introduction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
United Kingdom	1879, 1929-30s	USA	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	No	Kottelat & Freyhof, 2007; Everard, 2013
US Virgin Islands†	Unknown	Unknown	Unknown	Yes	Ogden, Yntema, & Clavijo, 1975 as cited in Froese & Pauly, 2019	No[E]	Smith-Vaniz & Jelks, 2014
USA	Native and Introduced-1800s-1900	USA	Sport	Yes	Robbins & MacCrimmon, 1974	Yes	Fuller & Neilson, 2019b
Venezuela	1935	USA	Unknown	Unknown	Robbins & MacCrimmon, 1974		
Zambia	1944	South Africa	Unknown	No	Robbins & MacCrimmon, 1974	Yes	Losse, 1998 as cited in Froese & Pauly, 2019b

Table 1.1. Distribution of Largemouth Bass (*M. salmoides)* continued.

Country	Date of Introduction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
Zimbabwe	1932	South Africa	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Skelton, 1993; Beamish et al., 2005; Scott et al., 2006; Marshall, 2011

† Denotes a territory held under jurisdiction by another country.

FishBase status as of 2019: ^{A} = new additions not currently in the database, ^{E} = established, ^{N} = not established, ^{Q} = questionable establishment.

Table 1.2. Distribution table detailing Smallmouth Bass (*M. dolomieu*) introduction history and current establishment.

Country	Date of Introduction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
Austria	1884-90	Germany	Unknown	No	Robbins & MacCrimmon, 1974	Uncertain[E]	Elvira, 2001; Kottelat and Freyhof, 2007; Rabitsch et al., 2013
Belgium	1885-90	Germany, USA	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	No[E]	Kottelat & Freyhof, 2007; Verreycken et al., 2007
Belize	1969	USA	Sport	Yes	Welcomme, 1988	Uncertain[E]	Loppnow et al., 2013
Bolivia	1966	Mexico	Unknown	No	Robbins & MacCrimmon, 1974	Probably Not[A]	Carvajal-Vallejos, 2014
Brazil	1911	USA	Unknown	Destroyed	Robbins & MacCrimmon, 1974		
Canada	Native and Introduced – 1869-1924	Unknown	Sport	Yes	Scott & Crossman 1973; Robbins & MacCrimmon, 1974	Yes	McPhail, 2007
Costa Rica	Unknown	Unknown	Unknown	Unknown	Robbins & MacCrimmon, 1974	No	Angulo et al., 2013

Table 1.2. Distribution of Smallmouth Bass (*M. dolomieu*) continued.

Country	Date of Introduction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
Czech Republic	post 1884	Germany	Unknown	No	Robbins & MacCrimmon, 1974	No[E]	Elvira, 2001; Kottelat & Freyhof, 2007; Hanel et al., 2011
Denmark	1958	Canada	Unknown	No	Robbins & MacCrimmon, 1974; Welcomme, 1988	No	Elvira, 2001; Kottelat & Freyhof, 2007; Hanel et al., 2011
Fiji	1962	Unknown	Unknown	Yes	Welcomme, 1988	No	Maciolek, 1984; Eldredge, 2000
Finland	1873, 1890, 1966	Canada, Germany, Sweden	Stocking	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	No	Elvira, 2001; Kottelat & Freyhof, 2007; Hanel et al., 2011
France	1869	USA	Unknown	No	Robbins & MacCrimmon, 1974	No	Elvira, 2001; Kottelat & Freyhof, 2007; Hanel et al., 2011

Table 1.2. Distribution of Smallmouth Bass (*M. dolomieu*) continued.

Country	Date of Introduction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
Germany	1880, 1883	USA	Aquaculture, Sport	No	Robbins & MacCrimmon, 1974; Welcomme, 1988	Uncertain[N]	Elvira, 2001; Kottelat & Freyhof, 2007; Rabitsch et al., 2013
Guam†	1962, 1963	USA	Unknown	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	No	Eldredge, 2000
Honduras	1967	USA	Unknown	Unknown	Robbins & MacCrimmon, 1974	Unknown	
Hong Kong†	1935	Unknown	Sport	Yes	Robbins & MacCrimmon, 1974	Unknown	
Hungary	1884-90	Germany	Unknown	No	Robbins & MacCrimmon, 1974	No	Elvira, 2001; Kottelat & Freyhof, 2007
Italy	1884-90	Germany	Unknown	No	Robbins & MacCrimmon, 1974	No	Elvira 2001, Kottelat & Freyhof 2007

Table 1.2. Distribution of Smallmouth Bass (*M. dolomieu*) continued.

Country	Date of Introduction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
Japan	1930	USA	Unknown	No	Robbins & MacCrimmon, 1974	Yes	Katano et al., 2015
Kenya	Unknown	Lake Victoria?	Diffusion?	Unknown	Fermon, 1996	Questionable[A]	Fermon, 1996
Lesotho	Unknown	South Africa?	Diffusion?	Unknown	Skelton, 1993	Yes[A]	Scott et al., 2006
Mauritius	1949	South Africa	Unknown	Unknown	Robbins & MacCrimmon, 1974	Yes	Fricke, 1999
Mexico	1975	USA	Stocking	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Miller et al., 2005
Netherlands	1884-90	Germany	Unknown	No	Robbins & MacCrimmon, 1974	No	Elvira, 2001; Kottelat & Freyhof, 2007; Soes et al., 2011
Norway	1887-95	Germany	To fill a vacant niche	No	Robbins & MacCrimmon, 1974; Welcomme, 1988	No	Elvira, 2001; Kottelat & Freyhof, 2007; Hanel et al., 2011

Table 1.2. Distribution of Smallmouth Bass (*M. dolomieu*) continued.

Country	Date of Introduction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
Poland	1884-90	Germany	Unknown	No	Robbins & MacCrimmon, 1974	No	Elvira, 2001; Kottelat & Freyhof, 2007
Slovakia	post 1884	Germany	Unknown	No	Robbins & MacCrimmon, 1974	No[E]	Holčík, 1996; Elvira, 2001; Koščo, 2010; Hanel et al., 2011
South Africa	1937-1945	USA	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	Yes	Skelton, 1993; Scott et al., 2006; Ellender & Weyl, 2014
South Korea	1973	USA	Unknown	Uncertain	Jang et al., 2002	Uncertain[A]	Jang et al., 2002
Swaziland	1938	South Africa	Sport	No	Robbins & MacCrimmon, 1974; Welcomme, 1988		
Sweden	1884-90, 1920-60	Germany, USA	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	No	Kottelat &Freyhof, 2007; Hanel et al., 2011

Table 1.2. Distribution of Smallmouth Bass (*M. dolomieu*) continued.

Country	Date of Introduction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
Switzerland	1885-90	Germany	Unknown	No	Robbins & MacCrimmon, 1974	No	Elvira, 2001; Kottelat & Freyhof, 2007
Tanzania	Not Introduced	-	Preserve native fishery	-	Robbins & MacCrimmon, 1974	Yes	Fermon, 1996
Uganda	1960	Unknown	Sport	No	Robbins & MacCrimmon, 1974	Questionable[A]	Fermon, 1996
United Kingdom	1878-90	USA	Sport	No	Robbins & MacCrimmon, 1974; Welcomme, 1988	No	Kottelat & Freyhof, 2007; Hanel et al., 2011; Everard, 2013
USA	Native and Introduced-early 1800s-1941	USA	Sport	Yes	Robbins & MacCrimmon, 1974	Yes	Fuller et al., 2019a
Vietnam	1952	USA	Sport	Yes	Robbins & MacCrimmon, 1974; Orsi, 1974	Probably Not[E]	Kottelat, 2001

Table 1.2. Distribution of Smallmouth Bass (*M. dolomieu*) continued.

Country	Date of Introduction	Origin	Reason	Introduction Successful?	Historical Source	Currently Established?	Recent Source
Zimbabwe	1940, 1942	South Africa	Sport	Yes	Robbins & MacCrimmon, 1974; Welcomme, 1988	No	Marshall, 2011

† Denotes a territory held under jurisdiction by another country.
FishBase status as of 2019: [A] = new additions not currently in the database, [E] = established, [N] = not established.

Table 1.3. Error matrix constructed from Largemouth Bass (*Micropterus salmoides*; LMB) distribution data found on FishBase and this study to determine the accuracy of online databases. Data contained on FishBase (n =76) was compared against the updated LMB distribution from this study based on three categories: established, absent, and uncertain. Highlighted cells indicate the number of regions where the distribution information on FishBase agreed with this study. FishBase falsely reports LMB establishment in 12 regions, absence in 5 regions, and uncertainty in 1 region for an overall error rate of 24%.

		Updated Largemouth Bass Distribution		
	n = 76	Established	Absent	Uncertain
FishBase	Established	**51**	4	8
	Absent	3	**6**	2
	Uncertain	0	1	**1**

Table 1.4. Error matrix constructed from Smallmouth Bass (*Micropterus dolomieu*; SMB) distribution data found on FishBase and this study to determine the accuracy of online databases. Data contained on FishBase (n =25) was compared against the updated SMB distribution from this study based on three categories: established, absent, and uncertain. Highlighted cells indicate the number of regions where the distribution information on FishBase agreed with this study. FishBase falsely reports SMB establishment in 6 regions and absence in 1 region for an overall error rate of 28%.

		Updated Smallmouth Bass Distribution		
	n = 25	Established	Absent	Uncertain
FishBase	Established	**7**	4	2
	Absent	0	**11**	1
	Uncertain	0	0	**0**

Figures

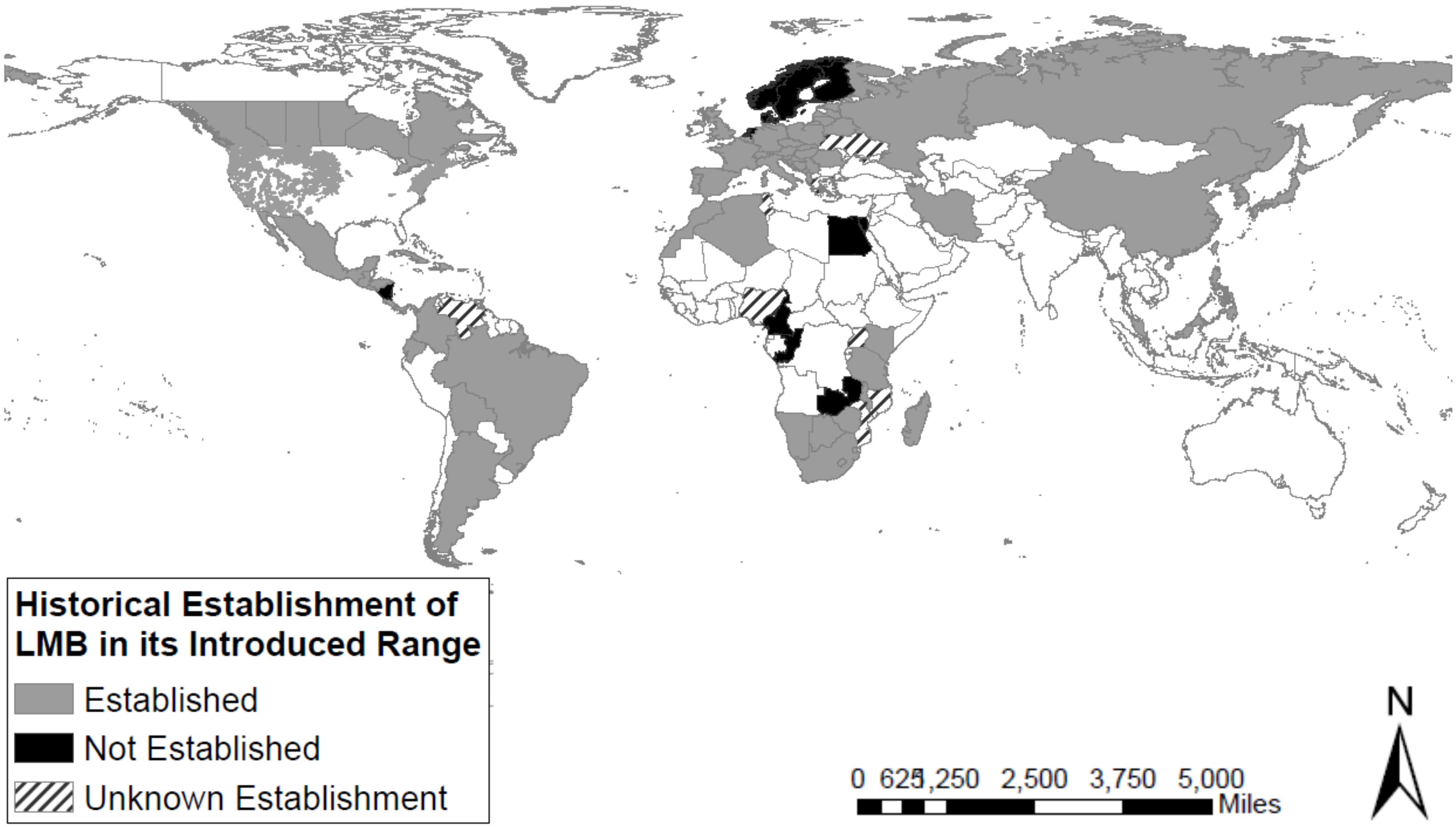

Figure 1.1. Historical introduction and establishment of Largemouth Bass (*Micropterus salmoides*; LMB*)* beginning in the early 1800s and continuing through 1994. Map based on data prior to 1988. Established indicates successfully introduced populations, not established indicates failed introductions, and unknown establishment indicates that LMB was introduced but it was unknown historically if they became established.

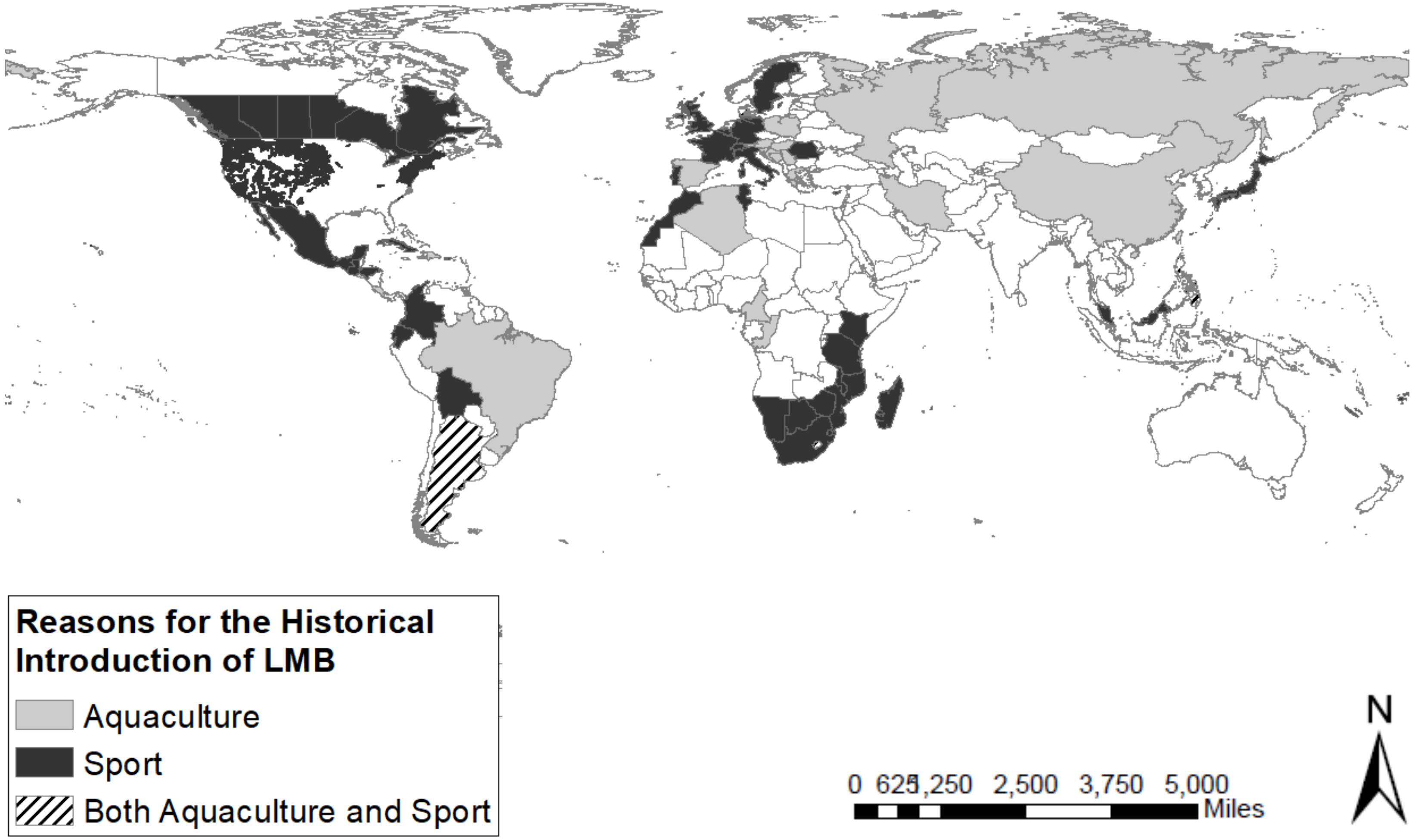

Figure 1.2. Reasons for the historical introduction of Largemouth Bass (*Micropterus salmoides*). Map based on data prior to 1988. Largemouth Bass was introduced for aquaculture in 21 regions, for sport in 37 regions, and for both aquaculture and sport in 5 regions.

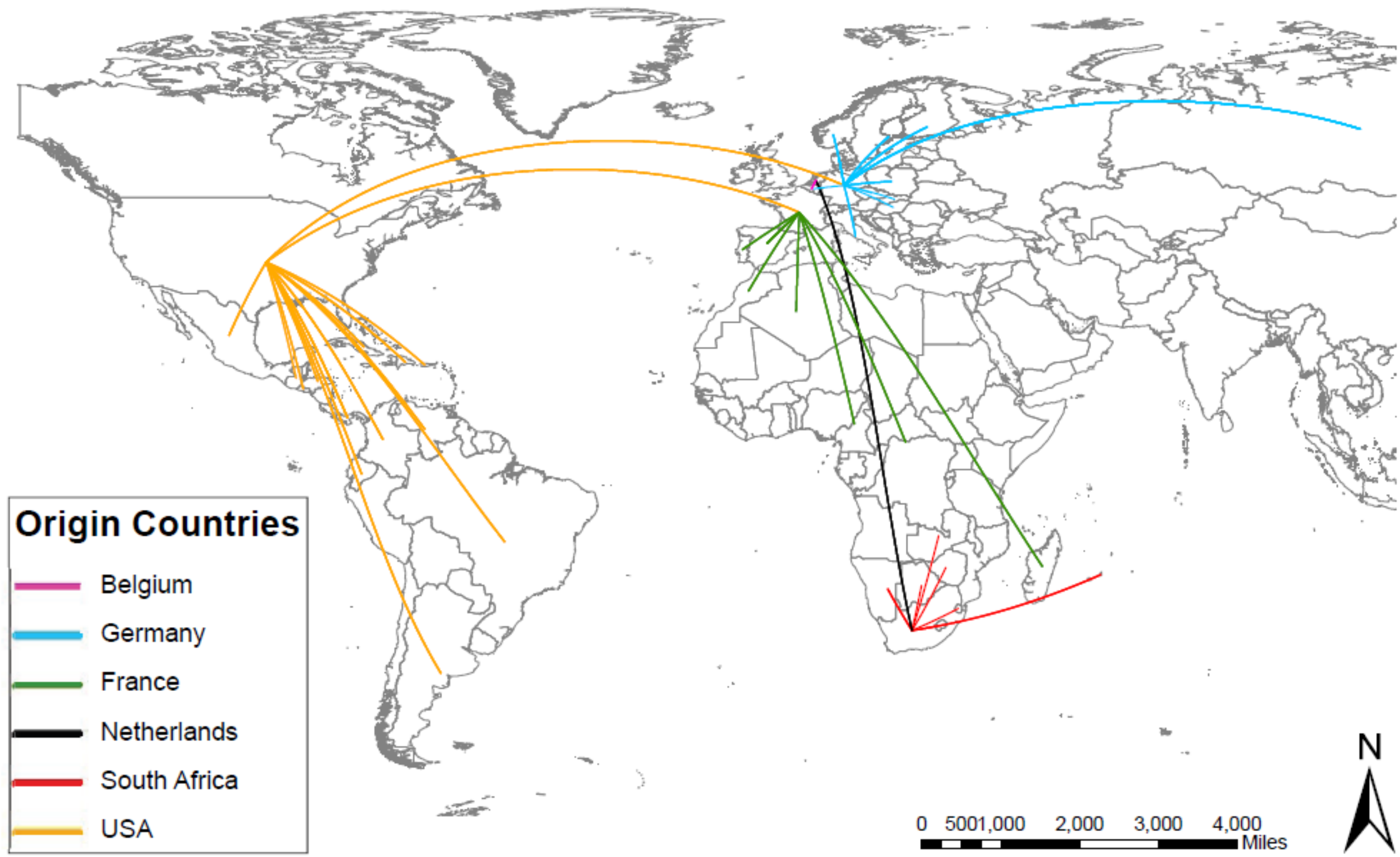

Figure 1.3. Largemouth Bass (*Micropterus salmoides*) dissemination. Map illustrating the degree of separation between Largemouth Bass origin countries and destination countries based on historical data prior to 1988.

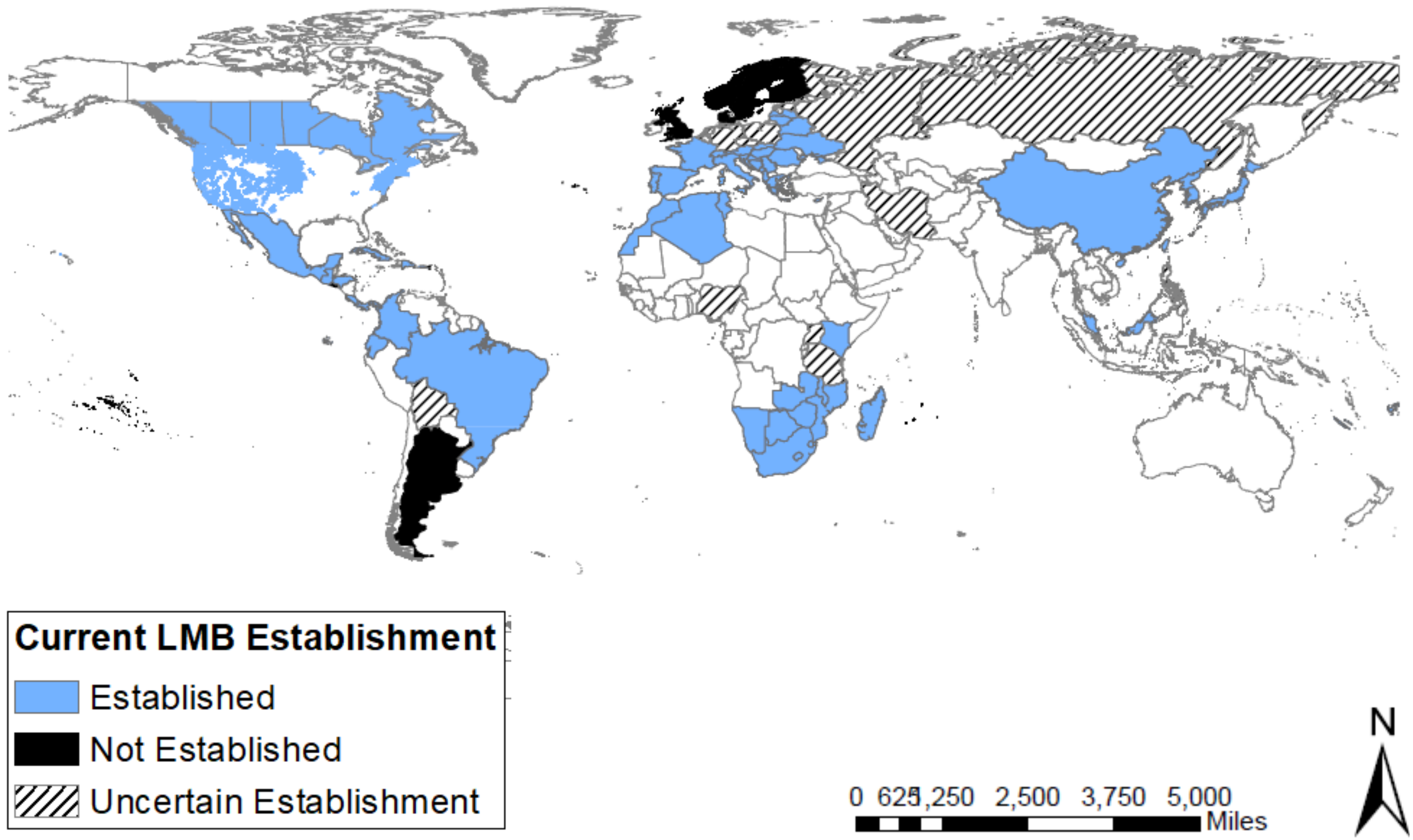

Figure 1.4. Current Largemouth Bass (*Micropterus salmoides*) establishment based on sources through 2019. Largemouth Bass is currently established in 54 countries and 7 territories. An additional 10 regions have an uncertain establishment due to conflicting documentation.

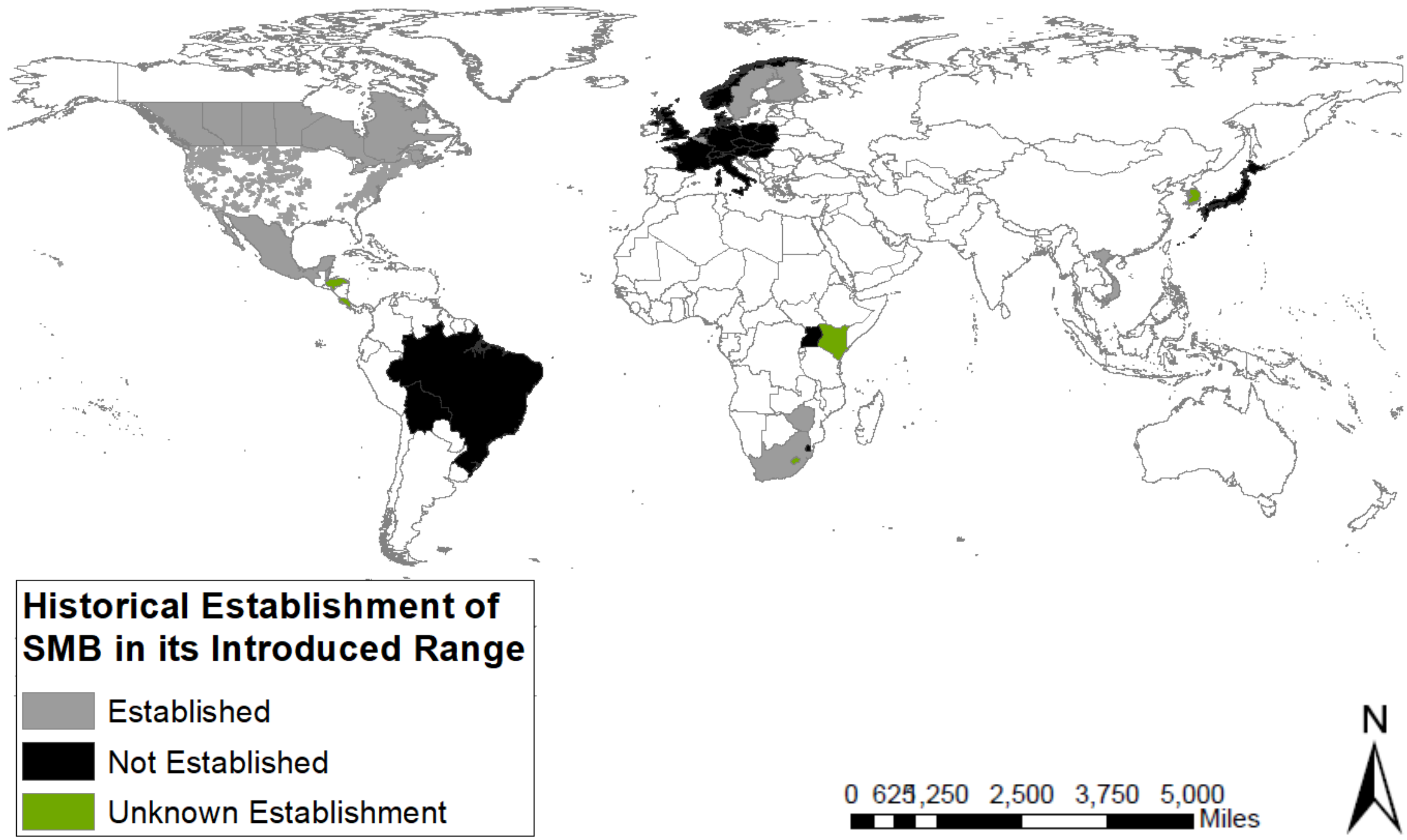

Figure 1.5. Historical introduction and establishment of Smallmouth Bass (*Micropterus dolomieu*; SMB*)* beginning in the early 1800s and continuing through 1945. Map based on data prior to 1988. Established indicates successfully introduced populations, not established indicates failed introductions, and unknown establishment indicates that SMB was introduced but it was unknown historically if they became established.

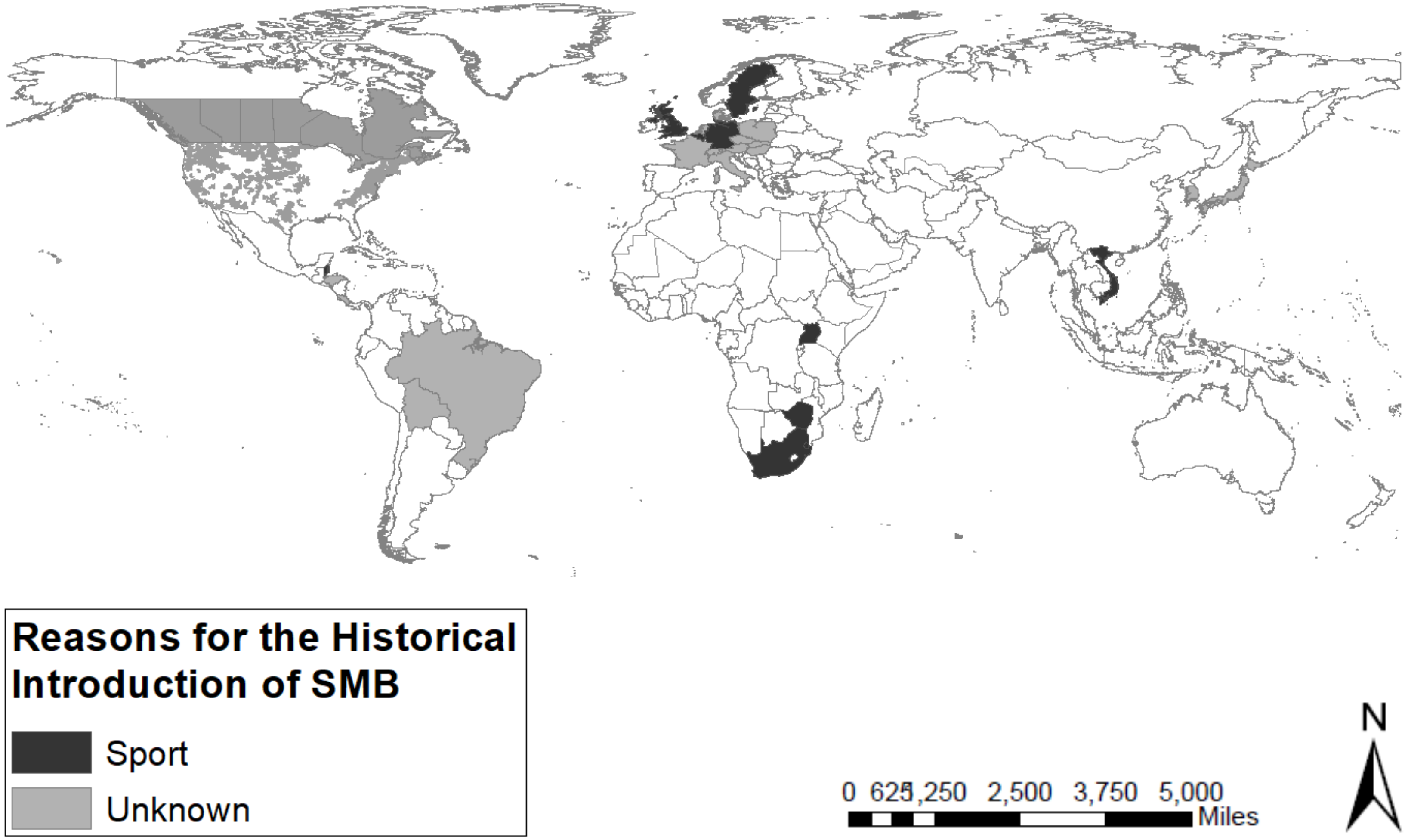

Figure 1.6. Reasons for the historical introduction of Smallmouth Bass (*Micropterus dolomieu)*. Map based on data prior to 1988. Smallmouth Bass was introduced for sport in 13 regions and for unknown reasons in 19 regions.

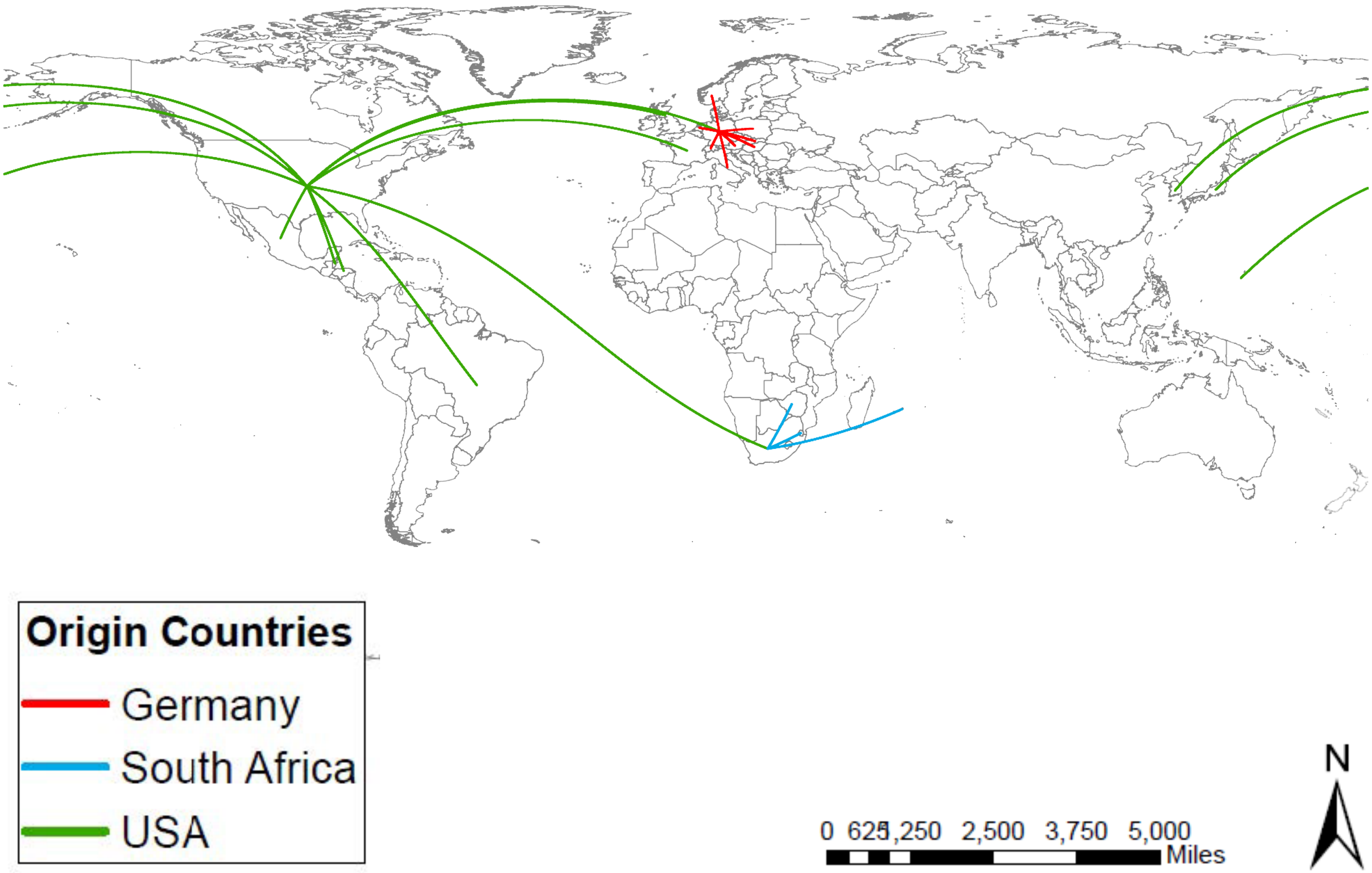

Figure 1.7. Smallmouth Bass (*Micropterus dolomieu)* dissemination. Map illustrating the degree of separation between Smallmouth Bass origin countries and destination countries based on historical data prior to 1988.

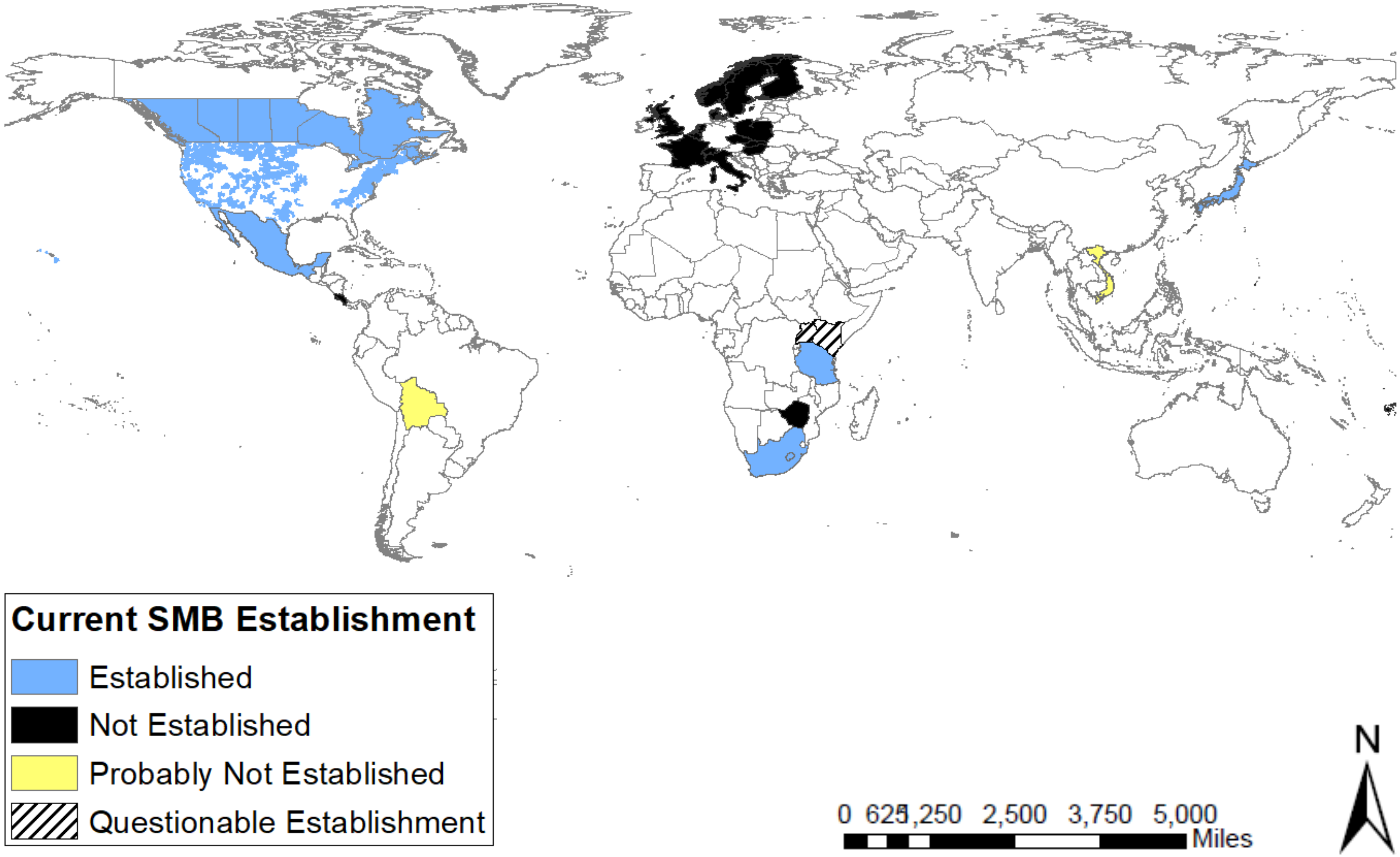

Figure 1.8. Current establishment of Smallmouth Bass (*Micropterus dolomieu)* based on sources through 2019. Smallmouth Bass is established in 8 countries, while 2 countries have questionable establishment due to possible diffusion through connected water bodies and 2 regions are probably not established due to incomplete field sampling.

CHAPTER II

ASSESSMENT OF NON-NATIVE BLACK BASS IMPACTS ACROSS THE UNITED STATES: ECOLOGICAL THREATS VERSUS ECONOMIC BENEFITS

Introduction

Freshwater fisheries management and conservation in the United States are governed by the North American Model of Conservation (NA Model). This doctrine affirms that wildlife is a common resource held in public trust primarily by state natural resource agencies (Geist et al. 2001). With its roots stemming from the 19th century when wildlife was scarce and being over-harvested commercially, sometimes to extinction (e.g., Passenger Pigeon *Ectopistes migratorius*), the NA Model put sportsmen as the foundational unit through influential leadership in the interests, values, and preservation of wildlife resources (Geist et al. 2001). The paradigm created under the NA Model still remains at the core of contemporary natural resource management, in that hunters and anglers fund wildlife conservation for the species they utilize.

Under the NA Model, funding for freshwater fish conservation is mainly comprised of revenue generated from fishing licenses (Jacobson et al. 2010). In addition, the Sport Fish Restoration Act administers excise taxes on fishing and boating equipment, which then is distributed to states based partly on license sales. This sets up a user-pay/user-benefit funding model where anglers who exploit fisheries then pay to preserve them. State wildlife agencies are, therefore, financially dependent on anglers as a key stakeholder group since revenue from fishing licenses support agency programs. For example, in 2018, fishing license sales generated over $724 million while the Sport Fish Restoration Act contributed over $351 million to state fisheries programs (U.S. Fish and Wildlife Service [USFWS] 2018a, 2018b). Justifiably, states seek to accommodate angler interests to secure angler recruitment and retention for financial security (Jacobson et al. 2010). Accordingly, one role of state wildlife agencies is to stock game fish species to restore population levels suitable for recreational exploitation while regulating the amount of take. Thus, the NA Model influences how game species are managed and perceived in the U.S since they are a valuable commodity to state fishery agencies. Perhaps the most emblematic group for the NA Model related to fisheries management are black bass (Centrarchidae, *Micropterus*), a piscivorous group of freshwater fishes.

Black bass have long been the most sought-after species group for fishing (Long et al. 2015) and its history has helped shape the NA Model. Historical exploitation of black bass included commercial fishing that forced this species down the path of extinction (U.S. House of Representatives 1925; U.S. Senate 1926). Anglers responded to these diminishing fisheries by forming sportsmen's organizations, such as the Izaak Walton League, to advocate for black bass protection. In turn, these angler groups became powerful proponents for the preservation of recreational fisheries by working with government representatives and state fish commissioners (Long et al. 2015) to pass conservation legislation at state and federal levels (Geist et al. 2001). Beginning with the Black Bass Act of 1926, which sought to curb illegal interstate commerce of fish, black bass transitioned from being a commercial fish to being a recreational game fish (Long et al. 2015). In 1968, the Bass Anglers Sportsman Society (B.A.S.S.) formed exclusively to develop angler interest and involvement into black bass fishing. Thus, anglers took a central role in the stewardship of freshwater fish by ensuring their sustainability for future generations to enjoy.

Reservoir construction across the United States in the 1930s-1970s created habitats and opportunities for fishing and stocking (Graf 1999), which coincided with the growing conservation movement to rebound black bass population declines. Efforts to recover black bass and expand fishing opportunities thus concentrated on building hatcheries to stock these impoundments with black bass, notably Largemouth Bass *Micropterus salmoides* (Long et al. 2015). By 1965, impoundments sustained 25% of freshwater recreational angling and became very important in supporting high quality black bass fisheries (Jenkins 1970). As a result, black bass gained lentic habitats across the country, which increased their range and ensured their population growth and stability.

The two most stocked species of black bass are Largemouth Bass (LMB) and Smallmouth Bass *Micropterus dolomieu* (SMB). The native range of these two species is within central and eastern North America, extending east of the Great Plains in the U.S., to the southeast of Canada, and the extreme northeast of Mexico (Scott and Crossman 1973; MacCrimmon and Robbins 1975; Jenkins and Burkhead 1994). However, humans have extensively transported black bass well outside their native range to satisfy recreational fishing demand (Robbins and MacCrimmon 1974; Welcomme 1988). Largemouth Bass, for example, have native ranges in 28 states within the U.S., and now are present in all 50 states (Robbins and MacCrimmon 1974; Alaska Department of Fish and Game 2018). Similarly, SMB have native ranges in 23 states within the U.S., and now have established populations in 47 states (Robbins and MacCrimmon 1974; Fuller et al. 2019).

With its distribution rapidly expanding in the U.S. and worldwide, the popularity of black bass quickly increased among recreational anglers. Ever since records have been kept, black bass have ranked as the most popular recreational freshwater fish in the U.S. (USFWS and U.S. Census Bureau 1991, 1996, 2001, 2006, 2011, 2016), making black bass anglers the predominant angling group nationwide. Due to their far-reaching non-native range, LMB and SMB are emblematic of the unintended consequences of stocking fish.

As top-level predators and highly competitive species, black bass alter predator-prey dynamics, reduce native species richness, modify nutrient cycling, and alter habitat structure in their introduced range (Jackson 2002; Loppnow et al. 2013). Ultimately, aquatic communities can become more homogenous when non-native black bass are present (Jackson 2002). Due to these attributes, LMB are regarded as one of the "100 World's Worst Invasive Alien Species", which is considered as a representative for the *Micropterus* genus, for their role in global biodiversity loss (Global Invasive Species Database 2018).

Non-native black bass can pose serious ecological harm to native biota in their introduced range. For example, in the United States, non-native LMB are considered to have negative ecological effects in California, Arizona, Nevada, and Virginia by reducing endemic species populations through direct predation (e.g. Owens Pupfish *Cyprinodon radiosus* (Miller and Pister 1971)), and SMB have extirpated numerous small prey fish in their introduced range including: Brook Stickleback *Culaea inconstans*, Fathead Minnow *Pimephales promelas*, Pearl Dace *Margariscus margarita*, Finescale Dace *Phoxinus neogaeus*, and Northern Redbelly Dace *Phoxinus eos* (Fuller et al. 1999; Loppnow et al. 2013).

Thus, non-native black bass regulated for recreational sport fishing create an enigma of competing impacts since the economic incentives and the potential ecological damages are fundamentally conflicting forces. Despite this, we continue to struggle to decide between conserving biodiversity and relying upon income derived from non-native species. Since these impacts are intrinsically different, non-native black bass create a conundrum of social values with a tendency to evade consistent policies across its introduced range. However, in some instances, managers have come to view the negative ecological effects more significantly than the economic benefits, and have sought to remove non-native black bass (e.g., SMB and Spotted Bass *Micropterus punctulatus* eradication in South Africa (Weyl et al. 2013; van der Walt et al. 2019)). How widespread this perception is in the U.S. though, is unknown.

My study seeks to assess how non-native black bass are currently viewed ecologically and economically in their environment by the agencies in charge of their management. Under the NA Model, state fisheries biologists are the trustees of our fisheries resources making their opinion on non-native black bass crucial to understanding how they are being managed. Thus, a survey of fisheries biologists was conducted to gain insights into their perspectives. Specifically, the objectives of this survey were twofold: (1) determine how fisheries managers perceive non-native black bass across the contiguous U.S., and (2) examine whether habitat plays a role in determining their status as harmful or beneficial. I was also interested in which management tools are currently used with non-native black bass to provide further support for my findings. To the best of my knowledge, this is the first broad scale study to understand the views that fisheries managers have on non-native black bass. By taking the initial step to quantify how managers are balancing these conflicting impacts, an important conversation can be sparked about the paradox of non-native black bass.

Methods

I administered an online survey (Appendix A) of fisheries biologists in the contiguous U.S. to assess the current state of management surrounding non-native black bass between two discrete habitat types: anthropogenic and natural water bodies. This survey was conducted via SurveyMonkey© and was available for a one-month period during July - August 2018. The survey frame was acquired by asking state fisheries chiefs for personnel who were most experienced in black bass management at a supervisory level. Respondent's survey answers corresponded to a single watershed (second level Hydrologic Unit Code [HUC]) where the majority of their non-native black bass management occurred. This HUC classification level contains 221 unique drainage sub-regions, which allowed responses to be spatially delineated. The format of the survey was then divided into two identical sections, natural and anthropogenic water bodies, containing mirrored questionnaires. Natural waters were defined as natural lakes, rivers or streams, while anthropogenic waters included reservoirs and impoundments.

A total of 16 species of black bass were represented in my survey as options for respondents: Alabama Bass *M. henshalli*, Altamaha Bass *M. sp. cf. cataractae*, Bartram's Bass *M. sp. cf. coosae*, Cahaba Bass *M. cahabae*, Chattahoochee Bass *M. chattahoochee*, Choctaw Bass *M. sp. cf. punctulatus*, Florida Bass *M. floridanus*, Guadalupe Bass *M. treculi*, Largemouth Bass, Redeye Bass *M. coosae*, Shoal Bass *M. cataractae*, Smallmouth Bass, Spotted Bass, Suwanee Bass *M. notius*, Tallapoosa Bass *M. tallapoosae*, and Warrior Bass *M. warriorensis*. Respondents were first asked to check all species of non-native black bass that were present within their specified watershed. For the subsequent parts of the survey, respondents answered each section based on a single species of non-native black bass that received the most management attention within either natural or anthropogenic waters.

First, respondents were asked for their perspective on the impact that the non-native black bass species had both economically and ecologically within their primary watershed, using a five-point scale ranging from "causes severe harm" to "of central importance". Questions assessing management tools used with non-native black bass were based on a five-point level of priority scale ranging from "not a priority" to "essential". Management tools assessed within the survey were chosen for their ability to represent both control and continued stability of non-native black bass populations. The twelve management tools included were: creel limits, length limits, catch and release, catch and kill, stocking native black bass, stocking non-native black bass, mechanical or chemical removal, black bass monitoring, black bass habitat alterations, forage stocking, tournament attraction, and angler education. Finally, respondents were asked to evaluate the current population level of their specified non-native black bass species per survey section.

All data were analyzed using statistical software package SPSS (IBM, Version 24). Chi-squared independence tests were run to determine the relationship between habitat (anthropogenic and natural) and impact variables (economic benefits and ecological impact), and Cramer's V was used to measure the strength of association between these variables. Results on management tool applications were analyzed using basic summary statistics. Using ArcGIS (Esri, version 10.5.1), maps were created to visualize the spatial extent of perceived economic and ecological impacts across the contiguous U.S. When watersheds received responses from more than one respondent, results were averaged.

Results

A total of 122 fisheries biologists from 33 states responded to this survey (Figure 1). Representatives from an additional 7 states opted-out of the survey, reporting that they did not have non-native black bass within their state: Alabama, Indiana, Illinois, Michigan, New York, Ohio, and Wisconsin. Thus, the overall response rate for my survey was 72%. The number of responses per state ranged from 1 to 9 with the average being 3.5. Data from 81 unique sub-region watersheds (second level HUC) were received with multiple responses occurring for several of these watersheds (29 repeated watershed responses in anthropogenic habitats and 19 repeated watershed responses in natural habitats). At a broader spatial scale, all of the 18 major geographic watershed regions across the contiguous U.S. were represented by respondents except for the Tennessee (HUC 06) watershed.

Of the 16 species of black bass represented in my survey, respondents reported that only 6 species of non-native bass received the most management attention: Largemouth Bass (LMB), Smallmouth Bass (SMB), Florida Bass (FLB), Alabama Bass (ALB), Spotted Bass (SPB), and Redeye Bass (REB). Furthermore, respondents indicated that only 7 black bass species had introduced ranges into watersheds beyond their native distribution (Table 1). The percentage of respondents reporting which non-native black bass was present within their designated watershed were: SMB (65%), LMB (59%), FLB (28%), SPB (19%), ALB (5%), REB (2%), and Shoal Bass (1%).

Natural Habitats

In natural habitats, 68 responses (56% of respondents) were received from fisheries biologists who managed these waters. Of the 49 unique watersheds represented within natural habitats, 11 watersheds received more than 1 response. There was little variation within these extra responses due to economic impact, as respondents largely agreed that non-native black bass were beneficial in natural habitats. In terms of variation due to ecological impact, the majority of respondents differed only slightly between degree of positive impact or between neutral to beneficial impact. The non-native black bass species that received management attention in natural waters were: SMB (52% of responses), LMB (31% of responses), FLB (10% of responses), SPB (4% of responses), ALB (1% of responses), and REB (1% of responses).

When describing ecological impacts in natural habitats, 27% of respondents indicated that non-native black bass “causes some harm”, while 6% of respondents chose “causes severe harm” (Figure 2). However, 29% of respondents also classified the ecological impact of non-native black bass as either “of central importance” or “causes some benefits", while 37% of respondents chose a "neutral" effect. In terms of species, SMB was perceived to be the most ecologically harmful non-native black bass followed by LMB, SPB, and ALB (Figure 3a). Conversely, LMB was found to have the most perceived ecological benefits followed by SMB and FLB.

Regarding economic benefits in natural habitats, the majority of respondents (81%) indicated that non-native black bass had a positive economic impact, choosing either "of central importance" or "causes some benefit" (Figure 4). However, 18% of respondents indicated that non-native black bass had a "neutral" effect, and 1 respondent indicated that they "caused some harm" in natural habitats. In terms of species, SMB was found to be the most economically beneficial non-native black bass followed by LMB, FLB, and RED (Figure 3b). Smallmouth Bass was the only species to have perceived negative economic impacts. In natural waters, non-native SMB was highlighted as having conflicting impacts within its introduced watershed by having, simultaneously, ecologically harmful and economically beneficial impacts.

Management tool use varied immensely across natural waters (Table 2). In general, black bass monitoring, creel limits, angler education, and length limits received higher priority levels. Efforts to control non-native black bass using "catch and kill" or "mechanical or chemical removal" were largely "not applicable" to most respondents, but were deemed "essential" and "high priorities" for a few respondents (5 and 3 respondents respectively). The watersheds where these control efforts were used include: Maine Coastal (HUC 0105) in Maine, Kanawha (HUC 0505) in West Virginia, Lower Mississippi-Hatchie (HUC 0801) in Arkansas, Colorado Headwaters (HUC 1401) in Colorado, Lower Green (HUC 1406) in Utah, and Lower Snake (HUC 1706) in Idaho.

Respondents found non-native black bass populations in natural waters to be 68% stable, 19% increasing, 9% decreasing, and 4% unknown.

Anthropogenic Habitats

In anthropogenic habitats, 96 responses (79% of respondents) were received from fisheries biologists who managed these waters. Of the 67 unique watersheds represented within anthropogenic habitats, 19 watersheds received more than 1 response. There was little variation within these extra responses due to economic impact, as respondents largely agreed that non-native black bass were beneficial. In terms of variation due to ecological impact, the majority of respondents differed only slightly between degree of positive impact or between neutral to beneficial impact. However, 5 watersheds received differences of opinion between respondents that varied from negative to neutral or negative to beneficial ecological impact including: Lower Chesapeake (HUC 0208), Rainy (HUC 0903), Lower Arkansas (HUC 1111), Red-Sulphur (HUC 1114), and Great Salt Lake (HUC 1602). The non-native black bass species that received the most management attention in anthropogenic waters were: LMB (52% of responses), FLB (28% of responses), SMB (15% of responses), ALB (3% of responses), and SPB (2% of responses).

Although some negative ecological impacts were present in anthropogenic habitats, this occurrence was less pronounced and drastically different from the impact perceived in natural waters. In anthropogenic habitats, 12% of respondents indicated non-native black bass "causes some harm", while no respondents chose "causes severe harm" (Figure 2). Non-native black bass had positive ecological impacts in anthropogenic waters with 57% of respondents indicating either "causes some benefits" or "of central importance", while 31% of respondents indicated a "neutral" effect. Largemouth Bass had the greatest number of perceived ecological benefits followed by FLB, SMB, and SPB (Figure 5a). Alabama Bass showed the most negative perceived ecological impacts in anthropogenic waters followed by LMB and SMB.

Non-native black bass in anthropogenic waters had an extremely positive economic impact with 91% of respondents indicating that they were either "of central importance" or "causes some benefit", while 9% of respondents indicated that they had a "neutral" effect (Figure 4). In terms of species, LMB had the greatest positive economic impact followed by FLB, SMB, ALB, and SPB (Figure 5b). It is noteworthy that non-native black bass did not cause any perceived economic harm in anthropogenic habitats. Overall, non-native black bass had few perceived negative ecological or economic impacts, but exhibited considerable beneficial impacts both ecologically and economically.

Management techniques varied across anthropogenic waters (Table 2). In general, black bass monitoring, creel limits, length limits, habitat alterations, tournament attraction, and angler education received higher priority levels. Efforts to control non-native black bass in anthropogenic waters using "catch and kill" or "mechanical or chemical removal" were largely "not applicable" for the majority of respondents, but were found to be a "high priority" for 7 and 1 respondents respectively. The watersheds where these control efforts were used include: Maine Coastal (HUC 0105) in Maine, Lower Chesapeake (HUC 0208) in Virginia, Pascagoula (HUC 0317) in Mississippi, Kanawha (HUC 0505) in West Virginia, San Juan (HUC 1408) in Colorado, Bear (HUC 1601) in Idaho, and Great Salt Lake (HUC1602) in Utah. Stocking non-native black bass in anthropogenic waters was a “high priority” for 25% of respondents, and “essential” for 12% of respondents. Respondents found non-native black bass populations in anthropogenic waters to be: 70% stable, 17% increasing, 8% decreasing, and 5% unknown.

Ecological Impacts and Economic Benefits

Habitat and averaged ecological impact were found to have a significant relationship ($\chi^2 = 21.201$, df = 4, $p < 0.01$) and were moderately associated (Cramer’s V = 0.429). My results indicate that negative ecological impacts were more abundant and more severe in natural than anthropogenic waters (Figure 6). In terms of species, ALB, LMB, SMB, and SPB caused the most ecological imperilment across both natural and anthropogenic habitats (Figure 7).

A significant relationship was found between habitat and averaged economic impact ($\chi^2 = 8.556$, df = 3, $p = 0.04$). Habitat and average economic impact were also low to moderately associated supporting my result (Cramer’s V = 0.272). My results found that black bass were considered economically beneficial in both anthropogenic and natural waters despite some perceived negative ecological impacts (Figure 8). However, economic benefits were more abundant and more positive in anthropogenic than natural habitats. In terms of species, FLB, LMB, and SMB provided the most economic benefits across both natural and anthropogenic habitats (Figure 9).

Discussion

My study highlights the conflicting impacts of non-native black bass, which can bring both economic benefits and ecological imperilments to their introduced range. Non-native black bass were generally viewed as an economic advantage regardless of habitat type. Thus, economic benefits did not appear to be tied to either natural or anthropogenic water bodies, but were inherent where black bass are present.

Since non-native black bass are an economic asset to fishery managers, conservation of these species becomes a priority under the NA Model. For example, my survey showed that non-native Florida bass was economically important to Texas in both natural and artificial habitats. At Lake Fork, TX, an anthropogenic water body, which contains both LMB and FLB, anglers spent over $27 million to experience a trophy LMB fishery (Chen et al. 2003). Further, stocking of non-native FLB into the indigenous range of LMB was often done intentionally to alter the genetic composition of LMB to create faster growing, trophy sized FLB/LMB hybrids (Chew 1975; Lamothe et al. 2012).

Other studies have found similar results that support the economic benefits of black bass. For example, in 2016, there were 9.6 million black bass anglers fishing over 117 million days making these anglers the primary group in both fish preference type and participation (USFWS and U.S. Census Bureau 2016). Moreover, Long and Melstrom (2016) found that black bass anglers contribute more to the economic value of recreational fishing compared to other angler groups through high participation, high spending on trips and equipment, and an increased rate of fishing trips taken. This implies that black bass anglers are disproportionately contributing more to state economies than other angler groups (Long and Melstrom 2016). With such a high angler preference of black bass, there is considerable effort to stock and manage black bass for angler satisfaction.

Stocked populations of LMB and SMB have economic incentives in terms of sport fishing tournaments, tourism, job creation, economic output, and angler license sales both in the U.S. and abroad. Nationally, freshwater fishing (excluding the Great Lakes) includes 29.5 million anglers participating in 373 million fishing days accounting for $27.5 billion spent annually (USFWS and U.S. Census Bureau 2016). In the U.S., freshwater fishing contributes $41.9 billion to the economy and sustains over 525,000 jobs annually (Southwick Associates 2018). Furthermore, with over 41,000 black bass fishing tournaments held annually in the U.S. (Driscoll et al. 2012), tournaments have added a significant source of economic value to communities. For example, at Sam Rayburn Reservoir in Texas, 66% of the total economic value of the fishery ($46.7 million) was due to black bass tournament angling (Driscoll and Meyers 2014). Moreover, in Lake Fork, Texas, 92% of over $15.5 million in fishing expenditures was due to the attraction of tourists who spent more money to experience a trophy LMB fishery (Chen et al. 2003).

On the other hand, the impacts of non-native fishes have contributed to economic losses in the United States. Non-native fishes, in aggregate, cause $5.4 billion in annual damages within the U.S. by altering water quality and contributing to extinctions of indigenous fish species (Pimentel et al. 2005). In addition, the costs to eradicate or control non-native fishes can be considerable. For example, in Colorado, non-native Smallmouth Bass threaten four endemic species (Colorado Pikeminnow *Ptychocheilus lucius*, Humpback Chub *Gila cypha*, Razorback Sucker *Xyrauchen texanus*, and Bonytail Chub *Gila elegans*) through direct predation and competition (USFWS 1987; Hawkins and Nesler 1991; Martinez et al. 2014). Current management actions to remove these invasive SMB are extensive, ranging from barriers to sponsoring fishing tournaments to electrofishing, with the goal of restoring the aforementioned endemic fishes (Upper

Colorado River Endangered Fish Recovery Program [UCREFRP] and San Juan River Basin Recovery Implementation Program [SJRBRIP] 2018). Since 1988, over $394 million has been used to fund the Upper Colorado River Endangered Fish Recovery Program, with over $2.5 million per year spent on efforts to control non-native fish, primarily SMB (UCREFRP and SJRBRIP 2018).

This study found that fisheries managers perceived more ecological imperilment from non-native black bass in natural waters compared to anthropogenic waters. Thus, the ecological threats of non-native black bass are skewed towards natural waters, with negative ecological impacts occurring across 20 unique watersheds. While ecological impacts are recognized, non-native black bass generally still resulted in perceived economic benefits in natural waters. For example, my study indicated that SMB caused ecological harm in the Willamette watershed of Oregon, while still producing economic benefits. In the Pacific Northwest, non-native SMB have caused the decline of commercially important native Pacific Salmon *Oncorhynchus* spp., which are now listed under the U.S. Endangered Species Act (Carey et al. 2011). However, in Oregon, 14% of anglers target black bass, which generates over $23 million in economic value (Carey et al. 2011).

Negative ecological impacts were also found in anthropogenic waters, primarily from ALB and SMB. For example, in Lake Norman, NC, after non-native ALB were illegally introduced into the reservoir, several ecological repercussions occurred including reductions in indigenous LMB abundance (Dorsey and Abney 2016). Alabama Bass was able to outcompete LMB for both resources and habitat, which allowed them to become the predominant black bass in this reservoir (Dorsey and Abney 2016).

Furthermore, some respondents differed in opinion concerning relative ecological impact of non-native black bass in anthropogenic environments. Two watersheds are highlighted where respondents reported competing positive and negative ecological impacts of non-native black bass: FLB in the Lower Arkansas (HUC 1111) and LMB in the Lower Chesapeake (HUC 0208). These discrepancies may be due to conflicting management goals, such as producing trophy fisheries and conserving endemic genomes. In instances where non-native black bass have been stocked within the ranges of endemic black basses, the resulting interspecific hybridization between congeners negatively affects the genetic integrity of native black basses (Whitmore 1983; Morizot et al. 1991; Philipp 1991; Koppelman 1994; Noble 2002; Alvarez et al. 2015; Dakin et al. 2015; Bangs et al. 2018). For example, Arkansas Game and Fish Commission set a management goal to change the genetic population structure of native LMB, attempting to have 40% of localized LMB populations integrate non-native FLB alleles into their genome (Lamothe et al. 2012).

My survey reflects the disparity in recognized ecological harm between natural and anthropogenic systems, where natural systems are perceived to endure more consequential negative impacts. This reasoning is supported by how society fundamentally values natural ecosystems and their processes as being higher than that of artificial ones (Angermeier 2000). This disagreement in values contributes to why degradation of natural ecosystems and of indigenous biodiversity is seen as an irreparable loss, and must instead be conserved (Angermeier 2000). Thus, the impact of invasive species in natural ecosystems are regarded more severely, especially when the threats can be far-reaching. For example, the severity of impact caused by non-native black bass in natural ecosystems can range from local extirpations (e.g., Clanwilliam Sawfin *Barbus serra* and Clanwilliam Sandfish *Labeo seeberi* (Marr et al. 2012)) to global extinctions (e.g., Alaotra Grebe *Tachybaptus rufolavatus* (Birdlife International 2016)).

Identifying the environment which non-native black bass inhabit is crucial to understanding the perceived differences in ecological threat. Not only did the expansion of reservoirs allow for artificial lakes to be created where standing water did not previously occur, but a novel set of ecological parameters resulted from their construction (Wetzel 1990). These highly altered environments contrast with natural lakes in respect to sediment loads, nutrient availability, temperature, water level fluctuations, and species diversity (Wetzel 1990). Since anthropogenic waters are young, unstable systems, its biotic community has not become well developed, as opposed to natural waters that have had thousands of years to reach an ecological balance (Noble 1986; Wetzel 1990). Habitat modifications resulting from the dynamic nature of reservoirs largely displaced the native fauna, thus creating concerns of aquatic "biological deserts" (Miranda 1996).

To mitigate low fisheries production in reservoirs, efforts were made to enhance fish populations via stocking throughout the 1930s-40s (Miranda 1996). Initial stocking of reservoirs focused on species that were useful for sport fishing especially piscivorous predators, namely LMB, (Noble 1986; O'Brien 1990) that would fill a vacant niche (Keith 1986). Such stocking practices have now evolved into "bio-manipulation" to provide trophy fish and to maximize yield for anglers (Miranda 1996). Since "nature knows no such organism as a 'reservoir species'" (Noble 1986), the current fauna in anthropogenic systems is a product of our own making, in which no indigenous biological community can be assigned. Thus, stocked populations of non-native black bass are generally not perceived as a threat in anthropogenic environments, and the proliferation of impoundments has allowed non-native species to flourish (Havel et al. 2005).

Reservoirs create the necessary propagule pressure to facilitate invasive species dispersal, and thus can act as stepping-stones for further invasions into connected water bodies (Havel et al. 2005). Due to a history of intensive stocking practices, most non-native black bass populations in reservoirs have self-sustaining populations, which allows for potential rapid invasion upstream (Havel et al. 2005). Recent studies have demonstrated the movement and hybridization between stocked populations of non-native black bass and endemic black basses upstream of reservoirs (e.g., Neosho Smallmouth Bass *M. dolomieu velox* hybridizing with non-native SMB (Taylor et al. 2018) and Shoal Bass hybridizing with non-native ALB (Taylor 2017)). Given that non-native congeners are the current driver of black bass imperilment (Alvarez et al. 2015; Dakin et al. 2015), reservoirs can act to promote the negative ecological impacts of non-native black bass through genetic introgression.

Conclusion

Implications of my survey suggest that challenges remain for managers attempting to balance the conflicting nature of non-native black bass as both a highly valuable sport fish under the NA Model and as a potentially harmful invader. However, my research has taken the important first step in characterizing the ecological and economic impacts of non-native black bass across the U.S and I have established a baseline of these perspectives. From this study, we have a better understanding of both current opinions and differences of opinions concerning these species which can inform management decisions in the future. Due to the paucity of data on this topic, more research must be completed to fully understand how non-native black bass are viewed between natural and anthropogenic habitats, as well as, the reasons behind these perspectives. Perhaps researching this topic on a finer scale will allow respondents to give more detailed responses about these conflicting interactions. For example, populations of non-native black bass that cause ecological harm but may also be of little economic importance could be identified and managed accordingly. In the future, we must strive to find a balance between socio-economic reliance and conservation priorities by better evaluating the level of risk associated with non-native species.

Tables

Table 2.1. Presence of non-native black bass (*Micropterus* spp.) in 2-digit hydrologic unit codes across the contiguous U.S. based on survey responses.

	Non-Native Black Bass Species						
2-digit HUCs	**ALB**	**FLB**	**LMB**	**REB**	**SHB**	**SMB**	**SPB**
New England (01)		x	x			x	
Mid-Atlantic (02)		x	x			x	x
South-Atlantic Gulf (03)	x	x	x		x	x	x
Great Lakes (04)			x			x	
Ohio (05)	x		x	x		x	x
Upper Mississippi (07)			x			x	
Lower Mississippi (08)		x				x	
Souris-Red-Rainy (09)			x			x	
Missouri (10)			x			x	x
Arkansas-White-Red (11)		x	x			x	x
Texas-Gulf (12)		x	x			x	x
Rio Grande (13)		x	x			x	
Upper Colorado (14)			x			x	
Lower Colorado (15)		x	x			x	
Great Basin (16)			x			x	x
Pacific Northwest (17)			x			x	x
California (18)	x	x	x	x		x	x

ALB = Alabama Bass, FLB = Florida Bass, LMB = Largemouth Bass, REB = Redeye Bass, SHB = Shoal Bass, SMB = Smallmouth Bass, SPB = Spotted Bass

Table 2.2. Priority level of management tools used with non-native black bass (*Micropterus* spp.) in natural and anthropogenic habitats based on survey responses. Management tools chosen to reflect both control and continued stability of black bass. All values are percentages of responses.

	Natural Habitats					Anthropogenic Habitats				
Management Tools	**Not a Priority**	**Low Priority**	**Medium Priority**	**High Priority**	**Essential**	**Not a Priority**	**Low Priority**	**Medium Priority**	**High Priority**	**Essential**
Creel Limits	4	21	29	28	15	2	10	27	35	24
Length Limits	12	16	18	29	10	6	13	17	28	24
Catch and Release	16	13	13	24	7	15	18	18	15	10
Catch and Kill	24	10	9	6	2	26	10	7	7	0
Stocking Native Black Bass	28	2	4	6	2	31	6	3	4	2
Stocking Non-Native Black Bass	27	10	18	9	2	23	14	13	25	12
Mechanical or Chemical Removal	43	9	0	2	3	30	13	3	1	0
Black Bass Monitoring	0	13	25	29	31	0	1	23	39	35
Black Bass Habitat Alterations	25	12	21	18	4	9	14	22	33	8
Forage Stocking	32	13	10	6	2	24	22	16	10	3
Tournament Attraction	22	15	28	13	6	13	20	32	20	7
Angler Education	6	12	38	24	13	5	22	32	25	13

Figures

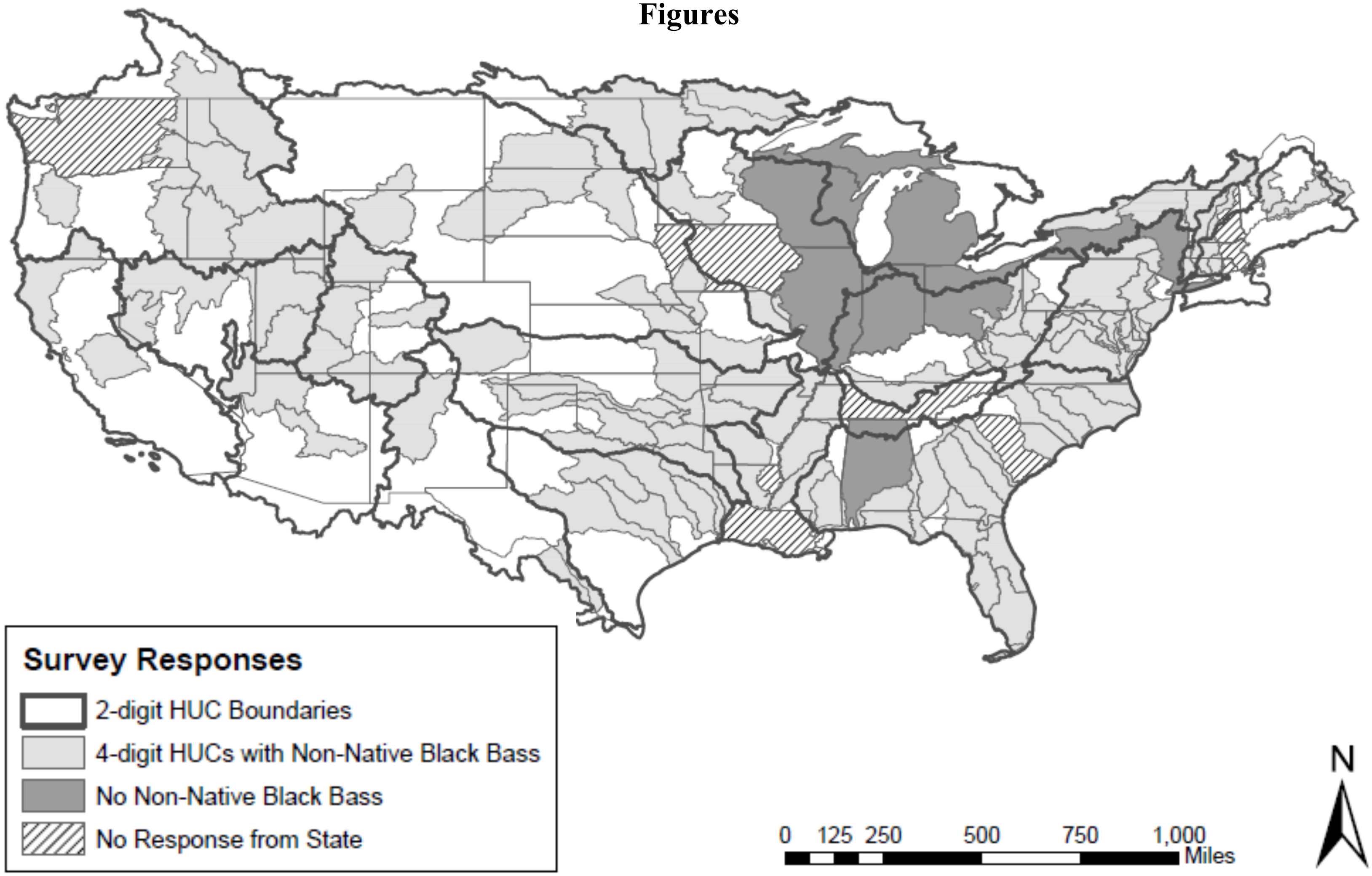

Figure 2.1. Survey response distribution map depicting where survey responses were received based on watersheds (4-digit hydrologic unit codes [HUC]), states who opted-out reporting that non-native black bass populations were not present in their state, and states who never responded to the survey request. White regions represent areas where no responses were received.

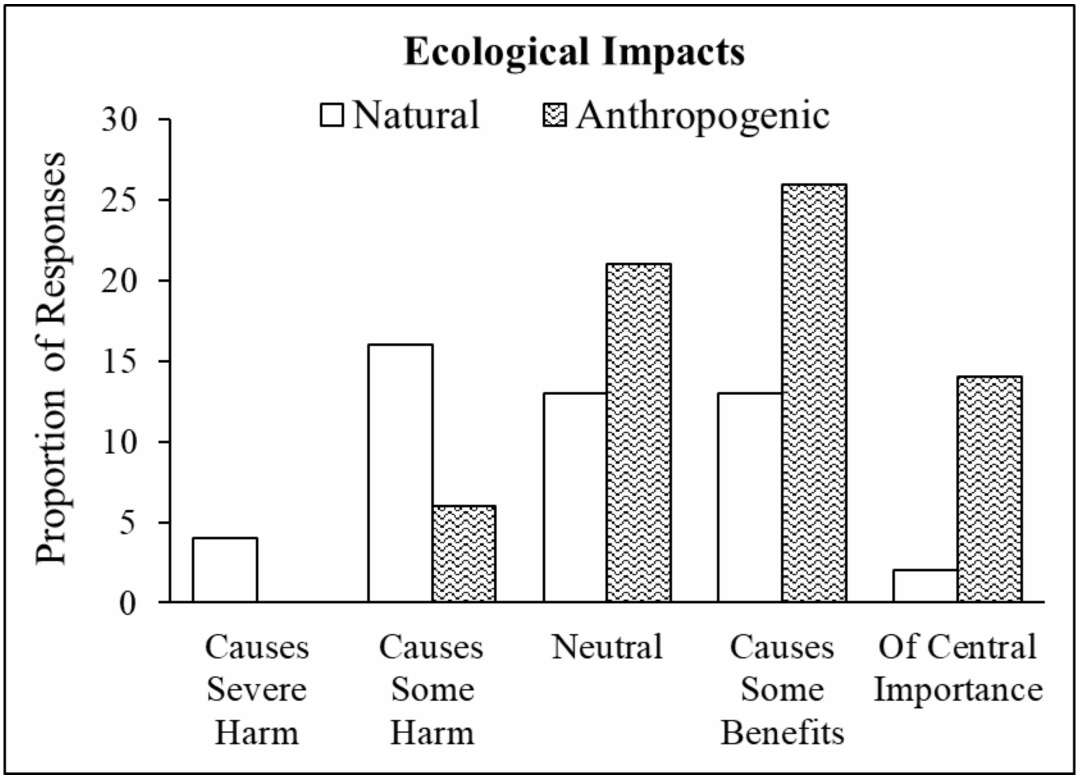

Figure 2.2. Perceived ecological impact of non-native black bass (genus *Micropterus*) in corresponding habitat types based on survey responses. Values represent averaged ecological impact from all black bass species assessed by respondents. A significant relationship was found between habitat type and ecological impact (χ^2 test; $P < 0.01$).

Natural Habitats

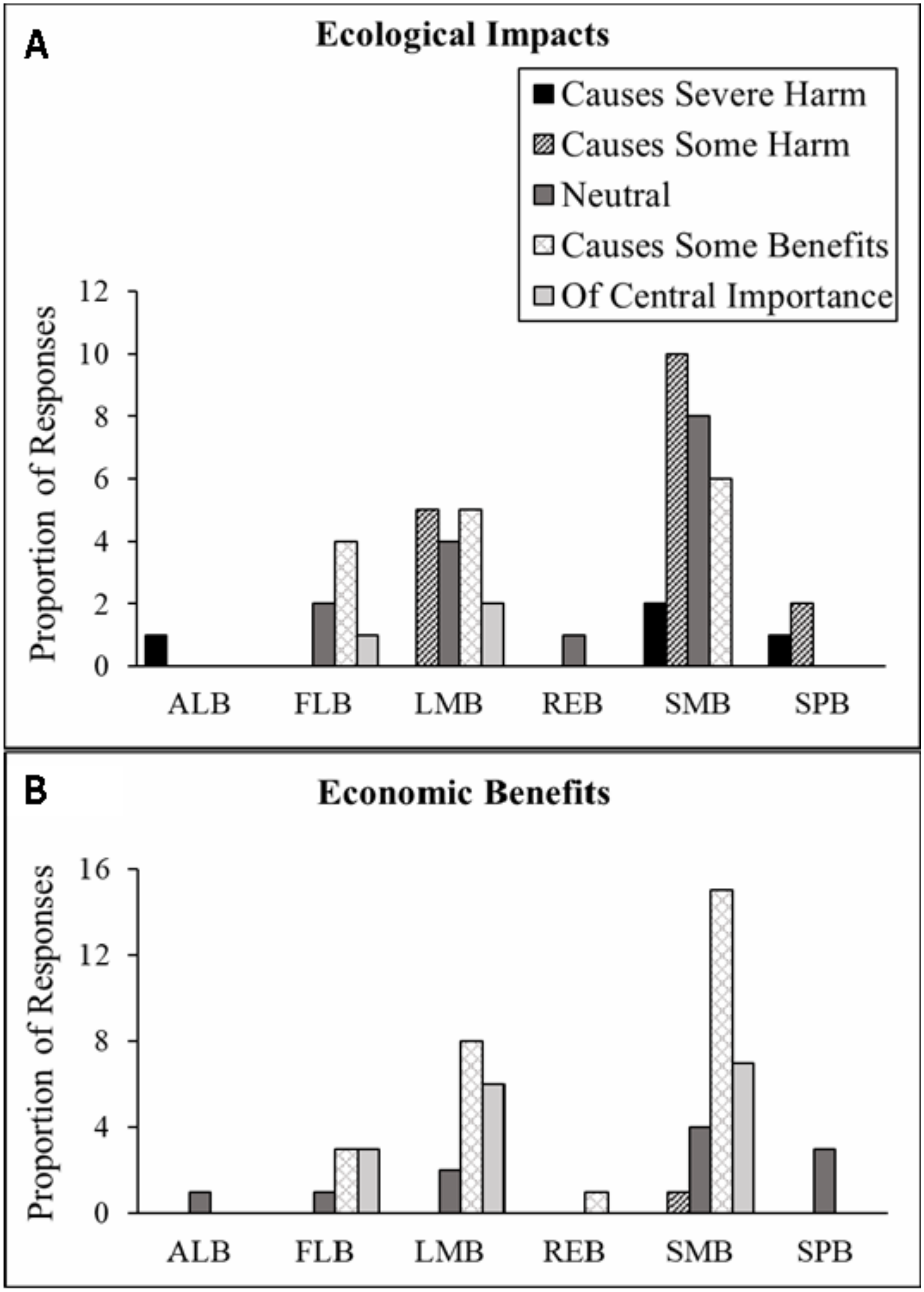

Figure 2.3. **(A)** Perceived ecological impacts and **(B)** perceived economic benefits based on individual non-native black bass species (*Micropterus* spp.) assessed by respondents in natural habitats. ALB = Alabama Bass, FLB = Florida Bass, LMB = Largemouth Bass, REB = Redeye Bass, SMB = Smallmouth Bass, SPB = Spotted Bass.

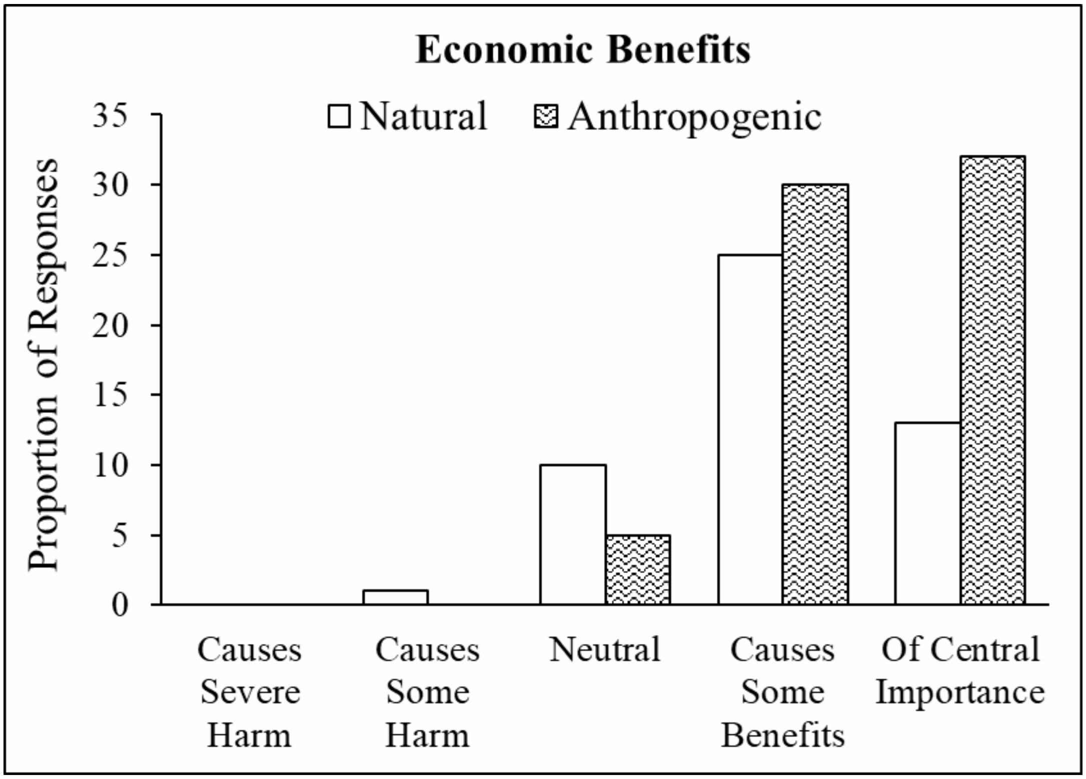

Figure 2.4. Perceived economic impact of non-native black bass (genus *Micropterus*) in corresponding habitat types based on survey responses. Values represent averaged economic impact from all black bass species assessed by respondents. A significant relationship was found between habitat type and economic impact (χ^2 test; $P < 0.04$).

Anthropogenic Habitats

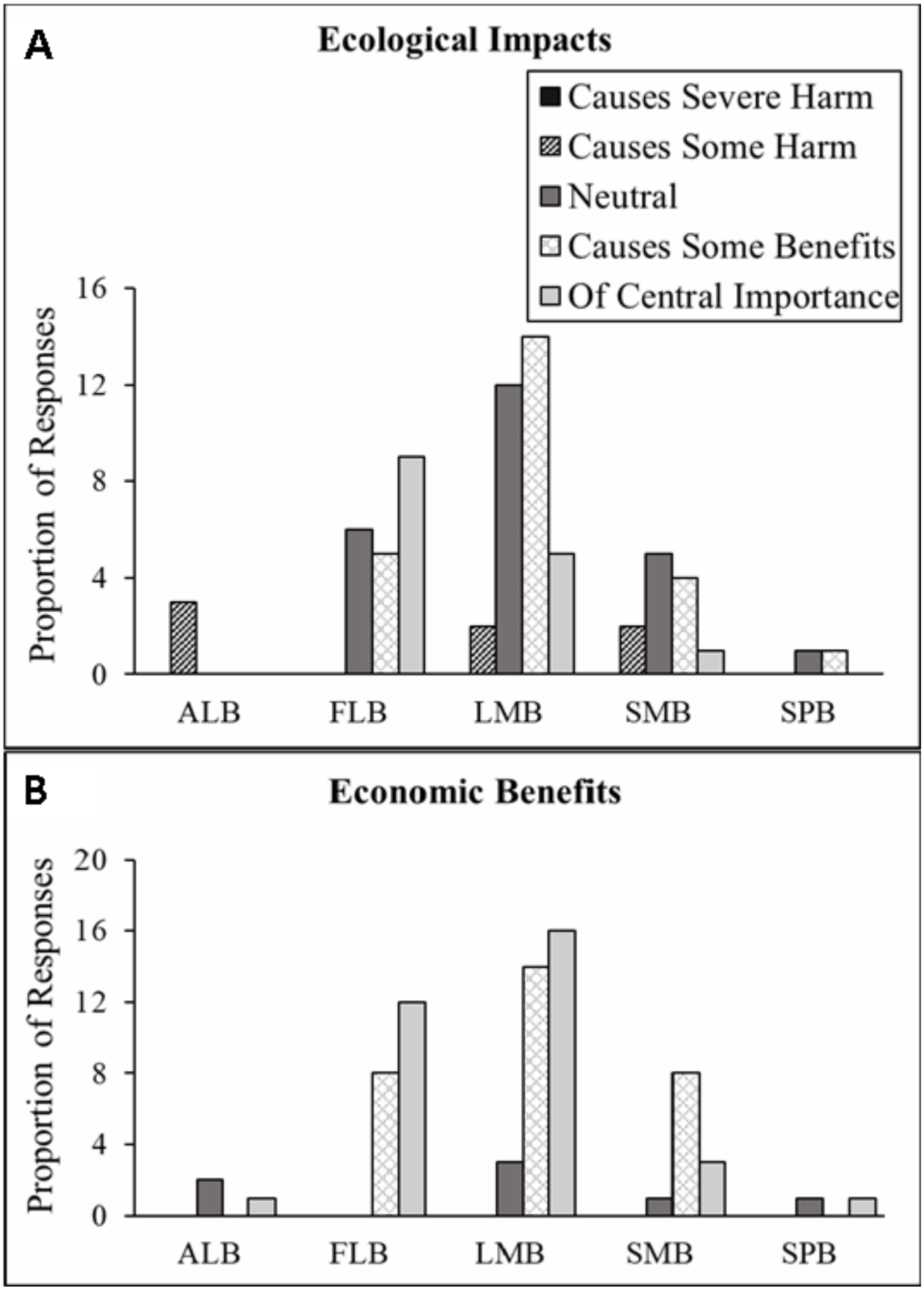

Figure 2.5. **(A)** Perceived ecological impacts and **(B)** perceived economic benefits based on individual non-native black bass species (*Micropterus* spp.) in anthropogenic habitats. ALB = Alabama Bass, FLB = Florida Bass, LMB = Largemouth Bass, SMB = Smallmouth Bass, SPB = Spotted Bass.

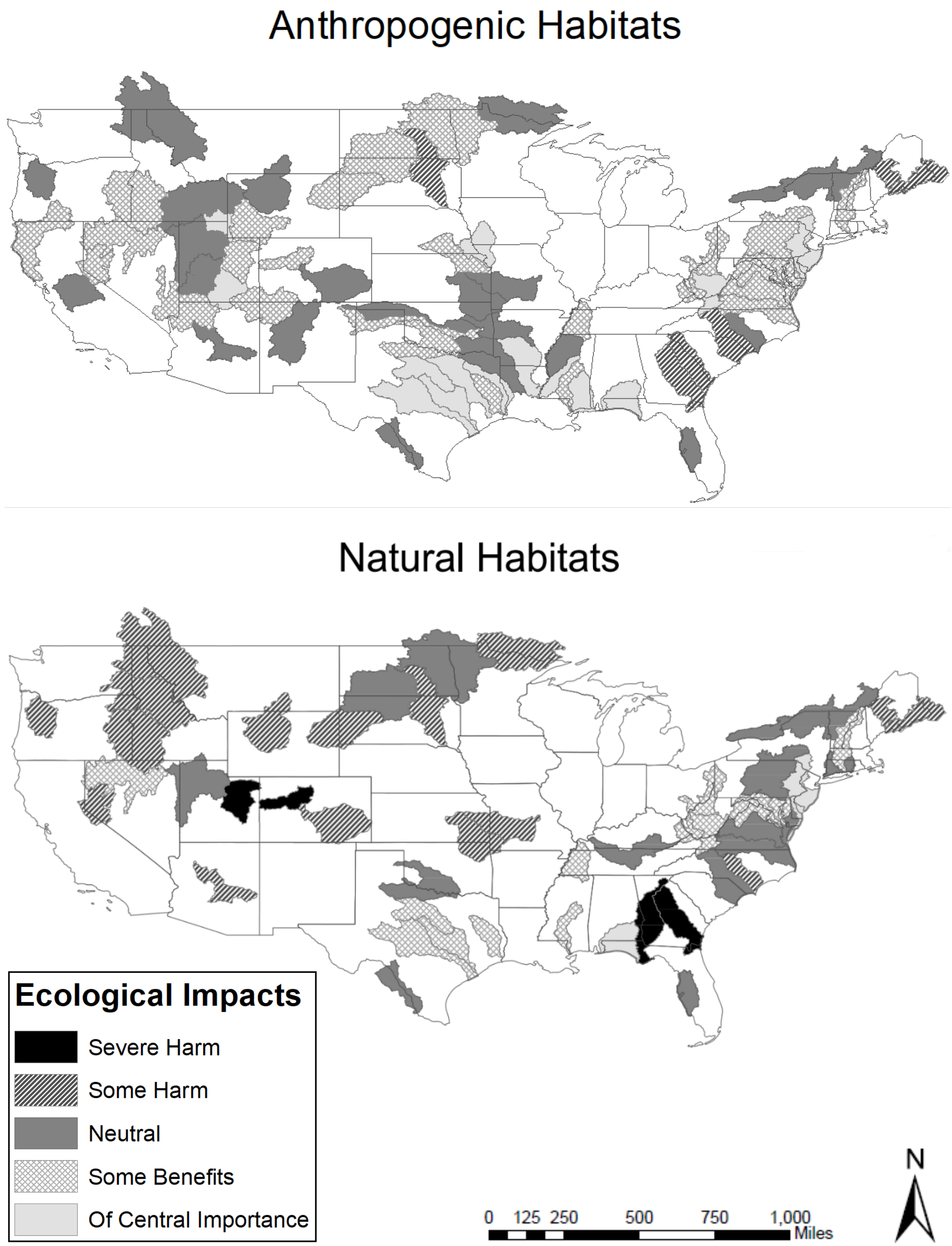

Figure 2.6. Map of **(A)** anthropogenic habitats and **(B)** natural habitats showing averaged perceived ecological impact, classified according to a 5-point scale, per watershed (4-digit hydrologic unit codes) based on all black bass species (genus *Micropterus*) assessed by respondents**.**

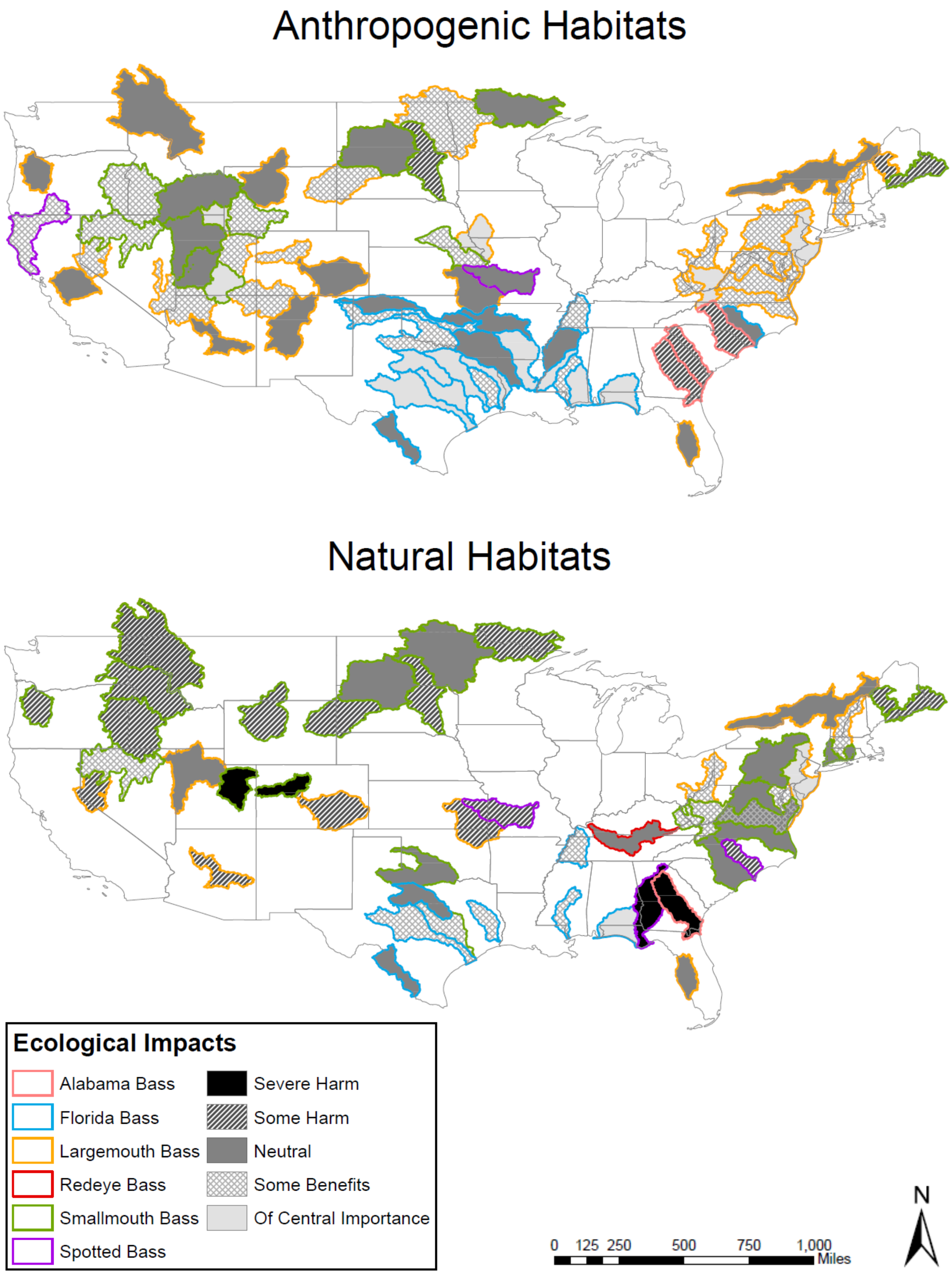

Figure 2.7. Map of **(A)** anthropogenic habitats and **(B)** natural habitats showing specific ecological impacts related to individual black bass species (*Micropterus* spp.) per watershed (4-digit hydrologic unit codes) assessed by respondents. Ecological impacts are classified according to a 5-point scale.

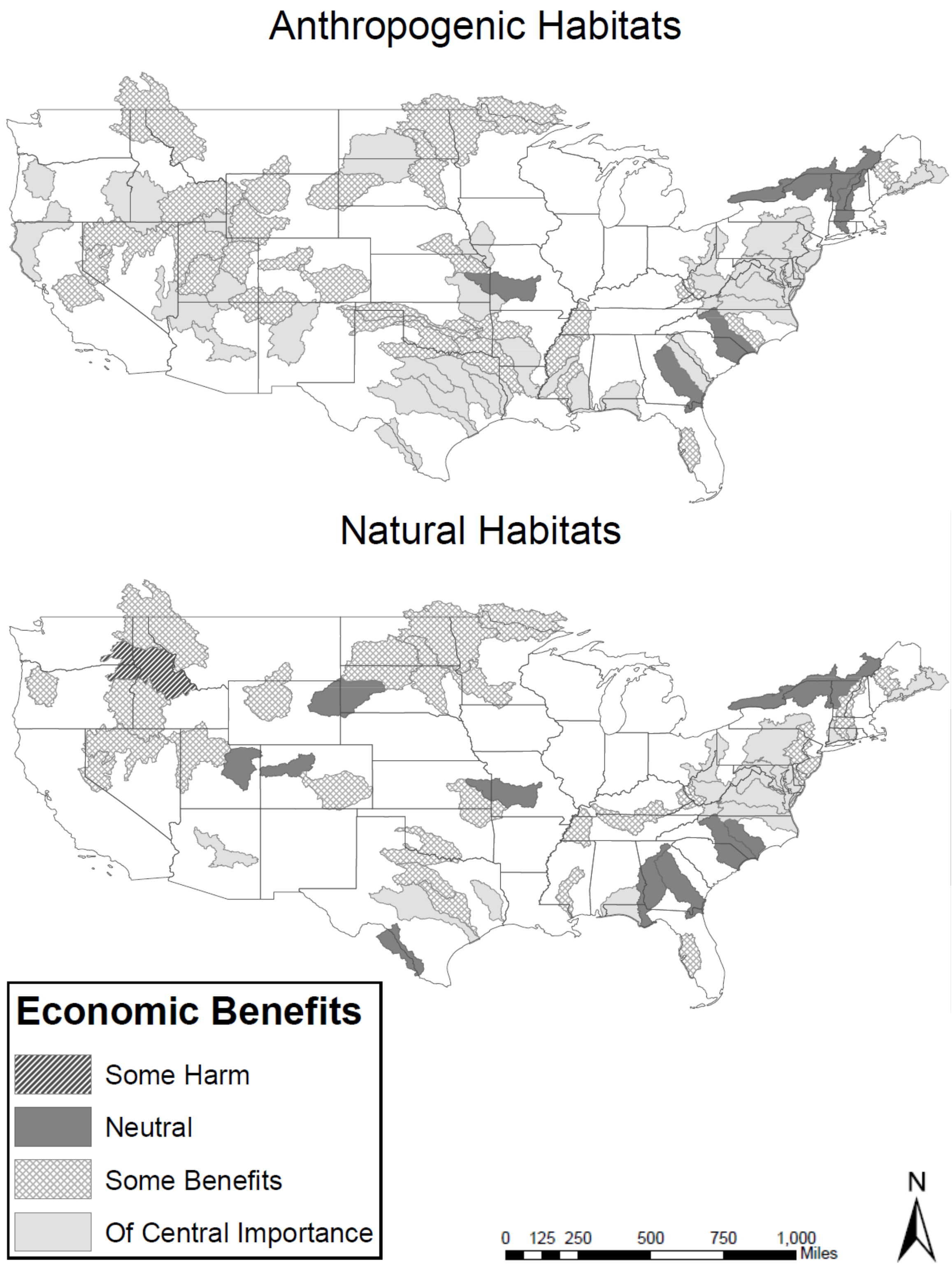

Figure 2.8. Map of **(A)** anthropogenic habitats and **(B)** natural habitats showing averaged perceived economic benefits, classified according to a 5-point scale, per watershed (4-digit hydrologic unit codes) based on all black bass species (genus *Micropterus*) assessed by respondents.

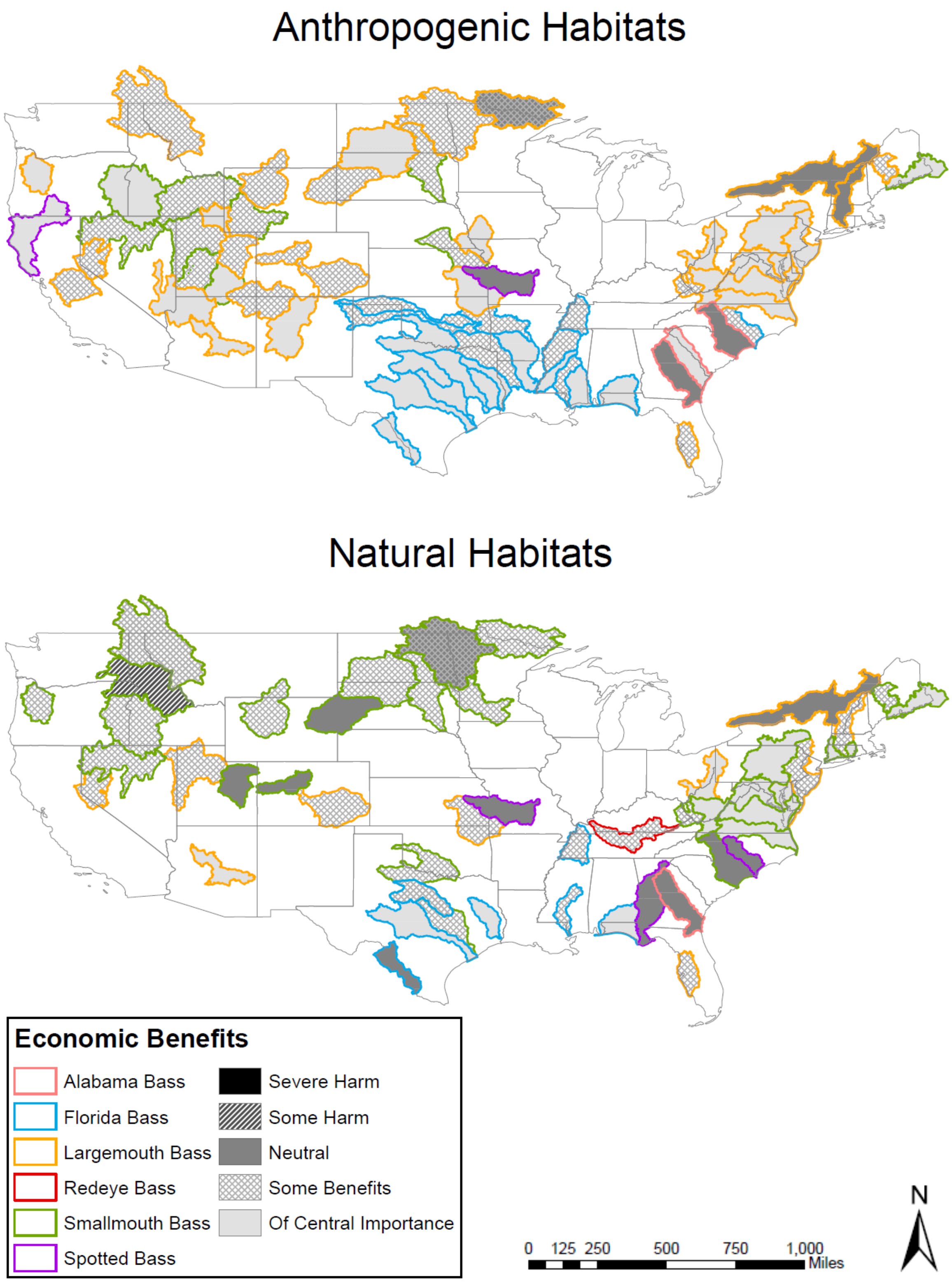

Figure 2.9. Map of **(A)** anthropogenic habitats and **(B)** natural habitats showing specific economic benefits related to individual black bass species (*Micropterus* spp.) per watershed (4-digit hydrologic unit codes) assessed by respondents. Economic benefits are classified according to a 5-point scale.

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APPENDICES

APPENDIX A
NON-NATIVE BLACK BASS MANAGEMENT SURVEY

Participant Information Form

Hello and thank you for taking the time out of your schedule to contribute to my research about non-native black bass management. We are inviting you to be a participant in an online research survey administered by myself, Lauren Seguy, Graduate Student at Oklahoma State University, under the direction of Dr. Jim Long, Research Fisheries Biologist with Oklahoma Cooperative Fish and Wildlife Research Unit. Participation in this survey is entirely voluntary. However, by completing this survey, you are giving consent to the researchers to use your responses. There are no foreseeable risks associated with this project. If you feel uncomfortable answering any questions, you can withdraw from the survey at any point without penalty. There is no compensation and there are no direct benefits to you for completing this survey.

If you agree to participate in this research study, we are asking you to: Complete an online survey that will take **10-15 minutes.** Please respond by **August *23*, 2018.**

Confidentiality: Your responses will be strictly confidential and will remain anonymous in this study. This means that your name or any other identifiers will not be connected to your responses. Further, only aggregated data will be reported. There is minimal risk to participate in this survey beyond that encountered in daily life. Our survey host (SurveyMonkey) uses data encryption to protect your identity and only authorized researchers will have access to the data on password protected computers. For further concerns, please consult the SurveyMonkey privacy policy at https://www.surveymonkey.com/mp/legal/privacy-policy/.

Contact Information and Questions: For questions regarding the research survey itself, please contact Lauren Seguy at (805) 427-5947 or at lseguy@okstate.edu. If you would like more information about your rights as a research participant, please contact the Oklahoma State University Institutional Review Board at (405) 744-3377 or at irb@okstate.edu.
Electronic Consent: By checking the "I Agree" box below, you acknowledge that you have read the Participation Information Form and agree to participate in this survey. If

you do not wish to participate in this survey, please check the "I Do Not Agree" box below and the survey will be terminated.

○ I Agree

○ I Do Not Agree

Non-Native Black Bass Management Survey

Introduction

Throughout the 19th and 20th centuries, non-native largemouth bass and smallmouth bass were introduced outside of their native range by state and federal sponsored programs for the interest of recreational fisheries. During these times, the goal of black bass management depended on maintaining stable, high quality populations for sport fishing. As such, black bass have become the most popular freshwater sport fish in the United States bringing job creation, tourism and economic revenue with it. Now, as greater importance is being placed on black bass diversity, conservation implications for rare, endemic black bass are being examined. To better understand current approaches for regulating non-native black bass in their environment, we are asking you to complete this survey about non-native black bass under your direction.

The attached survey will quantify current management strategies for non-native black bass within their corresponding habitat types. For example, non-native black bass occurring in artificial habitats (e.g. reservoirs) may receive different management strategies than non-native black bass residing in pristine water-bodies (e.g. natural rivers, streams, or lakes). This will bring insight into the current status of non-native black bass within the contiguous United States.

Please note that a species list has been provided to clarify the discrepancies within *Micropterus* genus. Specifically, this study considers Florida bass (*Micropterus floridanus*) its own species and not a subspecies of Largemouth bass (*Micropterus salmoides*) mainly due to genetic divergences. In addition, for the purposes of this survey, ponds are not a water body of interest. In this survey, ponds are defined as having an upper size limit of 5 hectares (~ 12 acres).

Thank you for your time and support.

1) In which state are you currently employed:

Alabama ▼

2) How long have you been employed in your current position?
(Round to the nearest year)

○ 0 - 1 ○ 2 - 5 ○ 6 - 10 ○ 11 - 20 ○ > 20

3) Choose the primary watershed (HUC 4) in which you conduct the majority of **non-native** black bass management activities. If you manage more than one watershed equally, please choose the watershed that focuses more on non-native black bass management.

Middle Tennessee-Elk ▼

4) What **non-native** species of black bass currently occur within your primary watershed? (Check all that apply)

☐ Alabama (M. henshalli) ☐ Altamaha (Micropterus sp. cf. cataractae)

☐ Bartram's (Micropterus sp. cf. coosae) ☐ Cahaba (M. cahabae)

☐ Chattahoochee (M. chattahoochee) ☐ Choctaw (M. haiaka)

☐ Florida (M. floridanus) ☐ Guadalupe (M. treculi) ☐ Largemouth (M. salmoides)

☐ Redeye (M. coosae) ☐ Shoal (M. cataractae) ☐ Smallmouth (M. dolomieu)

☐ Spotted (M. punctulatus) ☐ Suwannee (M. notius) ☐ Tallapoosa (M. tallapoosae)

☐ Warrior (M. warriorensis)

☐ None

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5) Do you manage **non-native** black bass in **NATURAL** water bodies (natural lakes, rivers or streams) within your primary watershed?
Please note that ponds (≤ 5 hectares) are not a water body of interest.

☐ **Yes.** If yes, please answer the remaining questions on this page.

☐ **No.** If no, please click "Next" at the bottom of this page.

6) Of the **non-native** species of black bass that occur in your primary watershed (Question 4), what one species receives the **most** management attention in **NATURAL** water bodies (natural lakes, streams, or rivers)?
(Choose ONE)

☐ Alabama ☐ Altamaha ☐ Bartram's ☐ Cahaba ☐ Chattahoochee ☐ Choctaw

☐ Florida ☐ Guadalupe ☐ Largemouth ☐ Redeye ☐ Shoal ☐ Smallmouth

☐ Spotted ☐ Suwannee ☐ Tallapoosa ☐ Warrior

☐ Not present

7) In **NATURAL** water-bodies (natural lakes, streams, or rivers) of the primary watershed you work in, please rank how this **non-native** black bass species is viewed ecologically and economically based on your professional opinion:

	Causes severe harm (1)	Causes some harm (2)	Neutral (3)	Causes some benefits (4)	Of central importance (5)
Ecological	○	○	○	○	○
Economic	○	○	○	○	○

8) In **NATURAL** water-bodies (natural lakes, streams, or rivers) of the primary watershed you work in, please rank the level of priority for how these management tools are used with the **non-native** black bass species designated in Question 6.
If a management tool is not used within your primary watershed, please choose "Not applicable".

	Not Applicable (0)	Not a Priority (1)	Low Priority (2)	Medium Priority (3)	High Priority (4)	Essential (5)
Creel Limits	○	○	○	○	○	○
Length Limits	○	○	○	○	○	○
Catch and Release	○	○	○	○	○	○
Catch and Kill	○	○	○	○	○	○
Stocking native black bass	○	○	○	○	○	○
Stocking non-native black bass	○	○	○	○	○	○
Mechanical or Chemical Removal	○	○	○	○	○	○
Black Bass Monitoring	○	○	○	○	○	○
Black Bass Habitat Alterations	○	○	○	○	○	○
Forage Stocking	○	○	○	○	○	○
Tournament Attraction	○	○	○	○	○	○
Angler Education	○	○	○	○	○	○

For other actions not listed that are directed toward management of this non-native black bass in **NATURAL** water-bodies (natural lakes, streams, or rivers) within your primary watershed, please specify:

____

9) Would you say the population of this **non-native** black bass in **NATURAL** water bodies (natural lakes, streams, or rivers) of the primary watershed you work in is:

- ☐ Unknown
- ☐ Decreasing
- ☐ Stable
- ☐ Increasing

10) Do you manage **non-native** black bass in **ARTIFICIAL** water bodies (reservoirs or impoundments) within your primary watershed?
Please note that ponds (≤ 5 hectares) are not a water body of interest.

☐ **Yes.** If yes, please answer the remaining questions on this page.

☐ **No.** If no, please click “DONE” at the bottom of this page.

11) In **ARTIFICIAL** water-bodies (reservoirs or impoundments), considering **ALL** non-native species of black bass that occur within your primary watershed, what one species of **non-native** black bass receives the **most** management attention? (Choose ONE)

☐ Alabama ☐ Altamaha ☐ Bartram's ☐ Cahaba ☐ Chattahoochee ☐ Choctaw
☐ Florida ☐ Guadalupe ☐ Largemouth ☐ Redeye ☐ Shoal ☐ Smallmouth
☐ Spotted ☐ Suwannee ☐ Tallapoosa ☐ Warrior
☐ Not Present

12) In **ARTIFICIAL** water-bodies (reservoirs or impoundments) of the primary watershed you work in, please rank how this **non-native** black bass species is viewed ecologically and economically based on your professional opinion:

	Causes severe harm (1)	Causes some harm (2)	Neutral (3)	Causes some benefits (4)	Of central importance (5)
Ecological	○	○	○	○	○
Economic	○	○	○	○	○

13) In **ARTIFICIAL** water-bodies (reservoirs or impoundments) of the primary watershed you work in, please rank the level of priority for how these management tools are used with the **non-native** black bass species designated in Question 11. If a management tool is not used within your primary watershed, please choose “Not applicable”.

	Not Applicable (0)	Not a Priority (1)	Low Priority (2)	Medium Priority (3)	High Priority (4)	Essential (5)
Creel Limits	◌	◌	◌	◌	◌	◌
Length Limits	◌	◌	◌	◌	◌	◌
Catch and Release	◌	◌	◌	◌	◌	◌
Catch and Kill	◌	◌	◌	◌	◌	◌
Stocking native black bass	◌	◌	◌	◌	◌	◌
Stocking non-native black bass	◌	◌	◌	◌	◌	◌
Mechanical or Chemical Removal	◌	◌	◌	◌	◌	◌
Black Bass Monitoring	◌	◌	◌	◌	◌	◌
Black Bass Habitat Alterations	◌	◌	◌	◌	◌	◌
Forage Stocking	◌	◌	◌	◌	◌	◌
Tournament Attraction	◌	◌	◌	◌	◌	◌
Angler Education	◌	◌	◌	◌	◌	◌

For other actions not listed that are directed toward management of this non-native black bass in **ARTIFICIAL** water-bodies (reservoirs or impoundments) of your primary watershed, please specify:

---

13) Would you say the population of this **non-native** black bass in **ARTIFICIAL** water-bodies (reservoirs or impoundments) of the primary watershed you work in is:

- ☐ Unknown
- ☐ Decreasing
- ☐ Stable
- ☐ Increasing

Please click "Done" to submit your answers. Thank you for completing the survey!

APPENDIX B
IRB APPROVAL FORM

Oklahoma State University Institutional Review Board

Date:	06/01/2018
Application Number:	AG-18-31
Proposal Title:	Non-native Black Bass Management Survey
Principal Investigator:	Lauren Seguy
Co-Investigator(s):	
Faculty Adviser:	Jim Long
Project Coordinator:	
Research Assistant(s):	
Processed as:	Exempt

Status Recommended by Reviewer(s): Approved

The IRB application referenced above has been approved. It is the judgment of the reviewers that the rights and welfare of individuals who may be asked to participate in this study will be respected, and that the research will be conducted in a manner consistent with the IRB requirements as outlined in section 45 CFR 46.

The final versions of any recruitment, consent and assent documents bearing the IRB approval stamp are available for download from IRBManager. These are the versions that must be used during the study.

As Principal Investigator, it is your responsibility to do the following:

1. Conduct this study exactly as it has been approved. Any modifications to the research protocol must be approved by the IRB. Protocol modifications requiring approval may include changes to the title, PI, adviser, other research personnel, funding status or sponsor, subject population composition or size, recruitment, inclusion/exclusion criteria, research site, research procedures and consent/assent process or forms.
2. Submit a request for continuation if the study extends beyond the approval period. This continuation must receive IRB review and approval before the research can continue.
3. Report any unanticipated and/or adverse events to the IRB Office promptly.
4. Notify the IRB office when your research project is complete or when you are no longer affiliated with Oklahoma State University.

Please note that approved protocols are subject to monitoring by the IRB and that the IRB office has the authority to inspect research records associated with this protocol at any time. If you have questions about the IRB procedures or need any assistance from the Board, please contact the IRB Office at 223 Scott Hall (phone: 405-744-3377, irb@okstate.edu).

Sincerely,

Hugh Crethar, Chair Institutional
Review Board

VITA

Lauren B. Seguy

Candidate for the Degree of

Master of Science

Thesis: NON-NATIVE BLACK BASS: POTENTIAL CONFLICTS IN FISHERIES MANAGEMENT

Major Field: Natural Resource Ecology and Management

Biographical:

Education:

Completed the requirements for the Master of Science in Natural Resource Ecology and Management at Oklahoma State University, Stillwater, Oklahoma in May, 2019.

Completed the requirements for the Bachelor of Science in Biological Sciences at California Polytechnic State University, San Luis Obispo, California in 2011.

Experience:

Sea Turtle Monitor at Ecological Associates, Inc. from April-August 2017, Sharp-tailed Grouse Project Volunteer at Colorado Parks and Wildlife from April-May 2016, Fish and Wildlife Biologist at RiverEdge Associates from June-November 2015, Sea Turtle Research Assistant at Latin America Sea Turtles from February-May 2015, Western Snowy Plover Monitor at California State Parks from 2014-2015, Sea Turtle Research Assistant at PRETOMA Turtle Trax S.A. from September-December 2013, Volunteer Educational Guide at Elephant's World from February-March 2013, Laboratory Assistant at Adelaida Cellars from April-December 2012, Student Research Assistant at Center for Coastal Marine Sciences 2011-2012, Volunteer Aquarist and Educational Guide at the Sea Life Center from 2010-2011