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Research Article

Pathways of fish invasions in the Mid-Atlantic region of the United States

Nicolas W.R. Lapointe[1,*], Pam L. Fuller[2], Matthew Neilson[2], Brian R. Murphy[1] and Paul L. Angermeier[1,3]

[1]*Department of Fish and Wildlife Conservation, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA*
[2]*U.S. Geological Survey, Wetland and Aquatic Research Center, Gainesville, FL, USA*
[3]*U.S. Geological Survey, Virginia Cooperative Fish and Wildlife Research Unit, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA*
**Corresponding author*
Present address: Canadian Wildlife Federation, 350 Michael Cowpland Dr, Ottawa, ON, K2M 2G4, Canada
E-mail: nlapointe@gmail.com

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Abstract

Non-native fish introductions are a major threat to biodiversity and fisheries, and occur through numerous pathways that vary regionally in importance. A key strategy for managing invasions is to focus prevention efforts on pathways posing the greatest risk of future introductions. We identified high-risk pathways for fish establishment in the Mid-Atlantic region of the United States based on estimates of relative probability of establishment among pathways and records of previous introductions, which were considered in the context of emerging socioeconomic trends. We used estimates of propagule pressure, species' environmental tolerance, and size of species pool to assess the risk of establishment by pathway. Pathways varied considerably in historic importance and species composition, with the majority of species introduced intentionally via stocking (primarily for sport, forage, or biocontrol) or bait release. Bait release, private stocking, illegal introductions intended to establish reproducing populations (e.g., of sport fish), aquaculture, and the sale of live organisms all create risks for future invasions in the Mid-Atlantic region. Of these pathways, bait release probably poses the greatest risk of introductions for the Mid-Atlantic region because propagule pressure is moderate, most released species are tolerant of local environmental conditions, and the pool of species available for transplantation is large. Our findings differ considerably from studies in other regions (e.g., bait release is a dominant pathway in the Mid-Atlantic region, whereas illegal introduction of sport fish is dominant in the western US and aquarium releases are dominant in Florida), demonstrating the need for regional-scale assessments of, and management strategies for, introduction pathways.

Key words: nonnative, invasibility, freshwater, introduced species, stocking, bait release, aquarium release

Introduction

Fish invasions incur significant ecological and social costs germane to most fisheries professionals, though important societal benefits are also derived from some introductions (see debate among Gozlan 2008; Leprieur et al. 2009; Vitule et al. 2009). Nonnative fishes threaten aquatic biodiversity in North America by imperiling native fishes (Miller et al. 1989; Jelks et al. 2008), homogenizing fish faunas (Rahel 2000), locally extirpating native fishes (Findlay et al. 2000), and altering food webs (Vander Zanden et al. 1999). Additionally, the introduction of novel species can threaten existing fisheries (Love and Newhard 2012). Preventing nonnative introductions most effectively reduces such effects (Puth and Post 2005).

Species invasion comprises multiple stages (Kolar and Lodge 2001). Species must first be transported from their native range and introduced elsewhere through any of a variety of pathways (Hulme et al. 2008). Once introduced, individuals may perish or establish a reproducing population, depending in part on the suitability of the receiving environment (Moyle and Light 1996). Propagule pressure, a function of the number of introductions and individuals introduced, correlates positively with establishment success (Colautti et al. 2006). Controlling invasions depends on understanding invasion pathways, including pathway stages and types, as well as species-specific establishment success, the species pool of potential invaders, and propagule pressure associated with each pathway.

Such knowledge can help inform development of effective and cohesive regulations, which currently vary widely in structure and intent among regions (ELI 2002).

Nonnative fishes invade via many pathways (Fuller 2003; Gozlan et al. 2010). Fishes are stocked for sport, food, forage, biocontrol/biomanipulation, or conservation, and such introductions may be officially sanctioned or illegal. Fishes are also released for compassionate reasons (e.g., pet or bait fishes; Kerr et al. 2005) or introduced by escaping ponds, being transferred in ballast water, or swimming through canals. The relative importance of pathways varies geographically and temporally with factors such as social attitudes and global trade (Keller et al. 2009). Understanding spatio-temporal trends in pathways of introduction is important in predicting and managing future invasions.

The types of species introduced vary among pathways, leading to the introduction of new species as alternate pathways emerge (Fuller 2003; Hulme et al. 2008; Olden et al. 2010). Intentional stocking of sport fishes has been a dominant pathway in North American since the end of the 19th century, though attitudes toward sport fish stocking have changed (Cambray 2003; Whelan 2004; Kolar et al. 2010). Despite this shift, the number of non-native fishes in the U.S. continues to rise each decade (Matlock 2014). Increases in global trade are generating new pathways and larger pools of potential invaders, resulting in introductions of novel species (Perrings et al. 2005; Hulme et al. 2008). Changing climates will alter environmental contexts for species establishment (Rahel and Olden 2008), leading to increased risk of establishment from pathways transporting sub-tropical species to temperate climates. New species introduced via emerging pathways may have unique traits, leading to novel impacts on recipient ecosystems.

Previous assessments of pathway importance have not necessarily accounted for biases associated with probability of establishment (e.g., Ribeiro et al. 2009), which can differ between intentional and unintentional introductions (Richardson and Pyšek 2006). Intentionally introduced species are more likely to establish because they are selected to match their receiving environment and often for their hardiness (Ruesink et al. 1995; García-Berthou et al. 2005; Moyle and Marchetti 2006). Propagule pressure is usually high for these introductions because many healthy individuals are frequently introduced (Hulme et al. 2008). However, even species introduced in small numbers can have high propagule pressure if introductions occur frequently (e.g., repeated releases of leftover bait fish at popular angling locations).

Analyses of invasion pathways can inform efforts to prevent the spread of nonnative fishes (Strayer 2010) but regions differ in their dominant pathways (Kerr et al. 2005; Keller et al. 2009; Ribeiro et al. 2009). For example, the aquarium trade is the most important source of freshwater introductions in Great Britain (Keller et al. 2009) and Florida (Shafland et al. 2008); illegal introductions of sport fishes dominate in Portugal (Ribeiro et al. 2009); illegal introductions are dominant in the western US (Rahel 2004); and ballast water and the live-food industry are important pathways in Ontario, Canada (Kerr et al. 2005). Such differences suggest that region-specific assessments of pathway importance can facilitate more effective management of fish invasions.

Our goal herein is to identify pathways posing the greatest risk for the establishment of non-native fishes in the Mid-Atlantic region, which is heavily invaded by this taxon (Fuller et al. 1999; Nico and Fuller 1999). Because few studies have examined fish invasions here, managers have little information to help predict and prevent future invasions. We identify temporal shifts in and species associated with dominant pathways of fish introductions, based on documented established species. We use qualitative estimates of propagule pressure and species-specific environmental tolerance to evaluate the risk of establishment of species in each pathway. This was coupled with estimates of the number of species involved in each pathway to evaluate the overall risk of establishment for each pathway.

Methods

Study site

The study area (Figure 1) included 78 eight-digit hydrologic units (HUC8s) delineated by the U.S. Geological Survey (USGS; Seaber et al. 1987) in the Chesapeake Bay subregion (henceforth the Mid-Atlantic region) of the Atlantic ichthyogeographic region in the U.S., as defined by Edwards et al. (1998). All HUC8s drain directly or through other HUC8s in the region into the Atlantic Ocean, and average approximately 3,000 km^2. The area is bounded by the Susquehanna River in Pennsylvania and New York to the north and the Neuse River in North Carolina to the south. Two HUC8s (Upper Chesapeake Bay, Lower Chesapeake Bay) were excluded because they were mostly brackish or marine.

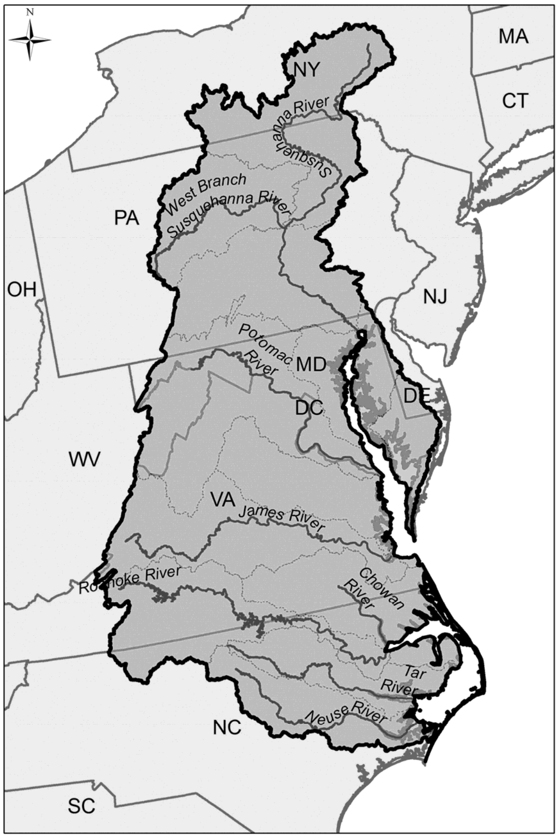

Figure 1. Map of the study area considered in this paper, which ranges from the Susquehanna River drainage in the north, to the Neuse River drainage in the south. Individual states are labeled by two-letter acronyms.

Data preparation

Records of species' introductions were obtained from the USGS Nonindigenous Aquatic Species Database (NASD) (USGS 2015) and were current as of May 1, 2013. The USGS gathers its information from published literature, personal communications with biologists, verified reports from the public, and museum data (see Fuller et al. 2013). Following USGS NASD protocol, species were considered established if they were known to reproduce and overwinter anywhere within the region; all other introduced species were treated as failed introductions. Hybrid species were excluded from counts of the number of species established by pathway and decade, but are listed in Appendix 1.

For each species, sources cited in the NASD were verified to confirm the earliest known date of introduction or detection, along with each of the pathways listed for that species (i.e., if the species was introduced more than once). Secondary sources were verified as necessary. Although many of the introductions and associated pathways presented here are documented, many others are presumed based on species identity, location, and expert opinion. Pathways associated with each species were estimated by the following methods, in order of preference: 1) documentation of the introduction (e.g., intentional stocking, or known aquaculture escape); 2) published estimates of the most likely pathway (e.g., in Jenkins and Burkhead 1994); 3) similarly documented or estimated pathways for the species in other regions; or, 4) documented or estimated pathways for congeners (e.g., bait release for *Notropis* spp.).

Temporal trends of establishment

To examine temporal trends among pathways, the first decade of introduction (either decade of detection or documentation, depending on species) was identified for each species by conducting literature searches and by searching museum holdings at American Museum of Natural History, New York State Museum, Academy of Natural Sciences, Philadelphia, and museums connected to FishNet2, particularly Cornell University, Smithsonian Institution, and North Carolina State Museum of Natural Sciences. For five species, a specific year of introduction or detection was not available; these were listed as introduced prior to the first documented date (e.g., <1957). Species listed as introduced <1980 and <1990 were considered to have been introduced in the 1970s and 1980s, respectively (two species), although they may have been present much earlier. For species known to have been introduced by more than one pathway, the most likely or dominant pathway was selected based on consensus among authors. Thus, for the purpose of the temporal graph (Figure 2) each species was associated with a single pathway. The number of species introduced through each pathway was calculated by decade.

Species and establishment success by pathway

Data presented on temporal trends of establishment show how dominant pathways change over time; however, they do not provide information on the complete suite of species associated with each pathway. We estimated the species-environment match for each pathway based on the likelihood that species associated with that pathway would tolerate environmental conditions in the Mid-Atlantic region. Knowledge of the species associated with each pathway informed estimates of species-

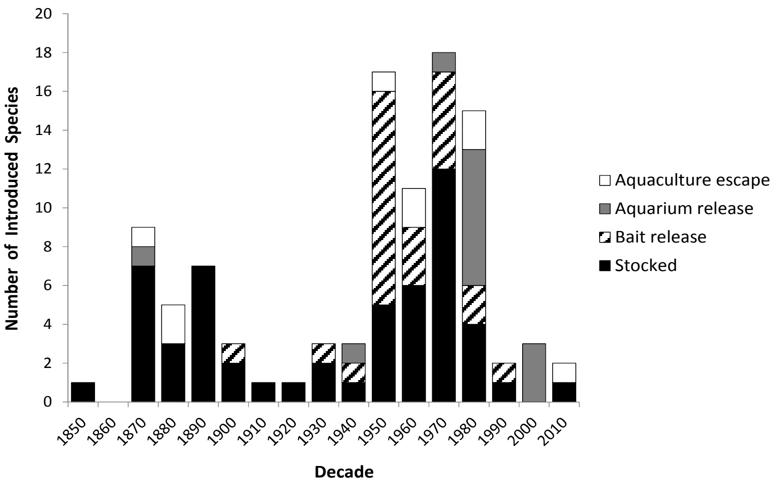

Figure 2. Historical trends of fish introductions in the Mid-Atlantic region by pathway and decade. All pathways associated with intentional stocking (for biocontrol, forage, sport, or as contaminant) were combined as "Stocked". Pathways that resulted in the introduction of less than three species were excluded, including "Canal" (*Nocomis biguttatus*, 1960's; *Morone americana*, 1970's), "Food fish release" (*Channa argus*, 2000's), and "Unknown" (*Ictiobus bubalus*, 1980's). Source: (USGS 2015).

environment match, which were based on the majority of species in a pathway. For example, even though Goldfish (*Carassius auratus* Linnaeus, 1758; a popular aquarium species) can survive in a temperate climate, species involved in the aquarium pathway were assumed to have a low species-environment match in the Mid-Atlantic region because the vast majority are tropical in origin. Introduced species were summarized by pathway, along with whether they established or failed to establish (Appendix 1). Species introduced through multiple pathways were listed under each, and considered as established through each if they were established anywhere in the region.

Relative probability of establishment

We estimated the relative probability of establishment for each known or potential pathway of fish invasions in the Mid-Atlantic region based on propagule pressure and species-environment match (Table 1). We estimated the relative propagule pressure of each pathway based on expected frequency of introductions and number of individuals introduced. The number of individuals was considered low if < 10 individuals were expected to be introduced at each event, moderate if 10–100 individuals were expected, and high if >100 individuals were expected. These numbers are based on release in proximity of other conspecific individuals to account for potential of reproduction. For example, hundreds of Goldfish may be released individually or in small groups, but if they are introduced into separate water bodies, individuals would have little potential to breed. Estimates of the relative probability of establishment of each pathway were based on estimates of propagule pressure and species-environment match. Pathways that were estimated to involve high or low propagule pressure and species-environment match were given a high or low probability of establishment, respectively. When estimates differed between the two criteria, the pathway was given a moderate probability of establishment.

Results

Fish introductions into the Mid-Atlantic region were widespread, taxonomically diverse, and often successful. One hundred species have been documented as introduced, plus two taxa identified to genus, and three hybrid species (Appendix 1). The numbers provided in this section represent only species that have been detected as established and recorded in the database, and should therefore be interpreted as the minimum number of established species per pathway. Of the introduced species, at least 71 have established within the region. Species were introduced through one to three pathways, with 58 species presumed to be introduced through a single pathway. The 1950s through the 1980s had the highest numbers of documented introductions (11–18 per decade; Figure 2). Excluding hybrids and taxa not identified to species, at least 61 species were stocked, 29 were released as bait, 14 were released from aquaria, 9 escaped from aquaculture, 2 were introduced via canal, and 1 was released as a food fish. These numbers exceed the total number of introduced species because some species were introduced through multiple pathways.

Table 1. Estimates of the relative probability of establishment among pathways. Probability of establishment was estimated relatively among pathways based on expected propagule pressure (the number of introductions and size [the number of individuals per release; Lockwood et al. 2009]) and species-environment match for the majority of introductions in each pathway. Estimates of percent established were derived from the total number of species that established and failed to establish in the Mid-Atlantic region via each pathway, based on USGS (2015).

Pathway	Intentional or Unintentional[a]	Propagule pressure - number	Propagule pressure - size	Species-environment match	Probability of establishment	Percent established[b]
Stocking for sport/food	Intentional	High [c] Low[d]	High [c] Low[d]	High [c] High	High [c] Variable	0.72
Stocking for forage	Intentional	High [c] Low[d]	High [c] Low[d]	High [c] High	High [c] Variable	0.82
Stocking for biocontrol	Intentional	Low	Moderate	High	Low[e]	
Stocked as contaminant	Unintentional	Low	Low-Moderate	High	Moderate	0.71
Bait release[d]	Intentional	Moderate	Moderate	High	High	0.90
Aquarium release[d]	Intentional	High	Low	Low	Low	0.43
Aquaculture escape	Unintentional	Low	High	Variable	Moderate	0.56
Canal connection	Unintentional	High	High	High	High	
Ballast water	Unintentional	Low	Moderate	Variable	Low	
Food-fish release[d]	Intentional	Low	Low	Variable	Moderate	
Prayer release[d]	Intentional	Low	Moderate	High	Low	
Classroom release[d]	Intentional	Low	Low	High	Low	

[a]Refers to action of the release, not necessarily the intent to establish a population; individuals who release organisms may or may not intend to establish a population.
[b]Not given for pathways associated with less than five species in the Mid-Atlantic region.
[c]If Agency sanctioned and/or conducted.
[d]Conducted by an individual or small group of people.
[e]When only sterile fish are used, as is the case with Grass Carp in the Mid-Atlantic region.

Intentional stocking

Historically, intentional stocking dominated (51%) fish introductions in the Mid-Atlantic region. This was the dominant pathway prior to the 1940s, and was responsible for frequent introductions between the 1950s and 1980s (Figure 2). Species from at least 13 families have been intentionally stocked in the region (Appendix 1). Species were intentionally stocked for sport, forage, biocontrol, or food, with others introduced as contaminants with stocked fishes. Most species were stocked for sport, especially centrarchids and salmonids, whereas clupeids and cyprinids were most often stocked for forage. Intentional stocking usually led to species establishment, with the exception of species stocked for biocontrol.

Pathways associated with stocking are known to involve high propagule pressure because species are often stocked repeatedly and in large numbers. Species stocked for biocontrol are an exception because this pathway is dominated by Grass Carp (*Ctenopharyngodon idella* Valenciennes, 1844), often stocked in low numbers as triploids (Mitchell and Kelly 2006). Additionally, species stocked as a contaminant with other fishes are now expected to be stocked infrequently and in low numbers because advances in stocking methods have reduced the occurrence of contamination. Illegal introductions of sport (or possibly forage) fishes likely occur frequently (Johnson et al. 2009), and multiple individuals are likely stocked at each occurrence or over time with the intent to establish a population.

Bait release

Bait release was the most common pathway for fish invasions in the Mid-Atlantic region, after intentional stocking. At least 26 fish species have established in the Mid-Atlantic region via bait releases, with most transplanted within the region or transferred from adjacent regions. Many of the species associated with this pathway were assumed to be introduced via bait release, because it is rarely possible to confirm actual introductions for this pathway. Unused bait fishes are commonly released (Litvak and Mandrak 1993), and several individuals are often released at each event. Twenty-nine species are assumed to have been introduced to the region through bait release. Of these, 60% are cyprinids, with catostomids, percids, gasterosteids also contributing multiple species. Of the species associated with this pathway, 90% have established; however, it is highly unlikely for failed introductions via this pathway to be detected because most species involved appear native to non-experts.

Aquarium release

Unwanted aquarium and ornamental fishes are also commonly released (Gertzen et al. 2008); however, fewer individuals are released at each event relative to bait releases, particularly for large-bodied species. Fourteen species were introduced via aquarium release, though many of these are tropical and would not likely survive in the Mid-Atlantic climate. Temperate species included four cyprinids, one centrarchid, and one poeciliid. Tropical taxa represented the Channidae, Characidae, Cichlidae, and Loricariidae families. Other tropical species may have failed to establish but were not detected or not reported.

Aquaculture escape

Slightly more than half (56%) of the nine species detected as introduced by escaping aquaculture facilities established reproducing populations. These were primarily cyprinids, but included one cichlid (Blue Tilapia *Oreochromis aureus* Steindachner, 1864). Of the four known species that did not establish, the majority had temperate origins. When species escape from aquaculture, high numbers of individuals may be introduced; however, such events are infrequent in the region (USGS 2015).

Other pathways

Few species were introduced via pathways other than those listed above. At least one species (Northern Snakehead *Channa argus* Cantor, 1842) was likely a food fish release, and has received widespread media attention. Release of unwanted food-fish is probably relatively rare, compared to bait or aquarium releases, and few individuals are likely involved.

At least two species spread within the region via canals (Hornyhead Chub *Nocomis biguttatus* Kirtland, 1841; White Perch *Morone americana* Gmelin, 1789). Where canals connect uninvaded habitats to habitats with established populations, both frequency and number of individuals may be high if a steady stream of propagules is available.

Although not documented in the Mid-Atlantic, additional pathways have been documented in other regions. Prayer release may involve the introduction of numerous individuals of the same species (Severinghaus and Chi 1999); however, this practice is not known to be common in the Mid-Atlantic region. The frequency of release of animals from classrooms is unknown in the region, but few animals are introduced at each event, and this pathway is probably dominated by taxa other than fish (Larson and Olden 2008). Ballast water can also provide a steady stream of propagules; however, the transfer of freshwater organisms in the region may be limited compared to other regions with high shipping traffic such as the Laurentian Great Lakes (Holeck et al. 2004), and this pathway may be more important for marine or invertebrate taxa in the Mid-Atlantic region.

All pathways associated with intentional stockings, including illegal introductions, likely involved high species-environment match because species would generally be selected based on expectations that they could survive in the region. We estimated that species stocked as contaminants would also survive in the region because they must survive under similar conditions as intentionally stocked species prior to stocking. Bait releases and canals mostly involve species that are already established or native to one part of the region and thus demonstrate high species-environment match. Most aquarium species would not tolerate local environmental conditions because they are primarily tropical, though some exceptions exist. In contrast, most aquaculture species are tolerant of local environmental conditions because they are selected for their ability to survive in outdoor aquaculture ponds. Similarly, most species found in the live food fish trade or readily available for prayer release originate from fresh waters, and are tolerant of the moderate temperate climate of the Mid-Atlantic region. Species kept in classroom settings are also likely to be robust to a range of conditions and suited for survival in the region's climate. Ballast water species may be transported from a variety of regions, including from within the Mid-Atlantic region, and their environmental tolerances may vary considerably.

Discussion

Intentional stocking of sport fish has been the most important pathway of fish invasions in the Mid-Atlantic region, but more species are now being introduced through once-minor pathways. New species continue to establish through bait and aquarium release, and aquaculture escape. The risk of establishment posed by individual pathways can be estimated by considering the probability of establishment associated with each pathway, along with analyzing historic data on pathway dominance. Such data must be considered in the context of current socioeconomic trends (e.g., an expansion of the diversity and prevalence of the aquaculture industry), and the detectability of introductions associated with that pathway. For instance, bait releases often involve cryptic species that are endemic to the Mid-Atlantic region, and are therefore difficult for even experienced ichthyologists to identify as nonnative to a given watershed (Courtenay 2007). Unique exotic species, such as many of those associated with the aquarium industry, are more likely to be identified as nonnative and reported, even by non-experts. Therefore, interpretation of pathway prevalence based on historic data must be tempered by consideration of detectability and changing social trends when predicting future pathway importance.

Our findings are consistent with other recent studies (e.g., Rahel 2004; Kerr et al. 2005; Keller et al. 2009; Ribeiro et al. 2009) that revealed considerable differences in dominant pathways of freshwater fish invasions among regions. These studies focused on species introduced from outside regions and generally ignored native species transplanted elsewhere in the region. Such transplants can have major consequences for the regional persistence of rare or endemic species, and warrant inclusion in assessments of pathway importance. For example, at least 65 fishes are introduced into parts of Virginia but only 19 of those are not native in another part of their Virginia range (Table 2, pages 39–42 in Jenkins and Burkhead 1994). Observed differences in dominant pathways among regions likely depend in part on how pathway importance was evaluated, including whether transplanted native species were assessed, and if probability of establishment was considered. Inherent differences also exist among regions in societal factors (e.g., prevalence of economic activities involving the transport of live organisms, stocking practices of natural resource management agencies) and degree of endemism. Such differences illustrate the value of assessing pathway importance and designing management strategies at regional scales, and suggest that assessments need to consider within-region transplants as equivalent to introductions from beyond the region in question.

Our approach to assessing the relative risk of establishment posed by various pathways of invasion complements established decision-support tools for evaluating risks posed by nonnative fishes (e.g., Kolar and Lodge 2002; Copp 2013). The Fish Invasiveness Screening Kit (FISK; Copp 2013) can be used to evaluate the risk of establishment and impact of individual species in a given region based on species traits and known impacts in other locations. Screening potential invaders can be time consuming. For instance, FISK includes 49 questions about each species' traits and documented ecological impacts. As such, recent applications of FISK have involved screening of only a small number (30–90) of species per Region, typically focusing on species already introduced to a region (e.g., Almeida et al. 2013; Puntila et al. 2013; Simonovic et al. 2013, but see Mendoza et al. 2015). Identification of pathways posing the greatest risk of introduction and establishment using methods developed here can help inform prioritization of species to screen using FISK. If managers lack the resources to conduct species-specific risk assessments, control and prevention efforts can be focused instead on high-risk pathways. Indeed, many regulatory tools for preventing invasions are pathway specific. For example, regulations aimed at preventing aquaculture introductions are necessarily different from those aimed at preventing bait release.

Pathways can be categorized in terms of human involvement and intent, with pathways involving the intent to establish a reproducing population clearly posing the greatest risk of establishment. Hulme et al. (2008) identified six types of pathways, applicable across taxa and biomes, to facilitate comparisons when developing management plans or assessing factors driving invasions. Under Hulme et al.'s (2008) framework, 85% of freshwater fish species introductions in the Mid-Atlantic region would be classified as 'releases', because they were intentionally released whether legally or illegally. These introductions were associated with multiple pathways that require different strategies for preventing invasions. We divide pathways into four broad categories (discussed below), based on similarities in options for managing, regulating, and otherwise preventing introductions. Invasions can be limited by focusing prevention efforts on pathways posing the greatest risk of establishment and developing management approaches and regulations that address multiple similar pathways (Lodge et al. 2006).

Intentional stocking

Historically, most intentionally stocked species were introduced to enhance recreational fishing. Stocking began in the 19th century and increased considerably in the 1950s. By the late 1970s, Mid-Atlantic state agencies began changing their approach to intentional stocking (T. Greene, Pennsylvania Fish and Boat Commission (PFBC); J. Odenkirk, Virginia Department of Game and Inland Fisheries (VDGIF); D. Besler, North Carolina Wildlife Resources Commission (NCWRC), pers. comm.), mirroring attitudes of fisheries professionals across the continent (Jackson et al. 2004; Kolar et al. 2010). Many agencies now consider stocking sterile individuals, or stocking sport fishes only in waters where native fishes are absent (LaBar and Frew 2004; Jackson et al. 2004; Whelan 2004; Kolar et al. 2010). These changes reflect both heightened awareness of the impacts of nonnative species and improved understanding of the limitations of stocking for enhancing recreational fisheries. Furthermore, agencies with public trust responsibilities and mandates for ecosystem-based management have shifted from focusing efforts entirely on stocking sport fish to a more holistic approach to managing freshwater resources (Whelan 2004).

Attitudes toward intentional introductions of sport fishes vary geographically, as do risks of subsequent invasions. The risk posed depends on the identity of the species stocked relative to the receiving ecosystem. Kerr et al. (2005) concluded that risks from this pathway were limited in Ontario, even though sport fish stocking is widespread there, and Gozlan (2008) described numerous socioeconomic advantages of this practice. Conversely, Clarkson et al. (2005) argued that ongoing stocking of established nonnative fishes undermines recovery of imperiled native fishes, and nonnative fish populations established by stocking may serve as sources for further spread of the species (Johnson et al. 2008). Most, if not all intentionally introduced nonnative fishes in the Mid-Atlantic region have at least not been detected as established in every watershed, suggesting that the region is not saturated in the distribution of established invaders. This creates an invasion debt (Strayer 2010), where established species have not yet spread throughout their introduced range, and the number of nonnative populations is therefore likely to increase in the future.

Aside from state-run (or sanctioned) stocking programs, anglers are known to intentionally transport and release sport fish with the intent to establish new reproducing populations (Johnson et al. 2009). In fact, illegal introductions of sport fishes are a major pathway of fish invasions globally (Madison 2003; Rahel 2004; Ribeiro et al. 2009). Illegal introductions of forage fishes also occur, including in the Mid-Atlantic region. In the 1980s, Gizzard Shad (*Dorosoma cepedianum* Lesueur, 1818) were introduced into Claytor Lake, VA; an act claimed in local media by an anonymous member of the public who aimed to improve angling by providing additional forage for piscivores in the reservoir (Bonds 2000). Members of the public may also release fish with the intent to establish populations of species they wish to consume; however, this likely occurs far less frequently, or species may be introduced for both sport and food. These pathways are particularly concerning because propagule pressure is generally higher compared to instances where fish are released simply because they are unwanted, and few management strategies exist to prevent such introductions.

Species are often released into the wild for convenience or compassionate reasons, even though the individual releasing them has no intention of establishing a reproducing population (and may not even consider this a possibility). Such pathways differ considerably in their relative probabilities of establishment. Bait release, aquarium release, and releases listed in the "other pathways" section fall into this category.

Bait release

The release of bait fishes may currently be the most important invasion pathway in the Mid-Atlantic region, though the greatest number of establishments occurred in the 1950s–1970s. Although this pathway is presumed for 26 established species, this number is probably an underestimate, given low detectability, and limited monitoring effort and historical data. Probability of establishment is high, but low detectability suggests that many additional undocumented introductions may have occurred in the Mid-Atlantic region. Limited detectability may have also led to underestimates of the risk posed by this pathway in other regions (e.g., Ontario; Kerr et al. 2005). This pathway is unique because most species are transplants within the region or from bordering drainages and are adapted to Mid-Atlantic climatic conditions. Though few fish are probably released at each introduction, bait releases probably occur frequently (Litvak and Mandrak 1993). Studies in other regions revealed the prevalence of bait releases and the likelihood of inter-basin transfers via this pathway. Of the surveyed anglers using live bait, 41% released unused bait in Ontario, with most assuming this benefited the ecosystem (Litvak and Mandrak 1993). Ludwig and Leitch (1996) demonstrated the near certainty of thousands of fish transfers annually between major basins in North Dakota and Minnesota through bait releases. Similar studies have not been conducted in the Mid-Atlantic region, but the propagule pressure of this pathway is likely large. Such introductions are not restricted to bait species; bait purchases commonly contain non-bait species as contaminants (Ludwig and

Leitch 1996). The potential for future bait-fish introductions is large. For example, only 13 of 63 cyprinid species native to Virginia are known to have been transplanted within the state, often to a limited number of watersheds (Jenkins and Burkhead 1994). Most of these species are indistinguishable to anglers who capture them by trap or net as bait, and may later transfer them.

Aquarium release

A moderate number of species were introduced in the Mid-Atlantic region through aquarium release compared to other pathways. Of the pathways discussed here, the aquarium and ornamental garden trade transports by far the greatest number of species to the Mid-Atlantic region. This could be explained by the large number of species in the trade. One study identified 730 ornamental freshwater fishes imported to the U.S. (Chapman et al. 1997), and one third of the world's worst invaders (Lowe et al. 2000) are associated with the aquarium trade (Padilla and Williams 2004). Aquarium fishes are commonly released; Gertzen et al. (2008) found that 5% of aquarium fish were ultimately released and estimated that 10,000 individuals were released per year in Montreal, Quebec. Species with characteristics associated with invasion success such as large size and aggressiveness are also more likely to be released (Duggan et al. 2006).

The risk of establishment posed by this pathway is increasing with globalization, through connection of new locations with greater speed and efficiency, and with the development of new technologies for care and transport of live animals (Ericson 2005; Hulme 2009). Introduction rates increase with economic growth and trade volume (Westphal et al. 2008) and species diversity increases with improvements in husbandry technologies and demand for novel species (Rixon et al. 2005). Fuller et al. (2013) found that aquarium release was the largest pathway for transplanting aquatic organisms to new locations in the US from 2004 to 2012. Most aquarium fishes are tropical and cannot tolerate winter; however, probability of establishment may increase with climate change (Hellmann et al. 2008), and water-garden species are likely selected based on their ability to tolerate local environmental conditions year-round.

Aquaculture escape

At least nine species have been introduced in the Mid-Atlantic region by escaping from aquaculture. The aquaculture industry, which includes production for the aquarium trade, is the most rapidly developing fisheries sector (Minchin 2007), doubling in volume and value over the 1990s in the U.S. (Naylor et al. 2001). Industry development is facilitated by technological advances (Minchin 2007), and there is widespread interest in establishing culture capabilities for new species (Tlusty 2002). When a species is transported to a region for aquaculture, it typically escapes, regardless of containment efforts (Townsend and Winterbourn 1992). Escape can occur if outdoor facilities flood, the outfall is not properly screened, accidents occur during transportation of the species to and from the facility, or they are transported by wildlife (e.g., osprey).

Other pathways

At least two species invaded the Mid-Atlantic region via canals. Though canals are not pathways of direct introductions of organisms by humans, canals facilitate dispersal that would otherwise be impossible (Hulme et al. 2008). One example in the Mid-Atlantic region is the Chesapeake and Ohio Canal, which connects the upper and lower Potomac River by surmounting barriers to fish migration such as Great Falls, and has already enabled dispersal of nonnative fishes (Starnes 2002).

Ballast water can also provide a steady stream of propagules; however, the transfer of freshwater organisms in the region may be limited compared to other regions such as the Laurentian Great Lakes (Holeck et al. 2004), and this pathway may be more important for marine or invertebrate taxa in the Mid-Atlantic region. Species at risk of being transported into Chesapeake Bay rivers by ballast include estuarine gobies and clupeids, which are susceptible to being taken into ballast tanks and can tolerate freshwater environments (Wonham et al. 2000).

There are several other pathways for fish introductions that have not been documented in the Mid-Atlantic region but do exist in other regions of the country. Introductions may have occurred through several of these pathways, but have not been documented because pathway identification is not always straightforward when a species is discovered in the wild. Any fish purchased alive may potentially be released. Aside from aquarium sales, live fish may be purchased from fish markets, or by mail or internet from biological supply depots (Keller and Lodge 2007). Live fish markets usually include nonnative species; 6 of 14 species found in a survey of Great Lakes markets were nonnative (Rixon et al. 2005). Although these fish may be released to intentionally establish a population, they may also be released for compassionate reasons or simply because they are no longer wanted (Dolin 2003). The Buddhist practice of prayer release involves releasing animals for spiritual or compassionate reasons and often requires the purchase of live animals (Crossman and Cudmore 1999). Species kept in classrooms may also be released when they are no longer needed for study or wanted, though this practice may be more prevalent for non-fish taxa (Larson and Olden 2008). Though each of these pathways is a concern in the region, there is little information available on their relative importance or the diversity of species involved.

Conclusions

We identified major temporal shifts in dominant pathways of fish introductions in the Mid-Atlantic region and differences in relative probability of establishment among pathways. Stocking was the dominant pathway from the 1850s to the 1970s, except in the 1950s when bait releases were most common. In the 1980s and 2000s, aquarium releases were the dominant pathway for fish invasions. All of the numbers presented here should be interpreted as minimums, because not all failed or established species have been detected and reported to the database. Species varied considerably among pathways, and new species are likely to be introduced via emerging pathways. Bait release, private stocking, illegal introductions, aquaculture, and the sale of live organisms all create risks for future invasions in the Mid-Atlantic region. Novel species are most likely to be introduced through pathways associated with economic activities such as aquaculture and the aquarium trade, and many native or established species will probably be transplanted to new drainages by bait release. Sanctioned and illegal private stocking will continue to facilitate the spread of sport fishes throughout the region. Of these pathways, bait release probably poses the greatest risk of introductions for the Mid-Atlantic region, because propagule pressure and species-environment match are moderate and high, respectively, and the pool of species available to be transplanted via bait release is large. This pathway could be addressed by regulations restricting the capture and transport of species among water bodies, or limiting the number of species that can be sold as bait. For example, New York State recently implemented regulations to limit the use of bait to a list of certified species, in part to reduce disease transfer, or the use of uncertified species in the same water body where they were captured (NYSDEC 2015).

Our findings differ considerably from studies of pathway-associated risks in other regions, demonstrating the need for regional-scale assessments of introduction pathways and the importance of accounting for probability of establishment when doing so. Records of pathways of introduction for existing invaders can inform predictions of future pathway dominance; however, emerging socioeconomic trends that could increase or decrease pathway importance should also be considered. Additional regional assessments would provide valuable information to managers seeking to prioritize prevention efforts by identifying pathways posing the greatest risk of establishment to a specific region.

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Supplementary material

The following supplementary material is available for this article:

Appendix 1. Fish species introduced by pathway in the Mid-Atlantic region.

This material is available as part of online article from:
http://www.reabic.net/journals/mbi/2016/Supplements/MBI_2016_Lapointe_etal_Supplement.xls