

Fish invasions in the Mid-Atlantic region of the United States

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ABSTRACT

Nonnative fishes are a major threat to biodiversity and new species continue to be introduced. In this dissertation, I described patterns and assessed determinants of fish invasions in the Mid-Atlantic region of the United States. Data on nonnative fish distributions were obtained from the United States Geological Survey's Nonindigenous Aquatic Species Database (NASD).

Nonnative fishes are introduced by a variety of pathways, and prevention efforts can be optimized by focusing on pathways posing the greatest risk of new invasions. To assess the importance of existing pathways, I described the species associated with each pathway, analyzed the number of species introduced by decade for certain pathways, and estimated the detectability and probability of establishment of species introduced by each pathway. Additionally, I reviewed the efficacy of existing regulations for preventing introductions via each pathway. Historically, the intentional introduction of centrarchids and salmonids for sport was the dominant pathway. Pathways currently posing the greatest risks included bait release, illegal introductions, stocking of private ponds, and several pathways associated with economic activities. These pathways involved cyprinids, catostomids, and species exotic to North America. Regulations varied considerably among states, and I suggest that region-wide prohibitions on the release of nonnative species into the wild would help prevent additional introductions.

Mid-Atlantic region watersheds differ considerably in nonnative species richness (NNSR), suggesting they are not equally invasible. I analyzed relationships between ecosystem characteristics and invasibility by compiling data on watershed characteristics and correlating these with NNSR. I included measures of colonization pressure (i.e., the number of species introduced) and research effort, which can bias patterns of NNSR. After controlling for these factors, the range in elevation in a watershed explained the greatest variation in NNSR. Highland watersheds had greater NNSR, probably because of greater habitat heterogeneity due in part to human activity. I suggest that NNSR can be reduced by restoration activities that reduce the diversity of artificial habitats available in highland watersheds

Ecosystems with similar NNSR may be invaded by different species, because differences in ecosystem characteristics may regulate the types of species that are able to establish. To explain differences in nonnative species among ecosystem types, I grouped Mid-Atlantic region watersheds by nonnative community and tested for differences in ecosystem characteristics among groups. Four groups were identified. A large, speciose group in the north-west portion region was characterized by smallmouth bass (*Micropterus dolomieu*). A large, speciose group in the south-west portion of the region was characterized by largemouth bass (*Micropterus salmoides*). Two smaller groups with few species were found on the coastal plain; one to the north, characterized by black crappie (*Pomoxis nigromaculatus*) and a second to the south characterized by white crappie (*Pomoxis annularis*). Nonnative community type was correctly predicted 80% of the time by models based on temperature and range in elevation. Relatively uninvaded watersheds in the south-east part of the region were predicted to host the most diverse nonnative community, suggesting that risks of invasion are high there. These results demonstrate the importance of species identity in determining ecosystem invasibility.

There is no consensus on how to estimate the relative impacts of nonnative species. I developed and compared several approaches for doing so. I estimated impact by surveying fish biologists regarding the abundance and socioeconomic and ecological impacts of each species. I obtained fish collection records as an additional estimate of abundance and consulted reports of impacts in the NASD. I consulted reports of impacts in global invasive species databases as a basis for comparison. I compared top-ranked species among approaches, and game and non-game biologists' ratings of game and non-game species for each survey question. Top-ranked species differed considerably among approaches. Non-game biologists gave higher ecological impact ratings to both game and non-game species. Approaches assessing socioeconomic impacts are most appropriate for informing social decisions, such as restricting the possession or trade of a species. A combination of data from approaches assessing ecological impacts and abundance is most appropriate for studies of ecological patterns, such as testing for differences in traits between high- and low-impact species. These approaches are transferrable to other regions and taxa, and can inform management decisions and improve efforts to identify factors correlated with high-impact invaders.

Collectively, my results can aid in reducing the effects of nonnative fish invasions by enabling managers to focus prevention efforts on high-impact species likely to invade particular ecosystems via known pathways. For example, bait releases, illegal introductions, private stocking, and several pathways associated with economic activities present the highest risks of future invasions, and warrant

attention aimed at preventing invasions. Prevention could also be focused on several watersheds in the south-east part of the region, which currently have few established species but were predicted to be invisable by bluegill (*Lepomis gibbosus*), bluntnose minnow (*Pimephales notatus*) channel catfish (*Ictalurus punctatus*), and warmouth (*Lepomis gulosus*). This work represents major advancements in invasion biology, including new links between species identity and ecosystem invasibility and the development of methods for quantifying impact.

Dedication

I dedicate this dissertation to my father, Claude Lapointe, who passed away many years before I began this work. I love him and miss him very much. He always pushed me to work hard and to pursue a good education, and I know he would be very proud. He would also be very surprised.

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General Introduction

Introductions of nonnative fishes are a major threat to biodiversity and were a contributing factor in 68% of recent fish-species and -subspecies extinctions in North America (Miller et al. 1989). Additionally, nonnative fishes contributed to declines in nearly 40% of imperiled fishes in North America (Jelks et al. 2008) and led to a homogenization of freshwater fish faunas across the United States (U.S.; Rahel 2000). Fuller et al. (1999) reported that 185 fish species have been introduced to the U.S. and another 361 have been transplanted beyond their native range. Introductions of large, piscivorous fishes often lead to extirpations of forage fishes through direct predation (Chapleau et al. 1997; Findlay et al. 2000). Nonnative species can also have more pervasive indirect effects resulting in shifts in abundance, habitat use, and diet of native fishes (Scott and Crossman 1979; Vander Zanden et al. 1999). Native organisms other than fishes may be affected directly or indirectly by nonnative fishes. For example, introduced rainbow trout (*Oncorhynchus mykiss*) fed on terrestrial prey in Japan; in response, Dolly Varden (*Salvelinus malma*) switched their foraging focus to algae-grazing benthic invertebrates, inducing further trophic cascades (Baxter et al. 2004). Economic costs of fish introductions can be high when recreational or commercial fisheries are disrupted, leading to social hardship in human communities that interact with these fisheries. For example, commercial and recreational lake trout (*Salvelinus namaycush*) fisheries in the Laurentian Great Lakes suffered great losses following the invasion of nonnative sea lamprey (*Petromyzon marinus*) (Lovell and Stone 2005). Eradication of nonnative species is generally impossible (Mack et al. 2000), and control is a perpetual expense. Preventing the introduction of nonnative species is the most effective way of eliminating negative effects (Puth and Post 2005). Slowing the rate of species introductions will require regulations and education directed at the most important pathways of introduction and species posing the greatest threat of invasion. A crucial role of invasion biologists is to identify and quantify these pathways and threats.

The invasion process is viewed as a series of stages, each with different filters that determine which species will advance. Stages may include transportation, introduction, establishment, spread, and impact (Kolar and Lodge 2002; Jeschke and Strayer 2006; García-Berthou 2007). The final stage is perhaps the most ambiguous. Richardson et al. (2000) defined invaders as nonnative species that established reproducing populations and spread, whereas Davis and Thompson (2000) suggested that an invasive species must also have a large impact in its new environment. Daehler (2001) argued that all nonnative species have ecological impacts, and defining invaders based on impact rather than spread is

an exercise in subjectivity. However, in a study of nonnative animals, Ricciardi and Cohen (2007) found no relationship between species that established and spread, and those that had an impact. For freshwater species in particular, spread is often rapid within an ecosystem but limited within a region unless additional introductions occur. Daehler (2001) suggested that most ecologists would not consider a species to be invasive if it had only local impacts; however, a species demonstrating major local impacts in a closed system is likely to have large impacts in other systems if spread occurs. I argue that, for freshwater and other closed systems (e.g., islands), the study of spread alone will not provide sufficient information for prediction or prevention of the negative effects of nonnative species. Impact must be considered, regardless of whether or not a species is labeled 'invasive'.

An understanding of the factors regulating ecosystem invasibility is needed for managers seeking to prevent or control nonnative species invasions (Marchetti et al. 2004a). Given that factors regulating invasions vary greatly among locations at global and continental scales, regional scales are ideal for analyses of ecosystem invasibility (Moyle and Marchetti 2006). Large-scale manipulative experiments with invasive species are impractical and potentially unethical; therefore, comparative studies offer a reasonable alternative (Light and Marchetti 2007). Freshwater ecosystems are ideal study subjects, given that natural migration of fishes is restricted among systems (Gido and Brown 1999).

Fish invasions have been studied for relatively few regions (García-Berthou 2007). My dissertation focuses on Atlantic Slope drainages in the United States, from New York south to North Carolina. Ichthyogeographic regions and subregions across North America were previously defined by Edwards et al. (1998) based on similarity in native fish assemblages. The Chesapeake Bay subregion (henceforth referred to as the Mid-Atlantic region) of the Atlantic ichthyogeographic region is among the regions most heavily invaded by nonnative fishes in the U.S. (Nico and Fuller 1999). Widely established nonnative fish species in this region include common carp (*Cyprinus carpio*; scientific and common names of fishes according to Nelson et al. [2004]), channel catfish (*Ictalurus punctatus*), smallmouth bass (*Micropterus dolomieu*), largemouth bass (*Micropterus salmoides*), and several *Lepomis* species. The coastal drainages in this region differ from highly connected inland drainages (e.g., Mississippi River basin, Great Lakes) because saltwater inhibits inter-drainage dispersal of freshwater fishes. Thus, drainages function as discrete units, each with distinctive ecological characteristics and histories of introductions.

Nonnative fishes are introduced through multiple pathways; each pathway may involve a unique set of species, and probability of establishment may vary among pathways. An evaluation of past and

present rates of establishment of non-native species by various pathways of introduction will provide information on which pathways pose the greatest risk for future invasions. In the first chapter, I document shifts in dominant pathways of fish introductions in the Mid-Atlantic region and describe differences in species composition among pathways. Additionally, I review regulations pertaining to nonnative species introductions, and compare their coordination and effectiveness for preventing invasions among states. I then forecast future patterns of introductions in the Mid-Atlantic region and evaluate the effectiveness of existing regulatory systems for preventing such introductions. Finally, I discuss options for addressing emerging pathways to prevent the introduction and spread of additional nonnative fishes in the Mid-Atlantic region.

Comparative studies of observed patterns of invasions are an important tool for understanding invasion processes at large scales. Nonnative species richness (NNSR) is commonly used as a measure of ecosystem invasibility and is regulated by ecosystem characteristics such as climate and range in elevation (Chytrý et al. 2008; Leprieur et al. 2008; Chiron et al. 2009). Nonnative species are thought to be more likely to establish in systems that are highly altered by human activities (Moyle and Light 1996); however, patterns of NNSR may be confounded by colonization pressure and bias in research effort. Colonization pressure is defined as the number of species introduced in a given location (Lockwood et al. 2009) and is an important determinant of the number of species established there. Similarly, documented patterns of NNSR can be biased if efforts to identify and record nonnative species vary across a region (Gassó et al. 2009). In the second chapter, I explore relationships among natural watershed characteristics, anthropogenic disturbance, colonization pressure, research effort, and NNSR to understand the relative contribution of these factors to ecosystem invasibility in the Mid-Atlantic region.

Despite Moyle and Light's (1996) assertion that predictions regarding native species depend on understanding the characteristics of invading species and the system being invaded, few studies consider differences among nonnative species when exploring patterns of ecosystem invasibility. Examining invasibility in relation to species identity should lead to better predictions of potential invaders. Differences in nonnative communities may arise in relation to ecosystem characteristics, when certain types of species are more likely to establish in ecosystems with particular characteristics. In the third chapter, I examine relationships between nonnative fish community composition and ecosystem characteristics. I group eight-digit hydrologic units (HUC8s) by similarities in their nonnative communities and test the hypothesis that species differ significantly among groups. I then test the hypothesis that groups of HUC8s with similar nonnative communities also share similar ecosystem

characteristics. Sufficient historical data do not exist to directly adjust for differences in species introduced to various parts of the region, but multiple records of failed and successful introductions exist for particular species. Therefore, I test the hypothesis that ecosystem characteristics determine the likelihood of establishment of individual species to provide further evidence that community-level patterns reflect environmental filters rather than simply patterns of historical colonization pressure.

The lack of rigorous, widely accepted methods for quantifying nonnative species' impact has hindered risk assessments and analyses of the characteristics of high-impact invaders, and standard approaches to quantifying impact are needed. There has been little consistency in methods for quantifying nonnative species impacts, leading to a paucity of studies exploring the traits associated with nonnative fishes that have significant impacts (García-Berthou 2007). Species that have ecological impacts may differ from those that have socioeconomic impacts, yet the distinction between these types of impact is often blurred in invasion biology (e.g., Kolar and Lodge 2002). In the fourth chapter, I develop five approaches for quantifying the degree of impact of nonnative fishes and compare their strengths, weaknesses, and biases. These approaches include: 1) reviewing documented impacts in an existing nonnative species database, (2-4) surveying fish biologists regarding the (2) socioeconomic impact, (3) ecological impact, and (4) abundance of nonnative species, and (5) estimating the proportional abundance of nonnative species based on existing collection records. I assess differences in my measures of impact by comparing average species ratings among approaches and to a global list of high-impact invaders. I compare variability in ratings among approaches to evaluate consistency in estimates of impact. Finally, I examine biases associated with survey respondents' professional focus by comparing ratings from game and non-game biologists for game and non-game fishes.

Results from these studies provide valuable information on the distributions and relative degree of impact of nonnative fishes in the Mid-Atlantic region. I identify pathways posing the greatest risk for future invasions, along with gaps in regulatory systems for addressing such pathways, and recommend options to reduce the risk of invasion for each pathway. I assess the invasibility of each ecosystem and identify high-risk ecosystems. I make specific predictions regarding the type of species most likely to invade particular areas of the Mid-Atlantic region, and the specific HUC8s where individual species are expected to establish reproducing populations if introduced. This information will inform management and prevention efforts, and potentially help to reduce the number of additional invasions in the Mid-Atlantic region.

Study area and data source

The study area includes 80 HUC8s nested within 11 larger HUC6s delineated by the U.S. Geological Survey (USGS; Seaber et al. 1987) in the Mid-Atlantic region. Each HUC6 corresponds to a major river drainage such as the Potomac or James river. The area, defined by Edwards et al. (1998), 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 from analyses because they were nearly entirely marine.

Nonnative fish distribution data were obtained from the USGS' Nonindigenous Aquatic Species Database (NASD; nas.er.usgs.gov accessed 17 September 2009). The NASD was created by compiling existing records from sources such as texts on state or regional fish assemblages, scientific journals, government documents, and personal communication with biologists (Nico and Fuller 1999).

Chapter 1: Pathways of fish invasions in the Mid-Atlantic region

INTRODUCTION

Nonnative fishes are introduced through a variety of pathways (Marchetti et al. 2004a; Gozlan et al. 2010). Fishes may be stocked intentionally for sport, food, forage, biocontrol/biomanipulation, or conservation, and such introductions can be sanctioned or illegal. Fishes may also be released for compassionate reasons, where the releaser may not necessarily intend for the species to establish a reproducing population. For example, pet or bait fishes are routinely released, as are fishes purchased for food or from biological supply depots (Kerr et al. 2005). Fishes may be introduced accidentally by escaping aquaculture or ornamental ponds, through ballast water transfers, or via canals and stream captures. The relative importance of these pathways varies temporally with social factors such as global trade and attitudes toward biological invasions. As new pathways emerge, additional species become potential invaders.

Establishment success can vary considerably between intentional and unintentional pathways (Marchetti et al. 2004a; Richardson and Pyšek 2006). Intentionally introduced species generally have a greater probability of establishment because they are selected for hardiness and appropriate physiological tolerances and habitat requirements (Ruesink et al. 1995; García-Berthou et al. 2005; Moyle and Marchetti 2006); however, some unintentionally introduced species may also share these characteristics. For example, species selected for aquaculture can generally tolerate local climates and may frequently escape (Hulme et al. 2008). Additionally, propagule pressure is usually high for intentionally introduced species because large numbers of individuals are frequently introduced, often in excellent condition (Hulme et al. 2008); however, even released pets introduced in small numbers can have high propagule pressure if introductions occur frequently (e.g., goldfish *Carassius auratus*).

The type of species introduced varies considerably among pathways and new pathways continue to emerge (Hulme et al. 2008; Olden et al. 2010). Intentional stocking of game fishes has remained a dominant pathway of fish introductions since the end of the 19th century (Cambray 2003) and although attitudes toward game fish stocking may be changing (Cambray 2003), continued sanctioned intentional introductions can be expected (Gozlan 2008). Concurrently, increases in global trade are leading to emerging pathways and the introduction of novel species (Perrings 2002; Hulme et al. 2008). The diversity of species transported for aquaculture and aquaria is increasing as these industries incorporate new products to meet consumer demand. Changes in climate will alter the types

of species that can establish (Rahel and Olden 2008), leading to increased importance of pathways such as the aquarium trade that predominantly involve tropical species. Novel species introduced via emerging pathways may have unique traits, leading to novel impacts on native ecosystems. Changes in dominant pathways and the species they involve can confound analysis and interpretation of historical invasion patterns, limiting the relevancy of historical patterns to predictions of future invasions. Accounting for temporal trends in pathways of introduction is critical to understanding and preventing invasions.

The probability of detecting invasions varies considerably among pathways, leading to uneven lag times in detecting, reporting and documenting invasions. Lag times are often defined as the time between an introduction and the spread and population increase of a nonnative species (Aikio et al. 2010); however, there are also considerable lag times between the introduction of a species and its detection, particularly when species are introduced illegally or unintentionally (Keller et al. 2009). Failed invasions are even less likely to be detected. Conversely, detection probability increases for established species after the initial lag between introduction and population increase. Additional delays arise between the detection and reporting or publication of nonnative species records, and their inclusion in nonnative species databases. Such lags must be considered when evaluating temporal trends of invasions.

Though invasions are a global issue, the importance of individual pathways varies among regions and taxa. Directed studies of invasion pathways have great potential for informing efforts aimed at preventing the spread of nonnative species (Strayer 2010). Recent reviews of pathways of fish and other aquatic invaders in Great Britain, Portuguese territories, and the province of Ontario have revealed considerable differences in dominant pathways among regions (Kerr et al. 2005; Keller et al. 2009; Ribeiro et al. 2009). All studies agreed that pathways associated with the aquarium trade were important, and it was the most important source of new introductions in Great Britain (Keller et al. 2009). Ribeiro et al. (2009) identified illegal introductions of game fish as the dominant pathway of new fish introductions in Portuguese territories, whereas Kerr et al. (2005) concluded that illegal stocking was rare in Ontario. Instead, ballast water and the live-food industries were found to be equally important to aquarium fish releases (Kerr et al. 2005). Such differences highlight the value of assessing introduction pathways at the regional scale.

In this paper, I document temporal shifts in dominant pathways of fish introductions in the Mid-Atlantic region and describe differences in species composition among pathways. Additionally, I review the regulations pertaining to each pathway, and compare coordination and effectiveness among states.

I then forecast future patterns of introductions in the Mid-Atlantic region and evaluate the effectiveness of existing regulatory systems for preventing such introductions. Finally, I discuss options for addressing emerging pathways to prevent the introduction and spread of additional nonnative fishes in the Mid-Atlantic region.

METHODS

Data preparation

Records of species' introductions in the Mid-Atlantic Region of the United States were obtained from the Nonindigenous Aquatic Species Database (NASD), which includes 8 categories of establishment status (definitions of each category provided in Shafland et al. 2008). Species listed as 'collected' (not known to have reproduced), 'stocked' (persist through repeated stocking) or 'failed' (not collected after an unspecified amount of time after introduction) were all considered failed. Other statuses had few records and were excluded from comparisons, including eradicated ($n = 5$), established? ($n = 1$), extirpated ($n = 4$), and unknown ($n = 5$). Duplicate records (i.e., for the same species, 8-digit hydrologic unit [HUC8], status, and pathway) were deleted.

The NASD listed 15 pathways and sub-pathways. I grouped these into four categories based on similarities in potential management and policy options for limiting introductions. All pathways associated with intentional state-sanctioned stocking were categorized as "intentionally stocked". Though hitch hikers with stocked fish were not intentionally stocked, they were included in this category because their introduction resulted from intentional stocking activities. Pathways involving species transported to the region through aquaculture, aquarium, and other industries were categorized as "economic activities". Bait releases were a dominant pathway of fish introductions in the Mid-Atlantic region, and were treated as a separate category. All other pathways were categorized as "other", including species introduced for unknown reasons.

Temporal trends of establishment

To examine temporal trends in pathways and evaluate lag times associated with documentation, the date of each record was considered. When multiple records existed for a species in a HUC8, only the first record of establishment was used. The majority (69%) of these records were based on one of three texts (Cooper 1983; Menhinick 1991; Jenkins and Burkhead 1994), and were listed under the date of publication of that text (i.e., 1983, 1991, or 1994, rather than the year the species actually established).

Records from these three texts that lacked an actual date of establishment were excluded because they biased evaluation of temporal trends by overestimating the number of records in 1983, 1991, and 1994, leaving 225 records of establishment by species and HUC8. After excluding records from these texts, insufficient aquarium-release ($n = 3$) and aquaculture-escape ($n = 1$) records remained to evaluate temporal trends; therefore, these pathways were grouped with other pathways to create a 'miscellaneous' category. The number of records by decade was calculated for intentionally stocked, bait release, and miscellaneous pathways.

Species and establishment success by pathway

Data for families and species introduced via each pathway were summarized to evaluate whether emerging pathways (i.e., those increasing in frequency in recent decades) involved novel species. Species were grouped by family when possible and the total number of established and failed introductions was listed for each species or family by pathway. These were used to calculate the proportion of introductions through a pathway for each species or family.

The proportion of introductions that led to establishment was calculated for each pathway. I estimated the expected probability of establishment for each pathway based on propagule pressure and the suitability of regional environmental conditions for most species in the pathway. I also estimated the probability of detecting an introduction (particularly if it failed) for each pathway based on the probability of the introduction being recorded and the species being identified as nonnative if observed.

I estimated the relative propagule pressure of each pathway based on the expected frequency of introductions and number of individuals introduced. I estimated that most pathways associated with intentional stocking involved high propagule pressure because species are often stocked repeatedly and in large numbers. Species stocked for biocontrol were an exception because it is dominated by grass carp (*Ctenopharyngodon idella*) that are often stocked in low numbers as triploids. Hitch hikers with stocked fish were another exception: I estimated low propagule pressure through this pathway because it is not intentional, and efforts were probably made to reduce contamination of stocked fish by unwanted species. I estimated low propagule pressure from aquaculture escapes because such events are probably infrequent. I estimated low propagule pressure from aquarium releases and other pathways associated with economic activities even though such introductions probably occur frequently, because low numbers of individuals are probably released each time. I estimated low propagule pressure from ballast water because federal regulations limit the transfer of untreated ballast water to U. S. waters. In contrast, I estimated high propagule pressure from illegal introductions and

bait releases because these practices are widespread (Litvak and Mandrak 1993; Johnson et al. 2009), and intermediate (i.e. less than intentionally stocked species but more than aquarium releases) numbers of individuals are released each time. I estimated high propagule pressure from canals because an established population at one end of the canal could continually provide individuals to disperse through the canal.

I estimated the species-environment match for each pathway based on the likelihood that the species associated with that pathway would tolerate the environmental conditions of the Mid-Atlantic region. All pathways associated with intentional stockings, including illegal introductions, likely involved species that could tolerate local environmental conditions because these species would generally be selected based on the expectation that they would survive in the region. I estimated that hitch hikers would also survive in the region because they must survive under similar conditions as intentionally stocked species prior to stocking. I expected that most species used in aquaculture would be tolerant of local environmental conditions because they must survive in outdoor aquaculture ponds. In contrast, I expected that most aquarium species would not tolerate local environmental conditions because they are primarily tropical. Pathways associated with other economic activities such as the live food trade and ballast water transfers may involve species with a wide range of origins and environmental tolerances; thus, I estimated a variable species-environment match for these pathways. Canals and bait releases mostly involve species that are already established or native to one part of the region; therefore, I estimated a high species-environment match for these pathways.

I then rated the probability of establishment of each pathway based on my estimates of propagule pressure and species-environment match. Pathways that were estimated to involve high or low propagule pressure and species-environment match were rated as having a high or low probability of establishment, respectively. When estimates differed between the two criteria, I rated the pathway as having a moderate probability of establishment.

I estimated the probability of introductions being recorded or otherwise documented for each pathway. Most intentional stockings are probably recorded in some format; however, many hitch hikers with stocked fish are probably not detected at the time of stocking, and records are probably not kept for this pathway. Introductions from all other pathways are not likely reported, save for aquaculture escapes, which may be documented in some cases (e.g., if aquaculture companies are required to report escapes, or if they file insurance claims after a flood).

I estimated whether species introduced through a given pathway could be readily identified as nonnative by an average ichthyologist. I expected that most intentionally stocked species, including

illegally stocked species, would be easily identified as nonnative because these species are primarily popular game fish whose native ranges are well known. Species stocked for unknown reasons and hitch hikers with stocked fish probably ranged considerably in the obviousness of their native status, depending on how well-known the species was and how far it was from its native range. Most species associated with economic activities would probably be easy to identify as nonnative because the majority are not native to the region. Conversely, species introduced by bait release would often be difficult to identify as nonnative because many bait species are transferred from adjacent basins, and the historic native ranges of many of these species are poorly understood (Jenkins and Burkhead 1994). I expect the obviousness of native status of species that disperse through canals to vary because species introduced through all other pathways may be involved.

I then estimated the detectability of nonnative species introduced through each pathway based on whether introductions were likely to be recorded and whether most species in the pathway were obviously nonnative. Pathways that were estimated to have high or low probabilities of introductions being recorded and obviousness of native status were rated as having a high or low detectability, respectively. When estimates differed between the two criteria, I rated the pathway as having a moderate detectability. When one criterion was variable, I based my estimate of detectability for that pathway on the other criterion.

Comparing regulations among states

I reviewed and summarized regulations relating to the importation, possession, sale and release of nonnative species by state, particularly with respect to aquaculture and private stocking. To evaluate the degree of coordination restricting species among states, I compiled data on “dirty-listed” species (i.e., those whose possession, importation, and/or release is legally restricted or prohibited) by state, including those listed as injurious under the Lacey Act (Lacey Act 2009). The potential for state regulations to prevent introductions was evaluated, based on the number of dirty-listed species coupled with the degree of restrictions regarding importing, possessing, and releasing nonnative species. For example, states that did not restrict the release of live organisms were considered to have low potential for preventing introductions.

Bait regulations were also reviewed and summarized by state. Regulations regarding anglers and methods of collection were obtained from state guides to recreational fishing regulations. Data on regulations for vendors were obtained through personal communication with state officials. The effectiveness of regulations for preventing introductions via bait release was compared among states.

States with regulations that restricted the use or prevented the transport or release of live bait were viewed as having greater potential to reduce bait release introductions.

RESULTS

There were 96 species in 20 families introduced to the region, and 68 of these established a reproducing population in one or more HUC8s. Of these, 46 failed to establish in at least one other HUC8. There were 898 recorded introductions (after other statuses and duplicate records were removed), including 606 established species and 292 of species that failed to establish. A large majority of introductions involved intentionally stocked fish ($n = 728$), with 50 introductions through economic activities, 79 through bait releases, and 41 through other pathways. Different species and families were generally introduced through different pathways (Table 1.1). Six of the twenty families were introduced through a single pathway. Species were introduced through 1-4 pathways, with 64 (66%) introduced through a single pathway and a further 15 introduced through only similar pathways (e.g., stocked for sport and stocked for unknown reasons).

Intentionally stocked fish

Historically, state-sanctioned intentional stocking was the dominant pathway of fish introductions (>80% of records). The majority were stocked for sport, which is the most likely reason for many species stocked for 'unknown reasons'. Virtually all introductions documented prior to the 1940s involved intentional stocking, and the number and proportion such introductions remained high through the 1990s (Figure 1.1). The number of intentional stocking records decreased in the past decade.

A wide variety of species were intentionally stocked (Table 1.1). Ten families were stocked for sport, particularly centrarchids and salmonids. Clupeids and cyprinids were most commonly stocked for forage and as hitch hikers with stocked fish. Common carp were most often stocked for food, and predominantly grass carp were stocked for biocontrol. Most intentional introductions resulted in established populations, save grass carp, which were probably stocked as sterile triploids (Table 1.2). Detectability of intentionally stocked fish was assumed to be high because these introductions are usually recorded.

Economic activities

Few records with reliable dates were available for pathways associated with economic activities, limiting interpretation of temporal patterns; however, one aquaculture-escape record dated to the 2000s, as did two of three aquarium-release records. The other dated to the 1980s, suggesting these pathways are increasing in importance.

Additional records without reliable dates provided further insight into pathways associated with economic activities. Species that escaped from aquaculture were both North American and exotic (Table 1.1) but only blue tilapia (*Oreochromis aureus*) and redbelly tilapia (*Tilapia zillii*) established reproducing populations. Goldfish were the primary species introduced by aquarium release (49%) though it established only 20% of the time. Most other aquarium-release species were tropical (e.g., red-bellied pacu *Piaractus brachypomus*, oscar *Astronotus ocellatus*) and did not establish. Overall, rates of establishment were low for pathways associated with economic activities (Table 1.2). Detectability was assumed to be particularly low for aquarium releases, especially for species that failed to establish.

Bait releases

Bait releases represented a small but consistent portion of introductions since the 1940s, with an apparent peak in the 1970s (Figure 1.1). No bait releases were reported from the 2000s; however, lag times in detecting introduced bait fishes are probably high and the number of bait releases has probably not declined.

Most bait releases were cyprinids, though catostomids were also common (Table 1.1). Sixteen cyprinid species were introduced, and bluntnose minnow (*Pimephales notatus*) and fathead minnow (*Pimephales promelas*) were the most common. Bluntnose minnow established 93% of the time, whereas fathead minnow established only 33% of the time. The proportion of species released as bait that became established was high (Table 1.2) but detectability was probably very low for species that failed to establish, suggesting that the proportion of species recorded as established is greater than the actual proportion of species that became established.

Other pathways

Other pathways have been recorded since the 1950s (Figure 1.1); however, all introductions in the 'miscellaneous' category prior to the 1980s were from an unknown pathway. Though the number remains small, the proportion of overall introductions from other pathways increased dramatically in

the 2000s, even if pathways associated with economic activities are excluded. Lag times for many of these pathways are also probably high, and the current importance of other pathways is probably underestimated.

The main pathways in the 'other' category included illegal introductions, movement through canals, stream captures, and introductions through unknown pathways. Most illegal introductions were of game fishes, though alewives (*Alosa pseudoharengus*) were illegally introduced as a forage fish (Table 1.1). Cyprinids were most the most common family dispersing through canals, and catostomids and percids were most frequently associated with an unknown pathway. Detectability and probability of establishment are difficult to estimate for introductions of unknown origin (Table 1.2), and likely vary among other pathways.

Comparing dirty lists among states

Dirty lists differed considerably among states (Table 1.3). Twenty five fish taxa (families, genera, and species) were restricted by at least one state or the Lacey Act. Virginia restricts the greatest number of fish taxa (18), though New York is currently developing new regulations and proposing assessments for 79 fish species, including initial assessments for 23 (NYISC 2010). I found no list for Washington DC or West Virginia, though West Virginia restricts importation of walking catfish (*Clarias batrachus*) and snakeheads (Channidae; Z. Brown, West Virginia Department of Natural Resources [WVDNR], personal communication). Delaware restricts only four species, though flathead catfish (*Pylodictis olivaris*) are additionally described as invasive (DDNREC 2010). Consistency among states was low; only snakeheads (Channidae) are restricted by all legal entities with dirty lists, though some restrict all snakehead species while others restrict only a small subset. Grass carp are restricted by all states with dirty lists, and other Asian carps are often restricted. Eight species are restricted only by a single legal entity.

In addition to having a dirty list of restricted species, North Carolina was the only state with a clean list, which lists species that are generally exempt from restrictions regarding importation, possession, and release; however, permits are still required to stock these species in private waters. This clean-list includes 17 fish species, 9 of which are exotic to the region (NCDACS 2010). Four other species are both native and nonnative to different parts of the Mid-Atlantic region.

Comparing nonnative species regulations among states

The Mid-Atlantic region states use multiple agencies and invoke a dizzying array of regulations for managing nonnative species. These regulations are summarized for a sub-set of Mid-Atlantic region states (Pennsylvania, Maryland, and Virginia) in the Environmental Law Institute's (ELI) review of aquatic invasions in the Chesapeake Bay (ELI 2007). The variety in regulations among these three states, coupled with a lack of readily available summaries for other states (regulations concerning nonnative species are not compiled in single, accessible files for any state), precludes a detailed analysis here. In general, regulations concerning nonnative species appear to be complex and confusing. For example, aquaculture regulations in the U.S. have been labeled elsewhere as a "regulatory quagmire" (Naylor et al. 2001). Instead, I provide a general analysis of the ability of state and federal regulations to prevent or reduce the risk of invasions.

Federal regulations apply to all states and reduce the risk of invasions, but regulate only certain dirty-listed species and ballast water exchange. At the federal level, the U.S. Lacey Act prohibits the transport of listed injurious species across state lines, but not their possession (Lacey Act 2009). Ballast water exchange is mandatory under the U.S. Nonindigenous Aquatic Nuisance Prevention and Control Act, and the adoption of new ballast water technologies is required under the U.S. Coastguard Authorization Act (Thomas et al. 2009).

Most states prohibit the release of all species not native to the state (e.g., Maryland, Virginia, and Washington DC) but apparently allow species to be transplanted among watersheds within the state. Pennsylvania and New York restrict the transplant of species among watersheds within the state, but allow the release of live species when that species is native to a given watershed. It is generally unclear whether naturalized species are restricted from release in any state. Most states have dirty lists of restricted species; however, these species can generally still be imported, possessed, sold, and even stocked with a permit or other written permission (e.g., Delaware, Virginia, and North Carolina). Existing regulations in New York are a notable exception; prohibited species may not be imported, possessed, etc. and temporary exemption permits are issued only for educational, exhibition, or scientific purposes with specific terms and conditions (NYSDEC 2010b).

In general, dirty lists appear to primarily focus on species transported for the stocking of private ponds and aquaculture; however, the list of species proposed for assessment for inclusion on dirty lists in New York includes a variety of aquarium species. The stocking of private ponds and small private impoundments with fishes by the public is generally allowed. Often, permits are required and native species must be stocked, though native status with respect to watershed is generally not specified (i.e.,

species native to any part of the state are considered native) and rules pertaining to naturalized species are not specifically addressed. Most states require licenses for aquaculture facilities, and some require facility inspections (e.g., Pennsylvania).

Comparing bait regulations among states

All states allow the sale and use of live bait fishes (Table 1.4). All but Delaware require a license to sell bait, and all except Virginia require a license or permit to collect bait fishes for resale, though I found no information on vendor regulations in Washington DC. Most states keep records of vendor licenses sold. Bait fishes may be imported from out-of-state in all states except Maryland, though New York and Pennsylvania require certification of VHS-free status (MDNR 2010; NYSDEC 2010a; PFBC 2010).

For personal use, all states permit the collection of bait fishes by seine and minnow trap, though regulations vary for other collection methods. All states except New York (see below) allow unrestricted transportation of bait fishes within the state. Most alarmingly, it is legal to dump unused bait in half of the Mid-Atlantic states (Table 1.4), and it is legal to release species in Pennsylvania watersheds when they are native to that watershed (PFBC 2010). Most state guides to fishing regulations do not mention the release of live bait, though Pennsylvania, West Virginia, and Maryland guides include notes to this effect (MDNR 2010; PFBC 2010; WVDNR 2010). No guides have figures or boxes describing the risks of releasing live bait, which could educate anglers about the risks and penalties associated with releasing live bait, helping to reduce the number of anglers who release live bait. One notable exception is New York, which has a specific guide to bait fish regulations and identification (NYSDEC 2010a).

New York has the most complex and restrictive bait regulations in the region; however, the use and transport of species beyond their native range is permitted in certain situations (NYSDEC 2010a). The state allows importation, sale and transport of certified live bait, provided the angler has a dated receipt listing abundance by species and the seller's name. In addition to certified live bait, 15 species (plus 5 other species in specific locations) may be collected and sold uncertified, provided they are sold and used only in the water body where collected. The seller must provide a similar receipt and inform the angler that fishes may not be transported overland in a motorized vehicle. Finally, a wide range of species can be collected for personal use in the same water body. Common carp, goldfish, lamprey larvae, and round goby (*Neogobius melanostomus*) may not be used as bait. The New York regulations seem to be the strongest among states with respect to bait releases because importation is highly restricted and live bait collected in the state may not be transported between watersheds. West

Virginia, Delaware, Virginia and Washington DC seem to have the weakest regulations because they do not restrict the transportation or release of live bait.

DISCUSSION

The majority of established species in the Mid-Atlantic region were intentionally stocked for sport, though a variety of other pathways have contributed to the regional pool of invaders. Pathways differed greatly temporally and in the species they involve, suggesting that future introductions via emerging pathways will involve novel species, which would further exacerbate impacts of non-native species in this already heavily invaded region. Despite apparent declines in the number of documented invasions after 1995, new species are probably being introduced throughout the region. For example, between 2002 and 2010 blue catfish (*Ictalurus furcatus*) and northern snakehead (*Channa argus*) were documented in the Plummers Island area of the Potomac River and flathead catfish are expected to disperse to the area soon (Starnes 2002; Starnes et al. in press).

I classified pathways of fish introductions into four broad categories. These differ considerably from the six pathway types proposed by Hulme et al. (2008), which were ordered according to decreasing human involvement. According to Hulme et al.'s (2008) framework, 97% of known introductions in the Mid-Atlantic region would be classified as 'releases'. Their framework was designed to facilitate comparisons of pathways across taxa and ecosystems; however, my results reveal serious limitations of this framework for freshwater fishes. The main limitation was that many pathways categorized as "releases" were found to involve unique species and require different strategies for preventing invasions. Instead of following Hulme et al.'s (2008) framework, I organized pathways in four categories by similarities in options for managing, regulating, and otherwise preventing introductions. These categories are discussed separately below.

Intentional stocking

Historically, the majority of intentionally stocked species were introduced for recreational fishing purposes. Stocking began in the 19th century and increased considerably in the 1950s. By the late 1970s and early 1980s, state natural resource agencies such as the Pennsylvania Fish and Boat Commission (PFBC), Virginia Department of Game and Inland Fisheries (VDGIF) and North Carolina Wildlife Resources Commission (NCWRC) had begun to change their opinion of intentional stocking (T. Greene, PFBC; J. Odenkirk, VDGIF; D. Besler, NCWRC, personal communication), mirroring attitudes of

fisheries professionals across the continent (Courtenay and Robins 1975; Kohler and Courtenay 1986). This change reflected both heightened awareness of the impacts of nonnative species and improved understanding of the limitations of stocking for enhancing recreational fisheries (D. Besler, personal communication). Blue catfish were one of the last major game fishes stocked into the region. Some states regulate this species as a game fish (PFBC 2010; VDGIF 2010; WVDNR 2010), while others restrict it as an invasive species (MDNR 2010; Table 1.3). Given the earlier change in attitude, the large number of intentionally stocked species recorded in the early 1990s in the NASD probably reflects lag times associated with detecting species that established from earlier introductions.

Intentional stocking occurs in the Mid-Atlantic region, but less focus is now placed on the establishment of new species in new waters by state agencies than in previous decades. Game fishes are stocked in the region to maintain put-and-take fisheries and occasionally to enhance native or naturalized recreational fisheries. Grass carp are often stocked by the public for biocontrol, though sterile triploids are often required (D. Besler, personal communication). However, new species are still introduced by the public. Many states allow the stocking of small private impoundments and ponds with nonnative species by the public, creating opportunities for escape into public waters. In Virginia, nonnative species that are not on dirty lists (ELI 2007, Lacey Act 2009) may be stocked in private ponds with written permission from the VDGIF and native species may be stocked without permission (ELI 2007). Several states in the region continue to recommend stocking small private impoundments with nonnative species, particularly largemouth bass and bluegill, and are developing new recommendations for alternative species, many of which are nonnative in the mid-Atlantic region (Dauwalter and Jackson 2005).

Attitudes regarding the intentional introduction of game fishes vary globally. Kerr et al. (2005) concluded that risks of future invasions from intentional stocking of game fishes were limited in Ontario, where such stocking is widespread, and Gozlan (2008) described numerous socioeconomic advantages associated with the intentional stocking of nonnative fishes. Conversely, Clarkson et al. (2005) argued that ongoing stocking of established nonnative fishes may prevent stabilization and recovery of imperiled native fishes. Nonnative fish populations maintained through intentional stocking may act as stepping stones for further spread of nonnative species (Johnson et al. 2008), either through natural dispersal or illegal transfers by anglers. The majority of intentionally introduced nonnative fishes in the Mid-Atlantic region are found in fewer than 50% of HUC8s, suggesting the region is not saturated. This creates an invasion debt (Strayer 2010), whereby the number of invasions is expected to increase as established nonnative species spread throughout the region.

Intentional stocking is likely to continue for the foreseeable future in the Mid-Atlantic region, particularly where habitat conditions and/or angling pressure preclude the re-establishment of native species. In these situations, put-and-take programs can meet demands for recreational fisheries and reduce angling pressure on other native fish stocks. In North Carolina, risks of establishment are reduced by stocking sterile triploid trout for sport (D. Besler, personal communication) where wild trout are not able to survive. The use of sterile, certified disease-free stocks in all intentional stocking programs would decrease the risk of further invasions. Even then, risk assessments should be conducted because these stocks are never 100% free of disease, non-sterile individuals, or other hitch hikers, and individuals have escaped from sterile stocks and established reproducing populations (Naylor et al. 2001).

The greatest threats from state-sanctioned intentional introductions likely arise from the stocking of private ponds by the public. The 2010 Delaware fishing guide describes “Fish Stocking Practices” under a section addressing general non-tidal fishing regulations (DNREC 2010). The passage reads “It shall be unlawful for any person to stock any species of fish into the nontidal public waters of this State without the written permission of the Director. This regulation does not prohibit the stocking of private impoundments” (DNREC 2010). Immediately below this caption is a description of the four dirty-listed species whose possession is prohibited without written permission. Upon reading, the layman would most likely interpret this to mean that any species (save the four restricted species) can be stocked into any private impoundment, regardless of the invasiveness of that species or the connectivity of that impoundment to natural waterways. Similar regulations and descriptions exist for other states in the region. Allowing private stocking is inherently risky because the status (native versus nonnative) of most species is unknown to most laymen. Furthermore, it sends the message that independent releases of live animals are acceptable. Full bans on private stocking are unrealistic given the number of pond fisheries in the region; however, regulations requiring permits for stocking, reporting of stocking activities, and provision of proof that a species is native could considerably reduce the risks associated with this practice.

Pathways associated with economic activities

A moderate number of species were introduced in the Mid-Atlantic region through pathways associated with economic activities. With the onset of globalization, several factors interact to increase the importance of these pathways. Invasions increase through development of new technologies for the care and transport of live animals and the connection of new locations with greater speed and

efficiency via air, land, and water (Ericson 2005; Hulme 2009). The number of introductions is increasing with economic growth and volume of trade (Levine and D'Antonio 2003; Rose 2005; Westphal et al. 2008) and the diversity of species involved in these pathways is increasing with improvements in husbandry technologies, and continual demand for novel species in the aquarium and food industries (Rixon et al. 2005). Pathways associated with economic activities are most likely to include novel exotic species. Many species are tropical and cannot survive in the Mid-Atlantic region; however, the probability of establishment may increase for some with climate change (Mandrak 1989; Hellmann et al. 2008). Most species introduced through pathways associated with economic activities are released by people assuming the act is humane (e.g., aquarium releases; Courtenay 1999; Padilla and Williams 2004), though some escape captivity accidentally (e.g., if an aquaculture facility is flooded).

The aquarium and ornamental garden trade transports by far the greatest number of fish species to the Mid-Atlantic region, though the majority are tropical and cannot currently tolerate winter temperatures (Chapman 2000). One study identified 730 ornamental freshwater fishes imported to the U.S. (Chapman et al. 1997), and over 4000 freshwater fish species are involved in trade (Sales and Janssens 2003). Hardiness is automatically selected for through surviving transport and captivity, and one third of the world's worst invaders (Lowe et al. 2000) are associated with the aquarium trade (Padilla and Williams 2004). Releases of aquarium fish are common. 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. Copp et al. (2005) found that an average of 3.5 species or varieties of fish per urban pond in London were released each year. Species with characteristics associated with invasion success such as large size and aggressiveness are more likely to be released (Duggan et al. 2006). Though most aquarium species are tropical, seven species for sale around the Great Lakes were predicted to survive winter (Rixon et al. 2005), and conditions are more hospitable in the Mid-Atlantic region; seven of the HUC8s evaluated in this study have average January low temperatures $>5^{\circ}\text{C}$. Despite these risks, the industry is largely unregulated (Padilla and Williams 2004).

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 freshwater fish species (Tlustý 2002). When a species is transported to a region for continual use in aquaculture, its escape to the wild can be expected regardless of containment efforts (Townsend and Winterbourn 1992). This pathway

differs from aquarium releases because fishes used in aquaculture are not generally released intentionally.

Fishes can be introduced through a variety of other economic activities. 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). Live fish can also be purchased by mail or internet from biological supply depots (Keller and Lodge 2007). Internet orders of aquarium fish are particularly widespread and difficult to control (Ericson 2005; Gertzen et al. 2008), and most species banned in a particular state or region can easily be purchased online. The Buddhist practice of prayer release involves releasing live animals for compassionate reasons and often requires the purchase of live species (Crossman and Cudmore 1999; Shiu and Stokes 2008). Though each of these pathways is a concern in the Mid-Atlantic region, there is little information available on their relative importance or the diversity of species involved. Directed research would provide valuable information on the risks posed by each pathway.

Fishes can be transported as hitch hikers in association with other economic activities, particularly in ballast water. Though no fish species has been recorded as establishing through ballast water transfers in the Mid-Atlantic region, this pathway continues to present a significant risk of future introductions in general despite existing ballast water regulations (Ricciardi 2001). Fishes have not been documented as hitch hikers on recreational boats (aside from transfers in livewells), yet this pathway is of major importance for other aquatic invaders (Rothlisberger et al. 2010). A juvenile northern snakehead was found in macrophytes attached to the motor of a trailered boat in the Mid-Atlantic region (J. Odenkirk, personal communication), suggesting this pathway involves at least a minor risk of invasion.

Those who profit from transporting live organisms are not responsible for the consequences of resulting invasions - a classic tragedy of the commons (Reichard et al. 2005). Dirty lists have been developed in many states; however, restrictions can be difficult to enforce, do not usually involve complete bans, and tend to focus on existing invaders after the damage is done. Screening procedures for dirty lists do not necessarily account for climate change or the rapid evolution of nonnative species (Whitney and Gabler 2008). Nonnative species can evolve rapidly in their introduced range, developing tolerances to harsh environmental conditions such as cold (Preisser et al. 2008). Clearly, additional efforts are required to reduce the number of invasions associated with economic activities.

The most rapid, efficient means for reducing invasions associated with economic activities is to develop education and outreach partnerships with industry members. These could include initiatives to educate vendors regarding risks of invasions (Chang et al. 2009) and develop labeling for packaging

materials used in the sale of live species. A recent study suggests that many vendors are receptive to the idea of selling alternative species in place of those known to pose major risks as invaders (Chang et al. 2009). Vendors and zoos/aquariums should be encouraged to accept unwanted live animals (Ribeiro et al. 2009). Participation in these initiatives could be advertised to customers as examples of corporate responsibility, further increasing educational opportunities. Legislation prohibiting the release of live animals is unlikely to affect trade and should be developed for all states. Legislation with moderate effectiveness for preventing invasions could include requirements for 'do not release' labeling and restrictions on particular species known to be harmful. Such restrictions (i.e., dirty lists) must be harmonized among states and adjoining regions (ELI 2007). Again, the economic consequences of such legislation are relatively minor, and these actions are less likely to be met with strong resistance than outright bans on the use of nonnative species.

The relatively cooperative measures described above are ideal for allowing rapid action and reducing risks; however, they are unlikely to prevent invasions outright. The development of clean lists, where only species shown to be unable to survive in the wild are permitted, is a more powerful solution. Listing procedures can be expensive, and costs should be borne by the industry, following polluter-pays regulatory models (ELI 2007). Such lists should be accompanied by more stringent measures to secure aquaculture facilities, greater inspection and enforcement efforts, and higher penalties (ELI 2007). Unfortunately, those involved in economic activities involving live species are unlikely to support such regulations, and few governments are eager to restrict trade (Padilla and Williams 2004). Regardless of the approaches used, greater efforts should be made to harmonize regulations, dirty lists, and management efforts among states and organizations, particularly those in adjacent regions (ELI 2007). Regulatory frameworks should follow catchment rather than political boundaries, as each constituency remains vulnerable to invasions through other jurisdictions with weaker regulations (Perrings 2002; Peters and Lodge 2009).

Given the complexity and differences among states in regulations and how stringently they are enforced, comparisons of effectiveness for preventing invasions are difficult. For example, North Carolina's clean list seems to facilitate rather than prevent certain invasions by allowing several nonnative species to be released throughout the state. The regulations under development in New York may be the most effective for reducing risks but are not yet official and still leave many gaps, such as allowing species that have not yet been assessed for inclusion on dirty lists to be imported. Specific research into the threats posed by each invasion pathway, including the risk of invasion, the type of

species likely to invade, and the potential socioeconomic and ecological impacts will support arguments in favour of stronger regulations regarding commercial trade of live species.

Bait release

The release of bait fishes may currently be the most important pathway in the Mid-Atlantic region. Probability of establishment is high, but low detectability implies that the importance of this pathway has been underestimated (e.g., Kerr et al. 2005). Though bait releases are associated with economic activities (recreational fishing and the bait industry), this pathway is unique because most species in this category are transplants within the region or from bordering drainages and are adapted to Mid-Atlantic climatic conditions. Additionally, bait releases are probably more common and involve a greater number of individuals than releases via most pathways associated with economic activities.

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 (Litvak and Mandrak 1993) and 25% released unused bait in Manitoba (Lindgren 2006). A majority of these anglers assumed that releasing bait benefited the ecosystem (Litvak and Mandrak 1993). Ludwig and Leitch (1996) demonstrated the near certainty of 1000 to 10000 bait-bucket transfers of fishes between major drainage basins per year in North Dakota and Minnesota. Such introductions are not restricted to bait species; Ludwig and Leitch (1996) found that 30% of bait purchases in North Dakota and Minnesota contained non-bait species, and Litvak and Mandrak (1993) found that 21% of species in bait-shop holding tanks in Toronto, Ontario were illegal for use as bait.

Historically, bait releases were the second-most important pathway in the Mid-Atlantic region. At least 20 fish species have established via bait releases and most are transplanted between watersheds in the region or transferred from watersheds adjacent to the region. This is probably an underestimate given limitations in detectability, monitoring efforts, and historical data. Such limitations have led to major uncertainties regarding native species distributions, even in the best-studied parts of the region (Courtenay 2007; Starnes et al. in press). The potential for additional bait release introductions is massive. For example, only 13 of 63 cyprinid species native to Virginia have been transplanted within the state, often to a limited region (Jenkins and Burkhead 1994). Though some cyprinids are not common bait fishes, contamination of bait buckets with non-bait species is common and can involve species from families other than Cyprinidae.

Variation in bait regulations among states is common, creating gaps in regulatory frameworks at regional levels. General regulations and variations in regulations among Mid-Atlantic states were similar

to those observed for 12 north-central states by Meronek et al. (1995) who argued that “variation in regulations among states confuses anglers, hinders the bait industry, and reduces credibility of management agencies”. Such variation particularly reduces the effectiveness of regulations when bordering states share watersheds.

Several options exist for reducing introductions via bait releases. Litvak and Mandrak (1993) suggest several options, ranging from education and research through to a full ban on the use of live or preserved baits, which can be hosts for the introduction of other aquatic organisms. There is an obvious and immediate need for Mid-Atlantic region-wide regulations banning the release of live bait, which would have no effect on anglers or the bait industry. Greater efforts could be made to educate anglers and bait vendors on the dangers and penalties associated with releasing live bait. Similar to other live fish sales, ‘do not release’ labels could be provided with all sales. The Pennsylvania Department of Agriculture (PDA) has provided invasive species training to bait dealers (ELI 2007), and the guide developed by New York is an excellent educational tool (NYSDEC 2010a). Unfortunately, anglers may have found the complexity of New York’s bait regulations confusing and frustrating, as the relatively new regulations are currently under review (L. Severino, New York State Department of Environmental Control [NYSDEC], Press Release). New York State’s policies on the use of bait fishes are similar to strategies proposed by Litvak and Mandrak (1993); however, the transport of certified fishes in the state may lead to introductions where these species are not native or established. The bait industry, along with many anglers, would probably strongly oppose a full ban on the use of live bait; however, this option is not unreasonable and has been adopted by at least 9 states and provinces in North America (Litvak and Mandrak 1993). This is probably the most controversial option, but is also most likely to reduce bait-release introductions.

Other pathways

Other pathways in the Mid-Atlantic region include introductions where the pathway is unknown, illegal stocking of game fishes, and dispersal through canals. Many unknown introductions likely resulted from known pathways, highlighting difficulties in tracking and preventing invasions. Globally, illegal introductions of game fishes are a major pathway of fish invasions (Johnson et al. 2009; Ribeiro et al. 2009) and the practice is far more common in the Mid-Atlantic region than NASD records suggest (N. Burkhead, United States Geological Survey, personal communication). Johnson et al. (2009) offer several recommendations for addressing illegal introductions, such as strict region-wide regulations (banning possession of live fishes, major penalties for offenders) that send a strong message regarding

the contemptibility of the practice. They also recommend a strong response once introductions occur, including closing bodies of illegally stocked waters to fishing or levying surcharges for fishing in waters with illegally stocked species. Given the largely riverine habitats and economic importance of reservoir fisheries in the Mid-Atlantic region, fishery closures are not a realistic management option. Convincing anglers that introductions are harmful rather than beneficial is challenging, given that most sport fisheries in the region are the result of historically sanctioned introductions. Policies allowing private stocking of small private impoundments do not help to discourage similar illegal behaviours in public waters.

Though canals do not represent direct introductions of organisms by humans, dispersal that would otherwise be impossible is facilitated by their creation (Hulme et al. 2008). The Chicago Sanitary and Ship Canal is currently in the limelight (Stokstad 2010) because it provides a pathway for dispersal of bighead carp (*Hypophthalmichthys nobilis*) and silver carp (*Hypophthalmichthys molitrix*) into the Laurentian Great Lakes. Solutions, particularly permanent closure of the canal, are being hotly debated, though carp may have already breached the multi-million dollar electric barrier designed to prevent their dispersal (Stokstad 2010). Similar concerns exist in the Mid-Atlantic region for the Chesapeake and Ohio (C & O) Canal, which connects the upper and lower Potomac River by surmounting barriers to fish migration such as Great Falls, and has already served as a pathway for the dispersal of nonnative species (Starnes 2002; Starnes et al. in press). The C & O Canal has probably received less political and media attention because recreational fisheries in the upper Potomac River are of minor economic importance relative to Great Lakes fisheries; however, the canal is a major potential pathway for the dispersal of several high-impact invaders, including northern snakehead, blue catfish, and flathead catfish (Chapter 4). Options for reducing these risks include barriers to dispersal (e.g., electric barriers) and permanent separation of the C & O Canal from the Potomac River. Unfortunately, the popularity of the C & O Canal as a recreational waterway limits many of these options.

Limitations

The NASD data had several limitations that hindered interpretation of the differences among pathways of fish invasions in the Mid-Atlantic region. Dates of introduction or detection were often unavailable, limiting analysis of temporal trends, especially for individual pathways. Differences in detectability among pathways limited comparisons of the probability of establishment. Furthermore, pathways appeared to be somewhat arbitrarily assigned to species. For example, numerous records exist for northern snakehead, a particularly high-profile invader. The actual pathway of introduction for

this species is usually unknown, except in Crofton Pond, Maryland where it was released for compassionate reasons. Here, several northern snakehead were purchased from a live-food market but later released when the customer decided not to eat them (Dolin 2003). The species is listed as “stocked for food”, “released for food”, and “released for unknown reasons”, none of which specifically match the one known reason for release. Pathway of introduction cannot be confirmed for most unsanctioned or unintentional introductions; thus, most records of bait or aquarium releases have likely been assigned a pathway based on species. This renders analysis of differences in species among pathways somewhat circular, at least for pathways involving unrecorded introductions. The NASD could be improved by including information on the source of pathway designations (known versus assumed), akin to data describing date of introduction (actual versus publication). Despite these limitations, the NASD represents the best available data on fish introductions in the Mid-Atlantic region. My assessments of temporal trends and differences among pathways were not critically impaired by such limitations, and the NASD was extremely useful in my evaluation of dominant pathways of invasion.

Lag times

The decline in number of records after 1995 suggests either a decrease in invasion rates or a lag time in detecting, reporting, and recording invasions in the NASD (Keller et al. 2009). Temporal data show that establishment rates peaked in the 1970s-90s and declined sharply afterwards; however, many records from these decades probably report earlier establishments, given the change in attitude toward intentional stocking in the 1980s. Before an introduction is listed in the NASD, it must be detected and reported either directly to the NASD or published in government documents, scientific journals or books. Most NASD records are based on texts of state or regional fish assemblages, which have the greatest cumulative lag between introduction and publication. For example, flathead catfish were intentionally stocked into the Occoquan Reservoir in 1965, but the only record in the NASD is from Jenkins and Burkhead (1994), nearly 30 years later. Additionally, many historical records were entered into the NASD immediately prior to publication of Fuller et al. (1999), and since then, staff have not been available to enter all records as they arrive (W. Courtenay Jr., USGS, personal communication). Given such delays, I perceive the decline in records after 1995 as indicative of lags in detection and recording, rather than as a reflection of declining invasion rates. Species established prior to 1995 have been present long enough to be recorded and incorporated into the NASD, but species established after that time may have not yet been entered into the database. Recent records are more strongly biased in favour of species or pathways with high detectability (Keller et al. 2009), further limiting analyses of

recent trends. Lag times suggest the number of invaders in the Mid-Atlantic region, already one of the most heavily invaded in North America (Nico and Fuller 1999), is far greater than listed in the NASD.

Conclusions and recommendations

I identified major temporal shifts in dominant pathways of fish introductions in the Mid-Atlantic region and differences in probability of establishment among pathways. Species varied considerably among pathways, suggesting that many new species are likely to be introduced via emerging pathways. Bait releases, private stocking, illegal introductions, and economic activities all create major risks for future invasions. Novel species are most likely to be introduced through pathways associated with economic activities, and large numbers of species will probably be transplanted by bait release. Sanctioned and illegal private stocking will continue to facilitate the spread of game fish throughout the region.

Given such risks, prevention efforts are warranted. Hulme et al. (2008) advocate a pathway-based approach to prevention, and I identified several groups of pathways requiring similar prevention strategies. I described several rapid and reasonable education, outreach and regulatory options for quickly reducing the risks of invasions; however, more extensive approaches including stringent regulations and penalties may be warranted in many cases. Regional integration of prevention efforts and policies across states and agencies is highly recommended (ELI 2007).

Unfortunately, such recommendations have a long history of being ignored; Magnuson (1976) identified the majority of pathways discussed in this study nearly 35 years ago, and Courtenay and Taylor (1986) called for greater interagency cooperation in preventing invasions nearly 25 years ago. These recommendations helped stem the flow of intentional, sanctioned introductions, but other pathways have increased in importance. The recent proactive efforts by New York State are promising, but still leave major gaps where the potential for new introductions is high.

Table 1.1 Common families and species introduced by each pathway, with pathway titles obtained (with modifications) from the Nonindigenous Aquatic Species Database (Fuller and Benson 2009). Pathways are grouped into four categories (in bold). Values in the “Established” and “Failed” columns represent the number of 8-digit hydrologic units where each species (or all species in a family) is established, or was introduced but failed to establish. Species and families contributing fewer than 10% of the introductions for a pathway were grouped under ‘Other’. Some species and families are recorded as introduced via multiple pathways.

Family	Species	Established	Failed	% of pathway
Intentionally stocked				
Stocked for biocontrol				
Cichlidae	<i>Tilapia zillii</i>		1	7
Cyprinidae	<i>Ctenopharyngodon idella</i>		10	67
Poeciliidae	<i>Gambusia holbrooki</i>	2	2	27
Stocked for food				
Channidae	<i>Channa argus</i>	1		9
Cyprinidae	<i>Cyprinus carpio</i>	8		73
Ictaluridae	<i>Ictalurus punctatus</i>	2		18
Stocked for forage				
Clupeidae	4 species	12	12	77
Cyprinidae	3 species	1	2	10
Osmeridae	<i>Osmerus mordax</i>	2	1	10
Salmonidae	<i>Coregonus artedi</i>		1	3
Stocked for sport				
Centrarchidae	13 species	222	41	52
Salmonidae	10 species	45	34	15
Other	8 families, 18 species	79	89	33
Stocked for unknown reasons				
Centrarchidae	6 species	81	8	58
Cyprinidae	2 species	47		31
Other	7 families, 10 species	9	9	12
Hitch hiker with stocked fish				
Clupeidae	<i>Dorosoma cepedianum</i>	2		29

Cyprinidae	2 species	4	1	71
Economic activities				
Aquaculture escape				
Amiidae	<i>Amia calva</i>		1	11
Catostomidae	<i>Ictiobus cyprinellus</i>		1	11
Cichlidae	2 species	2	1	33
Cyprinidae	<i>Ctenopharyngodon idella</i>		1	11
Ictaluridae	<i>Pylodictis olivaris</i>		1	11
Salmonidae	<i>Oncorhynchus mykiss</i>		2	22
Aquarium release				
Centrarchidae	<i>Enneacanthus gloriosus</i>	1	3	10
Characidae	3 species		10	24
Cyprinidae	<i>Carassius auratus</i>	4	16	49
Other	4 families, 5 species	1	6	17
Released food fish				
Channidae	<i>Channa argus</i>	1	1	100
Bait release				
Bait release				
Catostomidae	2 species	7	1	10
Cyprinidae	16 species	41	23	81
Other	3 families, 4 species	3	4	9
Other pathways				
Accidental				
Clupeidae	<i>Dorosoma cepedianum</i>		1	100
Canal				
Cyprinidae	2 species	2		66
Moronidae	<i>Morone americana</i>		1	33
Stocked illegally				
Clupeidae	<i>Alosa pseudoharengus</i>	1		25
Esocidae	<i>Esox lucius</i>	1		25
Ictaluridae	<i>Pylodictis olivaris</i>	1		25
Moronidae	<i>Morone chrysops</i>		1	25

Stream Capture

Percidae	<i>Etheostoma zonale</i>	3		100
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Unknown pathway

Amiidae	<i>Amia calva</i>		1	4
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Catostomidae	4 species	9	2	39
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Channidae	<i>Channa argus</i>	4	4	29
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Percidae	4 species	8		29
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Table 1.2 Estimates of probability of establishment and detectability by pathway. Probability of establishment was judged based on expected propagule pressure and species-environment match for the majority of introductions in each pathway. Estimates of proportion established were derived from the total number of established and failed invasions (by species and 8-digit hydrologic unit) in the Nonindigenous Aquatic Species Database (Fuller and Benson 2009) for each pathway. Detectability (particularly for failed invasions) was judged based on the expected probability of introductions being recorded, plus the obviousness of the native status of most species introduced via that pathway.

Pathway	Propagule pressure	Species-environment match	Probability of establishment	Proportion established in NASD	Probability of introductions being recorded	Obviousness of native status	Detectability
Intentionally stocked							
Stocked for food	High	High	High	100	High	High	High
Stocked (unknown)	High	High	High	89	High	Variable	High
Hitch hiker w/ stocked fish	Low	High	Moderate	86	Low	Variable	Low
Stocked for sport	High	High	High	68	High	High	High
Stocked for forage	High	High	High	48	High	High	High
Stocked for biocontrol	Low	High	Low ¹	13	High	High	High
Economic activities							
Aquaculture escape	Low	High	Moderate	22	Variable	High	High
Aquarium release	Low	Low	Low	15	Low	High	Moderate
Ballast water transfer	Low	Variable	Moderate	N/A	Low	High	Moderate
Other releases ²	Low	Variable	Moderate	N/A	Low	High	Moderate
Bait release							
Bait release	High	High	High	65	Low	Low	Low
Other pathways							

Unknown	Unknown	Unknown	Unknown	76	Unknown	Unknown	Unknown
Canals	High	High	High	N/A ³	Low	Variable	Low
Illegal introductions	High	High	High	N/A ³	Low	High	Moderate

¹When only sterile triploids are stocked

²Other releases associated with economic activities include food fishes, prayer, biological supply, ornamental garden fishes, and internet sales

³All other pathways combined had an establishment rate of 69%.

Table 1.3 Dirty lists of restricted species in each Mid-Atlantic region state, including species listed as injurious under the Lacey Act. Species listed for New York are not currently banned, but are proposed for review under a proposed regulatory system for nonnative species (NYISC 2010). Data for Pennsylvania, Maryland, and Virginia were obtained from the Environmental Law Institute’s (ELI) review of aquatic invasions in the Chesapeake Bay (ELI 2007). Data for Delaware and North Carolina were obtained from state guides to sport fishing regulations (NCWRC 2009; DDNREC 2010). The list of injurious fishes was obtained from section 16.13 of the Lacey Act (Lacey Act 2009). Data were not available on restricted species in West Virginia and Washington DC.

Scientific Name	Common Name	NY ¹	PA	DE	MD	VA	NC	Lacey Act
<i>Carassius auratus</i>	goldfish	√	√					
Channidae (family)	snakeheads	√ ²	√	√ ³	√	√	√	√
Clariidae (family)	air-breathing catfishes					√		√
<i>Clarias batrachus</i>	walking catfish	√		√	√		√	
<i>Ctenopharyngodon idella</i>	grass carp	√	√	√	√	√	√	
<i>Cyprinella lutrensis</i>	red shiner					√	√	
<i>Gymnocephalus cernuus</i>	Eurasian ruffe	√	√		√	√	√	
<i>Hypophthalmichthys molitrix</i>	silver carp	√	√		√	√		√
<i>Hypophthalmichthys nobilis</i>	bighead carp	√	√		√	√		
<i>Hypophthalmichthys harmandi</i>	largescale silver carp							√
<i>Ictalurus furcatus</i>	blue catfish				√			
<i>Ictiobus bubalus</i>	smallmouth buffalo					√		
<i>Ictiobus cyprinellus</i>	bigmouth buffalo					√		
<i>Ictiobus niger</i>	black buffalo					√		
<i>Leuciscus idus</i>	orfe/ide		√					
<i>Monopterus albus</i>	Asian swamp eel	√ ⁴			√	√	√	
<i>Mylopharyngodon piceus</i>	black carp	√	√		√	√	√	√
<i>Neogobius melanostomus</i>	round goby	√	√		√	√	√	
<i>Proterorhinus marmoratus</i>	tubenose goby		√			√	√	
<i>Pylodictis olivaris</i>	flathead catfish	√			√			
<i>Scardinius erythrophthalmus</i>	rudd	√	√			√	√	
Serrasalminae (subfamily)	piranhas (some genera)					√	√ ⁵	
<i>Tilapia spp.</i>	tilapia	√ ⁴	√			√		

<i>Tinca tinca</i>	tench	√
<i>Vandellia cirrhosa</i>	candiru	√

¹Current regulations prohibit only silver, bighead, and black carp and all snakehead (Channidae) species

²Only bullseye snakehead (*Channa marulius*) and giant snakehead (*Channa micropeltes*) are listed as assessment priorities, and northern snakehead are listed as a priority species for initial assessment.

³Only blotched snakehead (*Channa maculata*) and northern snakehead are listed

⁴Listed as priority species for initial assessment

⁵Genera not specified in North Carolina

Table 1.4 Summary of variability in regulations regarding use of live fishes as bait, across Mid-Atlantic region states. The overall effectiveness of regulations was judged as stronger (S), moderate (M), or weaker (W), based on the number of regulations that were in place in each state. States with no limit to the maximum abundance of bait fishes in possession for personal use are denoted by “NL”. Washington DC regulated only the methods that could be used to collect bait fishes and was excluded from the table. Information on regulations concerning vendors was obtained through personal communication with state officials, with “NR” representing “no response” (P. Hulbert, New York Department of Environmental Conservation; B. Preston, West Virginia Department of Natural Resources; S. Walton, Delaware Department of Agriculture; D. Samuels, Maryland Department of Natural Resources; contacts were not specified for Pennsylvania, Virginia, and North Carolina, and were not available for Washington DC). Information on regulations concerning anglers was obtained from state guides sport fishing regulations (NCWRC 2009; DDE 2010; DDNREC 2010; MDNR 2010; NYSDEC 2010a; PFBC 2010; VDGIF 2010; WVDNR 2010).

	NY	PA	WV	DE	MD ⁶	VA	NC
Vendors							
License required to sell bait?	Yes	Yes	Yes	No	Yes	Yes	Yes
License required to collect bait for resale?	Yes	Yes	Yes	Yes ¹	Yes	No	Yes
State keeps records of vendor licenses?	Yes	Yes	NR	No	Yes	Yes	No
Can bait be imported from out of state?	Yes ²	Yes ²	YES	Yes	No	Yes	Yes
Anglers							
Is it illegal to dump unused bait?	Yes	Yes ³	Yes	No	Yes	No	No
Is within-state transport of bait restricted?	Yes	No	No	No	No	No	No
Maximum abundance for personal use ⁴	NL	50	50	NL	50	50	200
Relative effectiveness of regulations	S	M	M	W	M	W	W
Methods of collection for personal use⁵							
Dip Net		√		√	√		√
Cast Net	√		√	√	√	√	√
Angling		√		√	√	√	√
Umbrella/Lift net				√	√	√	
Hand					√	√	
Hand-held bow net					√	√	
Hand line		√			√		

Push net	√	√
Spear	√	√

¹Tidal waters only

²If certified to be free of viral hemorrhagic septicemia (VHS) and other specified diseases

³If the species is not native to that watershed

⁴Per day, in possession, or in aggregate depending on state

⁵All states allow collection by seine and minnow traps

⁶Maryland only prohibits the use of seine nets exceeding 6 feet in length and 4 feet in depth for catching bait fishes

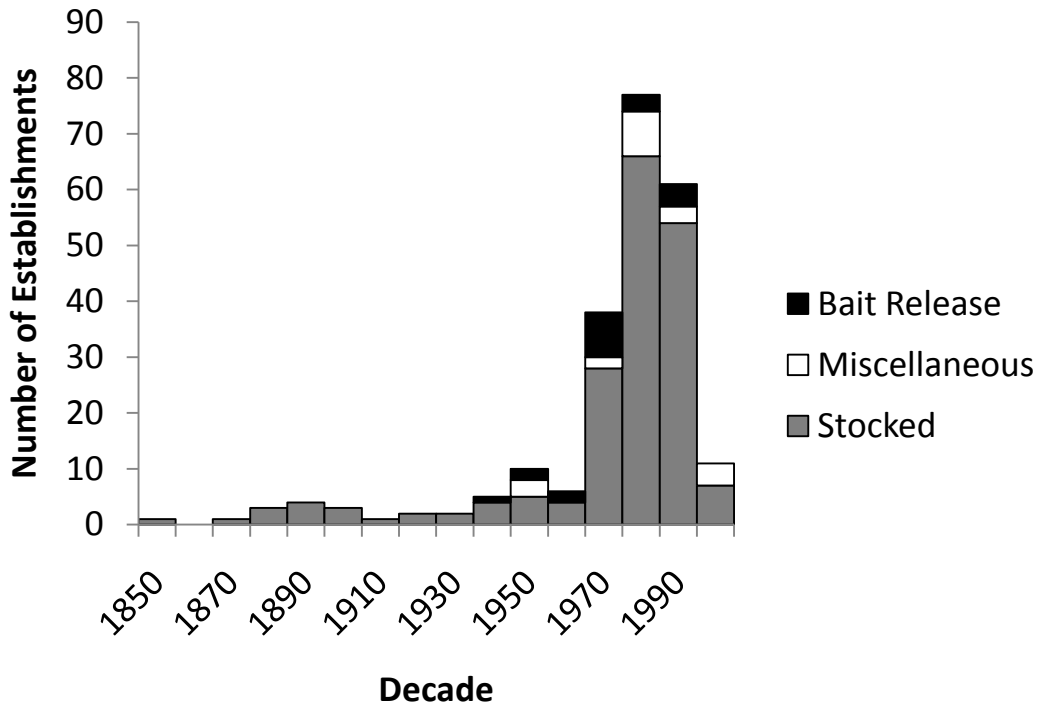


Figure 1.1 Historic trends in the number of records of establishment by pathway category and decade, with each establishment representing a fish species in an 8-digit hydrologic unit (HUC8). Records were obtained from the Nonindigenous Aquatic Species Database (Fuller and Benson 2009). When multiple records existed for a species in a HUC8, only the first record of establishment was used. The majority (69%) of these records were based on one of three texts (Cooper 1983; Menhinick 1991; Jenkins and Burkhead 1994), and were listed under the date of publication of that text (i.e., 1983, 1991, or 1994, rather than the year the species actually established). Records from these three texts that lacked an actual date of establishment were excluded because they biased evaluation of temporal trends by overestimating the number of records in 1983, 1991, and 1994. The number of records of establishment by decade was calculated for intentionally stocked pathways and bait releases; all other pathways were grouped as ‘miscellaneous pathways’.

Chapter 2: Interactions between natural and anthropogenic drivers of invasibility in freshwater ecosystems

INTRODUCTION

Introductions of non-native species are a form of human-mediated global environmental change, representing a top threat to biodiversity (Clavero and García-Berthou 2005). Eradication of established non-native species is unlikely (Mack et al. 2000) and control efforts are a costly, perpetual expense (Simberloff 2003); therefore, preventing unwanted introductions is critical (Puth and Post 2005). Better understanding of the factors regulating nonnative species richness (NNSR; Blanchet et al. 2009) is needed to help prevent invasions and conserve biodiversity (Marchetti et al. 2004a; Whittaker et al. 2005). Additionally, landscape-scale studies of nonnative species distributions can improve understanding of community assembly, because introductions provide the main large-scale experimental (albeit uncontrolled) evidence germane to assembly processes (Sax et al. 2007).

Several descriptive studies have explored abiotic, biotic, and anthropogenic processes regulating ecosystem invasibility at landscape scales (e.g., Marchetti et al. 2004a; Chiron et al. 2009). Comparative studies of observed patterns in NNSR are an important tool for understanding invasion processes at large scales (Fridley et al. 2007; Light and Marchetti 2007); however, confounding effects of colonization pressure (Chiron et al. 2009; Lockwood et al. 2009) and data biases have not always been accounted for (Pyšek et al. 2008; Richardson and Pyšek 2008; Sol et al. 2008). Disentangling such effects is critical to understanding mechanisms of species invasions. Here, I examine the relative influences of abiotic, biotic and human factors, colonization pressure, and data quality on patterns of nonnative fish species richness in watersheds in the Mid-Atlantic region of the United States.

Biotic factors may have little effect on invasibility at landscape scales. Native and nonnative species richness are often positively rather than negatively correlated across regions (Marchetti et al. 2004a; Leprieur et al. 2008; Chiron et al. 2009; Davis 2009), suggesting that biotic acceptance is more common than biotic resistance. The biotic acceptance hypothesis posits that ecosystems with heterogeneous habitats meet the niche requirements of many species, thus supporting speciose native and nonnative faunas simultaneously (Fridley et al. 2007). This scenario implies that abiotic rather than biotic mechanisms largely regulate invasibility at landscape scales.

Natural abiotic factors can contribute to invasibility by providing conditions that generally support high species diversity. Ecosystems with greater habitat heterogeneity support higher NNSR

because a wider range of species are more likely to encounter conditions that fulfill their ecological niche requirements (Davies et al. 2005). Environmental favourableness (lack of physicochemical extremes) can also contribute to invasibility (Fridley et al. 2007), and particular conditions at the time of an introduction can affect success (Moyle and Light 1996). The theory of fluctuating resource availability (Davis 2009) proposes that natural disturbances can free resources, providing opportunities for the establishment of nonnative species; however, frequent or extreme disturbance may inhibit establishment of most species (i.e., the intermediate disturbance hypothesis; Connell 1978; Davis 2009). Modification of natural disturbance regimes may play a stronger role in regulating invasibility than disturbance itself (Chytrý et al. 2008). In comparative studies of NNSR across landscapes, the role of measured abiotic factors is often secondary to factors representing human activity (Marchetti et al. 2004a; Leprieur et al. 2008; Chiron et al. 2009; Gassó et al. 2009); however, Blanchet et al. (2009) showed that abiotic characteristics were more strongly associated with fish NNSR than human activity in biogeographic realms with less economic development.

Ecosystem invasibility is expected to increase with anthropogenic disturbance (Lodge 1993; Moyle and Light 1996; Facon et al. 2006). Factors such as human population, urban and agricultural land use, and access are associated with invasibility in terrestrial ecosystems (Chiron et al. 2009; Gassó et al. 2009); however, many of these variables are also correlated with propagule pressure, leading to a general human activity hypothesis of invasion patterns (Leprieur et al. 2008). In aquatic systems, altered hydrological regimes, land development, and human population density are correlated with NNSR at landscape scales (Gido and Brown 1999; Whittier and Kincaid 1999; Marchetti et al. 2004a; Leprieur et al. 2008). Impoundment can greatly increase the invasibility of lotic systems by altering flow regimes and forming reservoirs, which are routinely stocked with nonnative fishes adapted to the novel, lentic conditions (Olden et al. 2006).

Observed patterns in NNSR across ecosystems largely depend on the number of species introduced, deemed 'colonization pressure' by Lockwood et al. (2009). Colonization pressure can be estimated using records of nonnative species introductions, including those that failed to establish reproducing populations, and is strongly correlated with landscape patterns of NNSR (Chiron et al. 2009). However, available colonization pressure data may have significant biases, which makes assessment of the role of this factor uncertain. Reliable and balanced data are difficult to obtain at landscape scales (Pyšek et al. 2008) because research effort is unlikely to be equal across landscapes (Gassó et al. 2009). Thus, patterns of NNSR are as likely to reflect research effort as propagule pressure or ecosystem characteristics. Failed invasions are more difficult to detect than successful ones,

especially in aquatic systems; thus, patterns of failed invasions may be particularly biased by research effort. I am not aware of any landscape-scale study examining the contribution of research effort to observed patterns of NNSR.

Freshwater ecosystems offer ideal landscapes for the study of invasibility, acting as biogeographical islands because natural dispersal among systems is restricted (Gido and Brown 1999; Olden et al. 2010). Though large drainage basins may be separated, natural dispersal may be possible among sub-watersheds within a given basin, leading to similarities in NNSR. Additionally, nearby watersheds in separate drainage basins may have been subjected to similar historical management policies (e.g., game fish stocking programs) or vectors of introduction associated with trade and commerce (e.g., pet releases). Such spatial autocorrelation of NNSR can confound landscape scale analyses of NNSR (Sol et al. 2008; Chiron et al. 2009; Gassó et al. 2009).

I examined ecosystem invasibility by fishes in the Mid-Atlantic region, one of the most heavily invaded regions in the U.S. (Nico and Fuller 1999). Compared to California and the Mississippi River basin, fish invasions have received little attention in this region. I explored relationships among natural watershed characteristics, anthropogenic disturbance, colonization pressure, research effort, and NNSR to understand the relative contribution of these factors to ecosystem invasibility in the Mid-Atlantic region. Based on previous studies of ecosystem invasibility, I predict that: 1) colonization pressure, research effort, and variables related to habitat heterogeneity and anthropogenic disturbance will have strong positive relationships with NNSR, and 2) biotic acceptance (i.e., positive relationships with native species richness) will be more evident than biotic resistance.

METHODS

Data collection

Nonnative fish distribution data were obtained from the Nonindigenous Aquatic Species Database (NASD). To reduce bias associated with lag times in detecting introductions (Keller et al. 2009), I included only species recorded as established by 1995 (Chapter 1). I calculated NNSR as the total number of nonnative species established in each 8-digit hydrologic unit (HUC8). Freshwater and diadromous species were included, while marine species were excluded. One hybrid (*Morone chrysops x saxatilis*) was included as an established species. Although colonization pressure is typically defined as the total number of species introduced to a given location, I excluded established species from my measure of colonization pressure because this information was already being used as the dependent

variable. Instead, colonization pressure was calculated as the number of nonnative species that failed to establish in each HUC8. This included species listed in the NASD as collected (not known to have reproduced), stocked (persist because of repeated stockings) or failed (not collected after an unspecified amount of time after introduction; definitions provided in Shafland et al. 2008).

I used ArcGIS 9.2 (ESRI Inc. Redlands, CA, USA) to compile data on ecosystem characteristics for each HUC8. Variables were related to land cover (proportion of land forested, developed, or in agriculture), habitat availability (proportion of land cover as lakes, reservoirs, and wetlands, density of small, large, and artificial streams), climate (minimum January temperature, mean annual precipitation), physical characteristics (watershed area, range in elevation), and other anthropogenic characteristics (human population density, number of dams; Table 2.1). Native species richness was defined as the total number of native species in each watershed (excluding marine species), as listed in NatureServe Explorer (www.natureserve.org). I obtained the Universal Transverse Mercator coordinates for the centroid of each watershed, and calculated the pair-wise Euclidean distances (km) among HUC8 centroids.

Research effort was estimated through detailed examination of NASD records and the NatureServe Explorer list of native species distributions. The NASD provides information on the distribution of nonnative aquatic species in the United States, based on personal communications and published reports, to inform the Aquatic Nuisance Species Task Force under the Nonindigenous Aquatic Nuisance Species Control and Prevention Act of 1990 (nas.er.usgs.gov/about/default.aspx accessed 6/30/2010). NatureServe Explorer provides similar information on the distribution of native species in the United States and Canada, based on published records and consultation with scientists in their natural heritage program (www.natureserve.org/explorer/aboutd.htm accessed 6/30/2010). Thirty eight species were listed as native by NatureServe and non-native in the NASD for at least one HUC8. For 25% (55 records) of the NASD records by HUC8 for these species, NatureServe also listed the species as native. Detailed descriptions in Jenkins and Burkhead (1994) based on historical collection records suggest that most are introduced (i.e., that NASD records are more accurate). The distribution of shared (NASD and NatureServe) records appears to reflect increased research effort in particular HUC8s because they are based on extensive contemporary collection efforts and scrutiny of detailed historic collection records. Most HUC8s had < 4 species with shared records, but the three HUC8s with the highest NNSR also had the highest number of such records (4-7). These HUC8s appear to have been subjected to relatively detailed research, based on information in the state-specific fish textbooks that were the primary sources for the NASD (Menhinick 1991; Jenkins and Burkhead 1994). The distributions

of many species demonstrating shared records suggest this pattern isn't merely spuriously correlated with NNSR (i.e., that the number of shared records doesn't automatically correlate with the number of nonnative species). For example, fallfish (*Semotilus corporalis*) and longnose dace (*Rhinichthys cataractae*) were native in 47 and 41 HUC8s, respectively. These species were each listed as non-native (and native) once, in drainages where higher research effort was expected. Thus, I interpret the number of shared records in each HUC8 as a measure of research effort.

Analytic methods

To explore relationships between ecosystem characteristics and NNSR, I used hierarchical partitioning (HP; Chevan and Sutherland 1991) and a Poisson error distribution to identify which explanatory variables had a significant, independent influence on nonnative species richness. HP assesses variable importance by partitioning variance explained into independent and joint contributions for all possible combinations of explanatory variables, and is useful for identifying variable importance rather than constructing a parsimonious predictive model (Pont et al. 2005). HP requires computation of $N!$ models (for N variables); thus, I first needed to reduce the set of explanatory variables. I did this using Akaike information criterion (AIC) stepwise model selection using the package MASS (Venables and Ripley 2002) and a Poisson-distributed generalized linear model (GLM). I then implemented HP using the HIER.PART package (Mac Nally and Walsh 2004; Walsh and Mac Nally 2008) within R (RDCT 2009) on the selected variables. I tested statistical significance for variable importance with randomization techniques (Mac Nally 2002) at 95% confidence.

To describe the direction of correlations and explore the sensitivity of HP to non-linear relationships and the direction of correlations, I applied generalized additive models (GAMs; Hastie and Tibshirani 1986). I implemented GAMs (using thin plate regression splines) by including both Poisson and negative-binomial error distributions and all explanatory variables in the MGCV package (Wood 2008) within R. I configured GAMs to automatically estimate a parsimonious degree of nonlinearity from generalized cross validation (Craven and Wahba 1979), and allowed automatic model building to penalize a variable out of the model (i.e., estimate an effect that was zero for all values of the independent variable). I then applied the AIC to final, fitted GAM models to select between Poisson and negative-binomial GAMs.

To explore the sensitivity of plausible spatial effects on variable selection and interpretation I also applied a generalized linear mixed model using a Poisson error distribution. This model included random effects for each HUC6 and a spherical semivariogram by latitude and longitude. The random-

effects structure accounted for dispersal of nonnative species to nearby watersheds, which could lead to similarities in NNSR among HUC8s within a given HUC6; the semivariogram estimated correlations between HUC8s based on linear distance, such as would be caused by changes in NNSR in HUC8s due to similar propagule pressure from shared management histories or nearby human activities. I estimated random effects using restricted maximum likelihood, which precluded further use of deviance-based model selection criteria such as AIC or Bayesian information criterion, in the NLME package (Pinheiro et al. 2009). Instead, based on a Wald test, I performed backwards model selection for all fixed effects (starting at the full model) with a significance threshold of 0.15 for all retained variables.

Different variables were selected by each analytical approach and variable importance changed considerably. No analytical approach is ideal for describing landscape patterns of invasibility; however, several variables were routinely important, suggesting that my principal findings are robust to limitations of analytical approaches and effects of spatial autocorrelation. Given the inter-correlated nature of landscape-scale data and the number of variables analyzed, variables selected in only one model likely represent spurious correlations (particularly when effects were weak). Thus, I focus my interpretation on variables that showed strong effects in at least two models.

RESULTS

There were 68 nonnative species documented in the study region, with a maximum of 21 nonnative species in a HUC8. The least-invaded HUC8s were in the southern coastal plain, east of Chesapeake Bay, and in central Pennsylvania; five had no nonnative species (Figure 2.1). HUC8s with the greatest number of invaders included the Upper Roanoke, Middle Roanoke, Upper James and Upper Dan in central and southern Virginia and North Carolina, and the Middle Potomac-Catoctin, Middle Potomac-Anacostia-Occoquan, and Rapidan-Upper Rappahanock in northern Virginia and Maryland. The most widely-distributed nonnative species included bluegill (*Lepomis macrochirus*; 66% of HUC8s), common carp (62%), largemouth bass (59%), smallmouth bass (58%), and rock bass (*Ambloplites rupestris*; 47%).

Stepwise model selection included nine variables in the HP analysis. Of these, six significantly explained the majority (91%) of independent effects on NNSR (Table 2.2). Variables describing research effort and colonization pressure were most important, followed by range in elevation and proportion of land forested. Of the other variables related to anthropogenic disturbance aside from proportion of land forested, only human population density and proportion of land in agriculture had a significant

independent effect on NNSR, though these were minor (~5% each). Other variables related to habitat availability and native species richness were identified by stepwise model selections, but did not explain a significant portion of the independent effects in HP.

The Poisson GAM was selected based on AIC. GAM results confirmed strong effects of range in elevation and proportion of land forested but the effect of colonization pressure was weaker and the measure of research effort was not selected (Table 2.2). Human population density, proportion of land developed, native species richness, and variables describing habitat availability also had strong effects. Most variables were positively correlated with NNSR at low values but demonstrated thresholds beyond which the relationship weakened or became negative (Figure 2.2). The density of small and large streams was negatively correlated with NNSR.

I found significant spatial effects, suggesting that HUC-8s nested within a HUC-6 are more likely to have similar NNSR, and that nearby HUC-8s have similar NNSR. The effects of geographic distance on NNSR similarity decreased until HUC-8 centroids were > 185 km apart, after which no spatial autocorrelation was detected. A nine-variable model was identified by AIC for the linear model after accounting for spatial effects. Colonization pressure, research effort, and range in elevation remained important but the correlation with proportion of land forested was negative and not significant. Native species richness was positively correlated with NNSR and the density of small and large streams was negatively correlated with NNSR. The proportion of land cover as wetlands and density of artificial streams were correlated with NNSR, though neither was selected by other analytical approaches.

DISCUSSION

Research effort as a determinant of NNSR

In this study, I demonstrate the importance of research effort, colonization pressure, and the interaction between natural abiotic characteristics and anthropogenic disturbance in structuring patterns of NNSR across landscapes. Previous studies have stressed that colonization pressure must be considered when examining large-scale invasion patterns (Chiron et al. 2009; Lockwood et al. 2009), though few studies quantitatively explore the effect of research effort (but see Moerman and Estabrook 2006; Pautasso and McKinney 2007). After controlling for the effects of research effort and colonization pressure, I demonstrate that invasion patterns are driven by a combination of natural abiotic factors and anthropogenic disturbance, in contrast to other large-scale studies where human activity such as

hydrologic alteration of aquatic systems appears to be the main determinant of ecosystem invasibility (e.g., Marchetti et al. 2004a; Leprieur et al. 2008; Chiron et al. 2009).

Understanding and accounting for biases in large-scale invasion datasets is challenging yet necessary. My measure of research effort (i.e., the number of species shared by a complementary database of native species) is indirect, but surrogates for variables such as propagule or colonization pressure have been effectively applied in landscape scale studies of invasions (Colautti et al. 2006; Leprieur et al. 2008). The presence of institutions of higher learning in a county has been used as a surrogate for research effort (Pautasso and McKinney 2007); however, research often occurs beyond the immediate environs of a particular institution. Here, close examination of the NASD database, its sources, and the specific details surrounding certain questionable records revealed a likely 'ichthyologist effect', similar to the 'botanist effect' suggested by Moerman and Estabrook (2006). Contemporary research effort and the availability of historical records are not uniform across the Mid-Atlantic region (Starnes 2002), leading to uncertainties in the ranges of some nonnative species, particularly those whose native ranges are poorly understood. Thus, unbalanced research efforts resulted in a notable bias in NASD lists of NNSR. Other large-scale databases/checklists of non-native species (e.g., DAISIE in Europe; Vilà et al. 2010) likely suffer from similar biases, which should be considered when analyzing regional patterns of invasibility (Pyšek et al. 2008; Sol et al. 2008).

To complement the colonization pressure hypothesis (Chiron et al. 2009; Lockwood et al. 2009), I suggest a research effort hypothesis: large-scale patterns of NNSR are influenced by geographic variation in research effort to document natural distributions of native species, especially effort occurring prior to widespread introductions. This hypothesis is relevant at both regional and global scales, and may be particularly relevant in regions with high endemism, where species transplanted between adjacent drainage basins may only be recorded as nonnative if detailed knowledge of their historical native range exists. Previous studies demonstrating positive relationships between measures of human activity such as GDP or international trade (e.g., Leprieur et al. 2008; Westphal et al. 2008) are particularly confounded by research effort. At global scales, wealthier countries or regions have greater resources to survey native biota and to monitor and record invasions (Westphal et al. 2008). Within regions such as the Mid-Atlantic, wealth and trade may not vary enough to be important drivers of research effort or invasions patterns themselves, yet research effort can vary considerably. At all spatial scales, failure to account for biases or errors in invasion records can lead to erroneous conclusions about ecosystem invasibility (Sol et al. 2008).

Colonization pressure was also a strong determinant of NNSR but may be particularly sensitive to research effort. Failed invasions are more difficult to detect (Sol et al. 2008), especially when species are introduced accidentally (Diez et al. 2009), leading to greater uncertainty in records of failed invasions. Thus, the veracity of records of failed invaders is particularly sensitive to research and monitoring efforts. I interpret the number of failed invaders as an additional measure of research effort, along with being a description of colonization pressure. Additionally, failed invasions are a measure of actual ecosystem invasibility (Lockwood et al. 2009) and can be more common in ecosystems with harsh abiotic conditions. Sufficient information does not exist to evaluate the relative contribution of research effort, colonization pressure, and invasibility to observed patterns of failed invasions; however, controlling for failed invasions allows for a more accurate assessment of the roles of anthropogenic disturbance and biotic/abiotic factors in regulating NNSR.

Abiotic factors as determinants of NNSR

After accounting for research effort and colonization pressure, abiotic factors explained significant variation in NNSR among watersheds. Notably, range in elevation and proportion of land forested were most important, while variables describing anthropogenic disturbance (e.g., human population density) had minor or no effects. Range in elevation and proportion of land forested were correlated (Spearman $r = 0.65$), and were greatest in highland watersheds in the western part of the region. Downstream watersheds in the coastal plain had low range in elevation, little forested land, and lower NNSR. In contrast with other studies of landscape-scale patterns of fish NNSR, watershed area and native species richness were not major factors (Gido and Brown 1999; Marchetti et al. 2004a). Watershed area probably had little effect because HUC8s had limited variance in area. Conversely, the limited effect of native species richness on NNSR could not be explained by low variance, because native species richness varied considerably among watersheds (20-76 species/HUC8).

Patterns of NNSR in the Mid-Atlantic region likely result from an interaction between anthropogenic and abiotic factors. The limited importance of anthropogenic factors may seem odd, given that invasibility of freshwater systems is widely considered to increase with anthropogenic disturbance (Gido and Brown 1999; Whittier and Kincaid 1999; Marchetti et al. 2004a; Leprieur et al. 2008), particularly in wealthy regions (Blanchet et al. 2009). The Mid-Atlantic certainly qualifies as wealthy but anthropogenic factors are not the primary determinants of NNSR throughout the region. Low-elevation lotic systems provide warm, often turbid, nutrient-rich conditions and support generalist species, whereas highland streams support specialist species adapted to cool, clear, nutrient-poor

waters (Scott and Helfman 2001). Watersheds with a large range in elevation naturally contain a wide variety of habitats suitable for colonization by a diversity of invaders (Davies et al. 2005; Leprieur et al. 2008). Moderate anthropogenic disturbance to highland streams can increase temperature, sediment, and nutrient loads (e.g., through deforestation) and create lentic habitats (e.g., through impoundment), all providing novel conditions suitable for generalist nonnative species (Angermeier and Winston 1998). Many species native to downstream sections were stocked in reservoirs after upstream sections were impounded (Jenkins and Burkhead 1994). Anthropogenic disturbance is not unique to watersheds with high range in elevation. For example, the number of dams and range in elevation were not correlated (Spearman $r = 0.13$). However, the effect of anthropogenic disturbance on ecosystem invasibility depends on the ecological context, especially the extent to which human alterations make available habitat more suitable for a wide array of potential invaders. Anthropogenic disturbance appears to have a greater effect on the invasibility of highland watersheds by creating novel, widely suitable habitats. The habitat diversity of coastal plain watersheds is not equally increased by disturbance and species requiring cool, clear waters cannot establish there. Additionally, many coastal plain streams and swamps are naturally harsh because of acidity, low dissolved oxygen, and dystrophic conditions which limit their suitability for many potential invaders (Smock and Gilinsky 1992).

The strong positive relationship between range in elevation and NNSR remained even after accounting for significant spatial autocorrelation in NNSR among watersheds in the region, both within and across larger drainage basins. Such autocorrelation likely reflects similarities in both abiotic characteristics and colonization pressure. Nearby watersheds are generally found in the same physiographic province, with comparable ranges in elevation and corresponding habitat heterogeneity. Colonization pressure is probably related to management practices, angling habits, and regulatory frameworks controlling vectors of introduction (e.g., baitfish, aquaculture, pet trade), all of which follow political rather than watershed boundaries. In addition, colonization pressure occurs within larger drainage basins when nonnative species disperse to connected watersheds. In the Mid-Atlantic region, numerous impoundments restrict upstream movement among watersheds; however, individuals can disperse downstream through turbines and spillways (Schmetterling and McFee 2006; Williams 2008). Thus, downstream watersheds may be subjected to particularly high colonization pressure because species introduced to highland areas may disperse downstream. That coastal plain watersheds generally had lower NNSR despite increased colonization pressure provides further evidence that abiotic factors (e.g., harsh conditions including high acidity and low dissolved oxygen in coastal plain watersheds) play a significant role in determining invasibility.

Non-linear effects and negative relationships with particular habitat types provided further evidence that habitat heterogeneity and suitability drive ecosystem invasibility. Range in elevation and proportion of land forested both exhibited thresholds beyond which NNSR did not increase. At a certain point, a large range in elevation and high forest cover may reflect steep channel gradients throughout the watershed, little disturbance and, therefore, little warm, lentic, nutrient-rich habitat and low habitat diversity. Similarly, NNSR increased with human population density up to 1000 people per km², and then decreased with further increases in human population density, supporting the intermediate disturbance hypothesis. Habitat quality and diversity can decrease with high human population densities (Nelson et al. 2009), limiting establishment even if colonization pressure is high. NNSR also decreased as the density of either small or large streams increased. Increases of one such habitat likely reflect decreases in other habitats, i.e., reduced habitat heterogeneity. Finally, native species richness had a weak positive correlation with NNSR, probably reflecting similar responses between native and nonnative species to habitat heterogeneity (Davies et al. 2005).

Biotic resistance/acceptance

The weak relationship of native species richness with NNSR provided little support for either the biotic resistance or acceptance hypotheses (Leprieur et al. 2008), and biotic characteristics appeared to have little effect on ecosystem invasibility at watershed scales. Native species richness probably has little effect on landscape-scale invasibility, and positive relationships between native and nonnative species richness likely reflect similarities in response to habitat heterogeneity (Fridley et al. 2007). Analyses involving functional diversity may be more relevant to assessments of biotic resistance, given that competition with native species may be reduced for nonnative species with novel traits (Olden et al. 2006). However, analyses of biotic effects are confounded by differences in the communities encountered by each invader. Early invaders primarily compete with native species, whereas successive invaders also compete with established nonnative species. Similarly, extirpations may alter the communities encountered by successive invaders. My results show that native species richness is a weak predictor of nonnative species richness and suggest that recent focus on such relationships (e.g., Leprieur et al. 2008; Blanchet et al. 2009) may be unwarranted.

Conclusions

Patterns of NNSR appear to be driven by natural ecosystem characteristics, human disturbance, and colonization pressure; however, biases in data quality must be accounted for before underlying

mechanisms are understood. My results primarily support hypotheses relating to colonization pressure and habitat heterogeneity, with human activity affecting invasibility by increasing both. In particular, I demonstrated how underlying abiotic characteristics mediated differential effects of anthropogenic disturbance on ecosystem invasibility. My results also illustrate the importance of examining invasion patterns of specific taxa, within regions delineated by ecologically relevant criteria (Moyle and Marchetti 2006; Hayes and Barry 2008). Different factors likely regulate terrestrial invasions in the region, and fish invasions in the Mid-Atlantic region appear to be regulated differently than in other regions (e.g., Marchetti et al. 2004a).

Watersheds in the region contain different habitats, which support different types of nonnative species. Though highland watersheds can support a wider range of nonnative species (and thus higher NNSR), invasibility of coastal plain watersheds may still be high for species with appropriate environmental tolerances (Moyle and Light 1996). Species identity is an important consideration in understanding invasibility and predicting future invasions.

These findings can aid in managing invasions in the Mid-Atlantic region, and suggest that management plans should account for abiotic conditions. Piedmont and coastal plain systems can be more effectively managed by focusing prevention efforts on species most likely to tolerate warm, turbid conditions. Targeted prevention efforts in highland watersheds are more difficult given the range of available habitats. Instead, reduction of novel conditions created by anthropogenic activities (e.g., impoundments) may reduce the invasibility of highland ecosystems by generalist invaders. Restoration activities such as dam removal and reforestation could help reduce the amount of warm, lentic habitats in highland watershed that favour many nonnative species.

Table 2.1 Ecosystem characteristics used as independent variables in analyses of patterns of nonnative fish species richness in the Mid-Atlantic region of the United States. The name of the variable is provided along with a description of the variable. The website is provided for the data source of each variable, along with the date accessed. Abbreviations used in the table include National Hydrography Dataset (NHD), National Land Cover Data (NLCD), National Oceanic and Atmospheric Administration (NOAA), National Spatial Data Infrastructure (NSDI), U.S. Department of Agriculture (USDA), and U.S. Fish and Wildlife Service (USFWS).

Variable	Description	Source, date accessed (URL)
Precipitation	Mean annual precipitation (cm)	All NOAA weather stations (1971-2000) in a watershed*, 10/26/09 (cdo.ncdc.noaa.gov/cgi-bin/climatenormals/climatenormals.pl)
JanTemp	Mean annual January low temperature (°C)	All NOAA weather stations (1971-2000) in a watershed*, 10/26/09 (cdo.ncdc.noaa.gov/cgi-bin/climatenormals/climatenormals.pl)
HUCArea	Total area of watershed (km ²)	USGS Water Resources NSDI Node, 10/12/09 (water.usgs.gov/GIS/metadata/usgswrd/XML/huc250k.xml)
Population	Number of people per km ²	National Atlas, 10/12/09 (http://www-atlas.usgs.gov/mld/ce2000t.html)
PropLake	Proportion of land cover as lakes	NHD Plus, 11/02/09 (www.horizon-systems.com/nhdplus/HSC-wth03.php)
PropReservoir	Proportion of land cover as reservoirs	NHD Plus, 11/02/09 (www.horizon-systems.com/nhdplus/HSC-wth03.php)
PropWetland	Proportion of land cover as wetlands	NHD Plus, 11/02/09 (www.horizon-systems.com/nhdplus/HSC-wth03.php)
PropForest	Proportion of land forested including deciduous, evergreen, and mixed forest, dwarf and scrub shrub	2001 NLCD, 03/05/09 (http://www.mrlc.gov/nlcd_multizone_map.hp)
PropAgricult	Proportion of land in agriculture including pasture hay and cultivated	2001 NLCD, 03/05/09 (http://www.mrlc.gov/nlcd_multizone_map.p)

	crops	hp)
PropDevelop	Proportion of land developed including low, medium, and high intensity, and open space developed	2001 NLCD, 03/05/09 (http://www.mrlc.gov/nlcd_multizone_map.p hp)
ArtifStream	Total length of canals/ditches per watershed area (km/km ²)	NHD Plus, Strahler Stream Order, 11/15/09 (www.horizon-systems.com/nhdplus/StrahlerList.php)
SmallStream	Total length of small natural streams (Strahler stream orders 1-3, Stream/River category) per watershed area (km/km ²)	NHD Plus, Strahler Stream Order, 11/15/09 (www.horizon-systems.com/nhdplus/StrahlerList.php)
LargeStream	Total length of large natural streams (Strahler stream orders 5-7, Stream/River category) per watershed area (km/km ²)	NHD Plus, Strahler Stream Order, 11/15/09 (www.horizon-systems.com/nhdplus/StrahlerList.php)
Dams	Number of dams > 1.83 m (6') in height	USFWS Fish Passage Decision Support System, 12/14/09 (fpdss.fws.gov/home;jsessionid=5F3F4144B8A3F8AB3680DCF6395CD177)
AltitudeRange	Difference between the minimum and maximum elevations in watershed (m)	USDA digital elevation models, 10/21/09 (http://datagateway.nrcs.usda.gov/)
NativeSR	Number of native species in a watershed, excluding marine species	NatureServe, 11/01/09 (naturereserve.org)
Shared	Number of species listed as both native and non-native	NatureServe, 11/01/09 (naturereserve.org) USGS NASD, 09/17/09 (nas.er.usgs.gov)
ColPressure	Number of nonnative species that failed to establish.	USGS NASD, 09/17/09 (nas.er.usgs.gov)

*If there were no stations in a watershed, the mean value from adjacent HUC8s was used.

Table 2.2 Results of analyses of patterns of nonnative fish species richness (NNSR) in the Mid-Atlantic region of the United States, with ecosystem characteristics as independent variables. NNSR data were obtained from the Nonindigenous Aquatic Species Database (Fuller and Benson 2009). Sources for ecosystem characteristic data are summarized in Table 2.1. Analyses included hierarchical partitioning (HP), generalized additive models (GAM) and generalized linear models (GLM) including spatial effects. The independent effect of each variable included in HP analysis is listed under % I. The direction of each relationship in the GLM is noted by plus/minus signs.

Variable	HP			GAM		GLM	
	% I	Z-score	p-value	X ²	p-value	t-value	p-value
ColPressure	29.8	11.80	<0.001	11.4	<0.001	+2.3	0.022
AltitudeRange	17.2	7.30	<0.001	25.6	<0.001	+2.6	0.011
PropForest	10.6	3.57	<0.001	27.8	<0.001	-1.8	0.071
Shared	24.7	11.95	<0.001			+2.9	0.005
Population	4.6	1.66	0.024	20.1	<0.001		
NativeSR	5.2	1.18	0.060	20.4	<0.001	+2.5	0.017
LargeStream	2.1	0.50	0.154	15.9	<0.001	-2.4	0.020
SmallStream	1.4	-0.05	0.260	7.3	0.007	-2.1	0.042
PropAgricult	4.4	1.30	0.048				
PropDevelop				23.5	<0.001		
Precipitation				6.7	0.034		
HUCArea				4.0	0.128		
PropWetland						-3.6	0.001
ArtifStream						+1.8	0.074

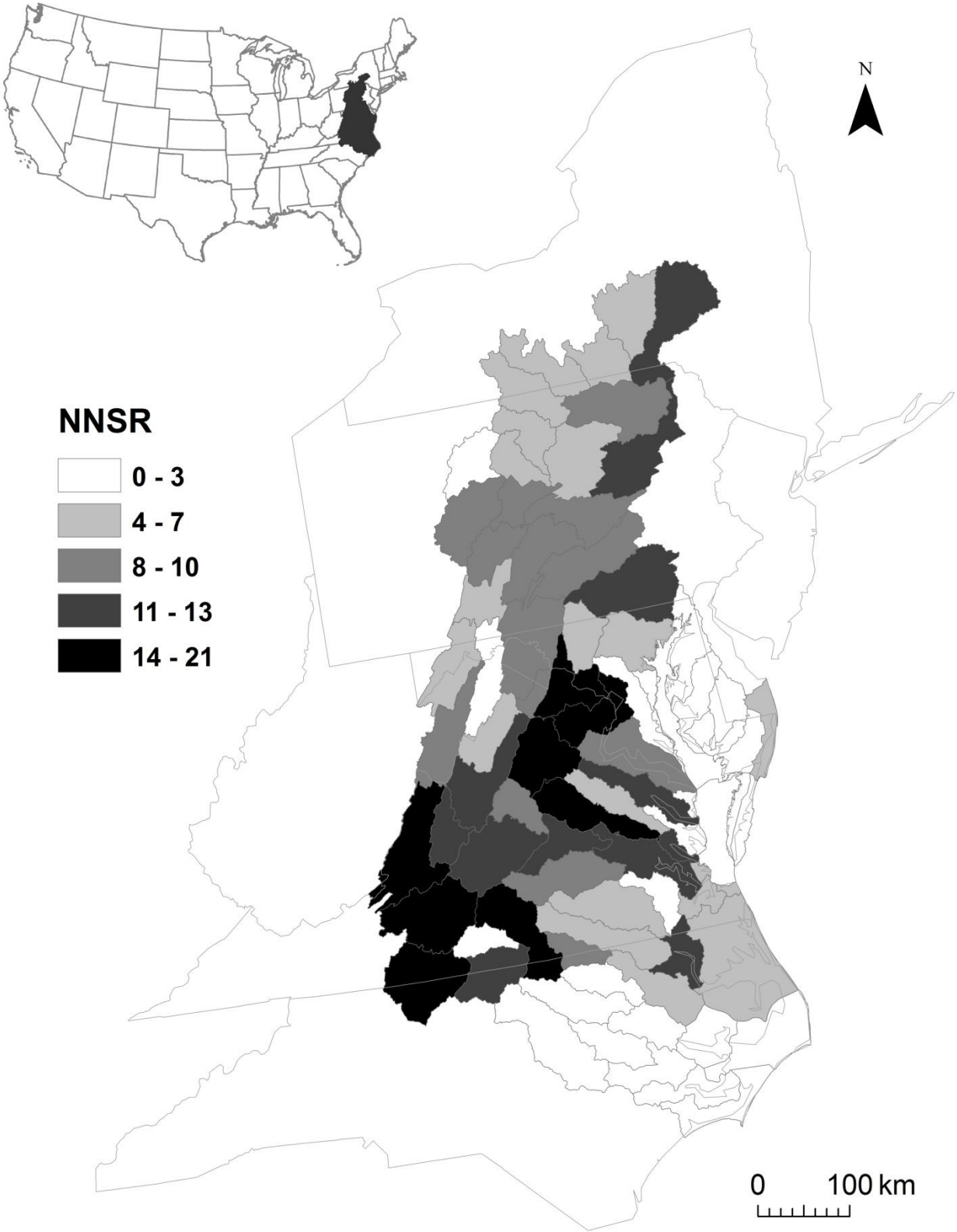


Figure 2.1 Map of the number of established nonnative fish species (nonnative species richness; NNSR) by 8-digit hydrologic units in the Mid-Atlantic region of the United States. NNSR data were obtained from the Nonindigenous Aquatic Species Database (Fuller and Benson 2009).

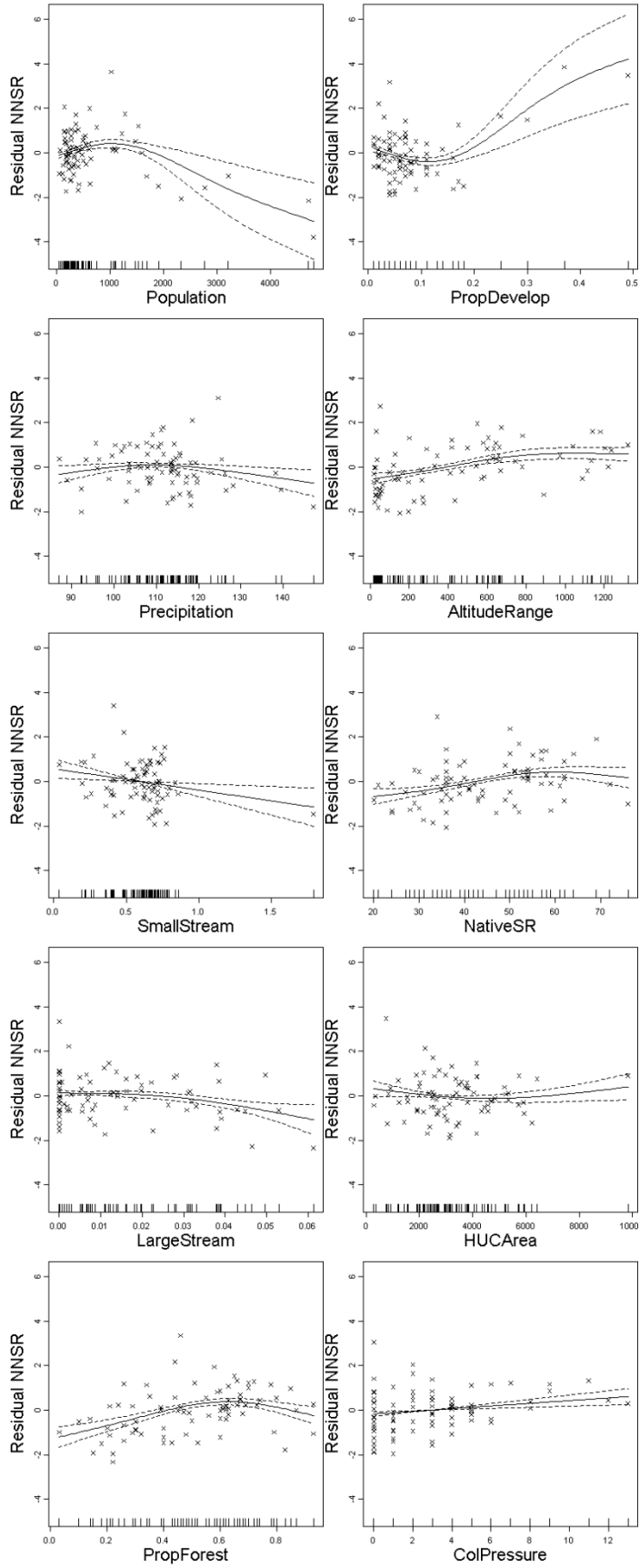


Figure 2.2 Partial dependence plots of the relationships between individual ecosystem characteristics and nonnative fish species richness (NNSR) in 8-digit hydrologic units in the Mid-Atlantic region of the United States. NNSR data were obtained from the Nonindigenous Aquatic Species Database (Fuller and Benson 2009). Sources for ecosystem characteristic data are summarized in Table 2.1. Plots were generated from the results of a generalized additive model of NNSR based on ecosystem characteristics, and show the predicted relationship between NNSR and each characteristic after accounting for the effects of all other characteristics. Explanatory variables are shown on the x-axes. Y-axes represent the difference between actual and predicted (i.e., residual) NNSR. Solid lines represent the estimated relationship, and dashed lines represent 95% confidence intervals. Residual values for each HUC8 are marked by 'x's, and hash marks above the x-axes represent the deciles of each explanatory variable.

Chapter 3: Landscape-scale determinants of nonnative communities

INTRODUCTION

Nonnative species are widely perceived as a global threat to biodiversity (Vitousek et al. 1997), and knowledge of the factors regulating invasions can improve interpretation of risk assessments and inform prevention efforts. The study of ecosystem invasibility is a major focus of invasion biology (Richardson and Pyšek 2006). Studies generally rely on nonnative species richness (NNSR) as a measure of invasibility, and seek explanations for patterns of NNSR across ecosystems or landscapes (e.g., Chytrý et al. 2008; Leprieur et al. 2008; Chiron et al. 2009).

In addition to NNSR, species identity is an important determinant of ecosystem invasibility. Drivers of invasion success differ among taxa and region (Kolar and Lodge 2002), and the invasibility of an ecosystem depends on characteristics of both the ecosystem and of the invading species. Ecosystems with equal NNSR may contain very different nonnative communities. Such patterns may be attributed to differences in invasion history (i.e., the species that were introduced differed among locations) and environmental filters affecting the type of species that can establish (Moyle and Light 1996). Each species introduced to a given system has a different likelihood of establishing a reproducing population, depending on propagule pressure (Colautti et al. 2006), the match between species traits and ecosystem characteristics, local community composition (Fridley et al. 2007), and the timing of introduction in relation to local disturbance regimes (Davis 2009). Community composition is often considered alongside richness and abundance in analyses of biotic responses to habitat loss, degradation or restoration (Houlihan and Findlay 2003; Moerke and Lamberti 2003). Similarly, the inclusion of species identity in analyses of ecosystem invasibility would provide important insight into the invasion process (i.e., how ecosystem characteristics regulate the type of species likely to invade).

Researchers have begun to consider the match between ecosystem characteristics and species identity in studies of invasibility (Vander Zanden and Olden 2008). Recent studies have examined invasions from both ecosystem-invasibility and species-invasiveness perspectives (Chong et al. 2006; Gassó et al. 2009); however, in each case NNSR was the only measure of ecosystem invasibility, and species invasiveness was considered in separate analyses. In a study of European nonnative fish communities, Leprieur et al. (2009b) analyzed patterns of nonnative species turnover in relation to dispersal limitation and environmental filters. They found that distance explained most of the variation

in nonnative communities, while environmental characteristics had little effect, and concluded that human-mediated dispersal was the main driver of nonnative fish distributions across Europe.

The relationship between nonnative species identity and ecosystem characteristics may differ among spatial scales. The regional scale is an appropriate starting point because regions are large enough to exhibit strong environmental gradients, yet small enough to have similar histories of species introductions throughout. Regions may also be subjected to similar invasive species management protocols that would benefit from assessments of patterns of invasions. For example, the Mid-Atlantic Panel on Aquatic Invasive Species addresses nonnative species issues for the Mid-Atlantic region (<http://www.midatlanticpanel.org> accessed 07/28/2010), the focus of my study. At regional scales, aquatic systems are ideal units of study because they act as biogeographic islands with distinct natural boundaries (Gozlan et al. 2010), and within aquatic systems, fishes are often the best-studied taxon. The existence of databases of nonnative fish distributions such as the Nonindigenous Aquatic Species Database (NASD) facilitates analysis of the factors structuring nonnative communities.

In this study, I examine relationships between nonnative fish community composition and ecosystem characteristics. I begin by grouping 8-digit hydrologic units (HUC8s) by their nonnative communities and describing the species associated with each group. I then test the hypothesis that groups of HUC8s with similar nonnative communities also share similar ecosystem characteristics. Nonnative communities may be structured by colonization pressure (Lockwood et al. 2009), rather than ecosystem characteristics, if historical introductions of particular species varied spatially. Sufficient historical data do not exist to account for such patterns at the community level in the Mid-Atlantic region, but multiple records of failed and successful introductions exist for certain species. Therefore, I also test the hypothesis that ecosystem characteristics determine the likelihood of establishment of individual species to provide further evidence that community-level patterns are not simply a reflection of colonization pressure.

METHODS

Data collection

Non-native fish distribution data were obtained from the NASD. To reduce bias associated with lag times in detecting introductions, I included only species recorded as established by 1995 (Chapter 1). I created a presence/absence matrix of established species by HUC8. Additionally, I calculated the total number of HUC8s where each species established or failed to establish. The latter designation included

species listed in the NASD as collected (not known to have reproduced), stocked (persists because of repeated stockings) or failed (not collected after an unspecified amount of time after introduction; definitions provided in Shafland et al. 2008). Species native to some HUC8s yet introduced elsewhere within the Mid-Atlantic region were considered native transplants. Species introduced from outside of the region were considered exotic, regardless of their continent of origin. Ecosystem characteristics described in Chapter 2 were used for analysis, excluding native species richness, the number of shared species, and colonization pressure (Table 2.1).

Data preparation

Certain species and samples were removed prior to multivariate analyses. Two HUC8s (Upper Chesapeake Bay, Lower Chesapeake Bay) were removed because they were nearly entirely marine, and five HUC8s were removed because they had no established non-native species. Rare species found in <5% of the remaining samples (HUC8s) were removed to reduce their influence on multivariate analyses (McCune and Grace 2002). Common species retained for analyses are listed in Table 3.1. After deleting rare species, one additional HUC8 was removed because it had no common species.

Canonical correspondence analysis

I initially described the relationship between species and ecosystem characteristics by applying canonical correspondence analysis (CCA) with CANOCO 4.53 (ter Braak and Smilauer 2004). To improve normality, proportional variables (9) were arcsine transformed and other variables (6) were $\log_{(x+1)}$ transformed. Biplot scaling was selected, focusing on inter-species distances. The stepwise significance ($\alpha = 0.05$) of adding ecosystem characteristics to the model was tested by 999 Monte Carlo permutations (ter Braak and Smilauer 1998). Ecosystem characteristics identified by forward selection as contributing significant variation were retained. Biplots were generated to provide a visual assessment of the relationship between nonnative species and ecosystem characteristics.

Defining nonnative communities

To find and describe groups of HUC8s with similar nonnative communities, I conducted hierarchical cluster analysis and Indicator Species Analysis (ISA) in PC-ORD 5.2 (McCune and Mefford 2006). Groups of HUC8s were first defined by hierarchical cluster analysis using flexible beta linkage ($\beta = -0.25$) based on a Sorenson distance matrix, which is appropriate for species presence/absence data (McCune and Grace 2002). Two- to four-group solutions were explored, but lower-level groupings were

not considered further because they included groups with <4 samples. ISA was then conducted for two-, three-, and four-group solutions by calculating the indicator value (I_v) of each species for each group. A perfect indicator species ($I_v = 100$) would be found in all of the samples in one group and in no other samples (McCune and Grace 2002). The significance ($\alpha = 0.05$) of each indicator species was determined by 999 Monte-Carlo permutations. The four-group solution appeared to be ecologically sound and had the highest number of significant indicator species; thus, it was selected for further analyses (Figure 3.1).

Nonnative communities and ecosystem characteristics

I explored associations between ecosystem characteristics and nonnative communities with Random Forests (RF) analysis (Breiman 2001). RF is a modification of classification and regression trees where predictions are generated by creating multiple trees, each based on a bootstrapped subsample of the data and a random subset of predictor variables at each node. In this study, the categorical response variable was nonnative community type (as defined by hierarchical cluster analysis), with untransformed ecosystem characteristics as predictor variables. RF analyses were implemented through the randomForest package in R (Liaw and Wiener 2002; RDCT 2009). The default setting was used for m_{try} , the number of predictor variables available for selection at each node ($m_{try} = 3$; the square root of the total number of predictor variables) and 1000 trees were generated. Classification accuracy was estimated by comparing the predicted nonnative community for each sample to the actual nonnative community. For the six HUC8s that were excluded from analyses for having no common nonnative species, I used the RF model to predict the expected nonnative community.

RF offers strong predictive and explanatory power without overfitting models (Breiman 2001; Prasad et al. 2006; Cutler et al. 2007); however, estimates of variable importance (derived by permuting each predictor variable in turn and calculating the resulting increase in misclassification rate) can be biased by differences in scale or correlations among predictor variables (Strobl et al. 2007; Strobl et al. 2008). An alternate conditional variable permutation scheme based on RF of conditional inference trees (cRF) was developed in the party package in R to account for such biases (Hothorn et al. 2006; Strobl et al. 2007; Strobl et al. 2008). I applied this approach to evaluate the relative importance of predictor variables. Multiple analyses were conducted with different values for the parameter m_{try} because the importance of correlated predictor variables can be overestimated when m_{try} is small (Strobl et al. 2008). Partial dependence plots based on RF results were created to visually describe the relationship between the most important predictor variables and each nonnative community, independent of other predictor variables.

Individual species and ecosystem characteristics

I developed RF models to predict establishment versus failure of individual species, based on ecosystem characteristics. Analyses were conducted on species that had at least three records of both establishment and failure to establish, and variable importance was estimated. Variables that had negative importance values (implying they decreased model fit) were removed, and analyses were repeated (Goldberg and Waits 2009). Classification accuracy was estimated, and the relative importance of retained variables was verified in cRF using Strobl et al.'s (2008) approach, as described above. Partial dependence plots were created from RF models for the most important predictor variables. RF models were used to predict whether a species would establish a reproducing population if introduced to HUC8s where there were no records of introduction.

RESULTS

Canonical correspondence analysis

Six variables contributed significantly to the model, including temperature, range in elevation, proportion of land cover as lakes, population density, number of dams, and precipitation. Only the first two canonical axes were presented because they explained 64% of the variance in the relationship between species and ecosystem characteristics (45 and 19%, respectively; Table 3.2). The first axis represented a gradient of HUC8s with high-to-low temperature and precipitation, low-to-high range in elevation, and few-to-many dams (Figure 3.2). The second axis represented a gradient of HUC8s with a low-to-high proportion of land cover as lakes, and high-to-low range in elevation and human population density.

Rainbow trout and brown trout (*Salmo trutta*), smallmouth bass, rock bass, fathead minnow and banded darter (*Etheostoma zonale*) were all strongly associated with a high range in elevation and a large number of dams, and low temperature and precipitation (i.e., the first axis), whereas threadfin shad (*Dorosoma petenense*), white crappie (*Pomoxis annularis*), walleye (*Sander vitreus*), warmouth (*Lepomis gulosus*) and blue catfish had opposite associations (Figure 3.2). Warmouth and blue catfish, along with torrent sucker (*Thoburnia rhotroeca*), bluntnose minnow and bluehead chub (*Nocomis leptocephalus*) were associated with a low proportion of land cover as lakes and high human population (the second axis), whereas quillback (*Carpionodes cyprinus*) and white bass (*Morone chrysops*) had opposite associations. Several species, including widespread species such as largemouth bass and

bluegill, were found at the center of the biplot, implying relatively neutral relationships with ecosystem characteristics.

Defining nonnative communities

Four distinct groups of HUC8s with similar nonnative communities were identified with hierarchical cluster analysis (Figure 3.1a) and described by significant indicator species (Table 3.3). Each community was named for the species with the highest indicator value. The largemouth bass community was most widespread (found in 34 HUC8s) and included bluegill, channel catfish, bluntnose minnow, and warmouth as significant indicator species. The smallmouth bass community was also widespread (found in 24 HUC8s) and included rock bass, brown trout, and banded darter as significant indicator species. The two remaining communities were relatively uncommon (found in 7 HUC8s each) and had a single significant indicator species each: black crappie (*Pomoxis nigromaculatus*), and white crappie.

Species that were not significant indicators provided additional insight into differences among nonnative communities. White crappie community HUC8s were species-poor, containing only species that were common throughout the Mid-Atlantic region (bluegill and common carp). A few additional species were found in black crappie community HUC8s (e.g., walleye, rainbow trout), though these species were also common in HUC8s with bass communities. Many species not found in HUC8s with crappie communities were present in HUC8s with bass communities (especially largemouth bass community HUC8s), including threadfin shad, gizzard shad (*Dorosoma cepedianum*), green sunfish (*Lepomis cyanellus*), striped bass (*Morone saxatilis*), bluehead chub, and torrent sucker. Quillback, flathead catfish, and bull chub (*Nocomis raneyi*) were only found in largemouth bass community HUC8s and fathead minnow were only found in smallmouth bass community HUC8s. Significant indicator species were sometimes found in HUC8s with other communities (Table 3.3). Largemouth bass and bluegill were found in many smallmouth bass community HUC8s, whereas smallmouth bass had the opposite distribution. Both crappie species were found in a considerable portion of largemouth bass community HUC8s.

Nonnative communities and ecosystem characteristics

RF models correctly classified the nonnative community of 80.6% of HUC8s (Table 3.4). Black crappie and white crappie community HUC8s were the most commonly misclassified, particularly as having largemouth bass communities. Misclassifications often involved outlying HUC8s with

communities that differed from the surrounding HUC8s (e.g., the black crappie community HUC8 at the northern tip of the region, Figure 3.1a).

Variables associated with climate, physical characteristics and land cover had the greatest explanatory power (Figure 3.3a). At low (2-3) m_{try} values, cRF models had >97% classification success, suggesting overfitting. Classification success decreased as m_{try} increased, but differences in variable importance became more pronounced. Temperature and range in elevation were consistently important, regardless of analytical approach (RF versus cRF) or m_{try} value (Figure 3.3a). Precipitation, proportion of land forested and proportion of land cover as wetlands were also often of secondary importance; however, the first two were highly correlated with temperature and range in elevation, respectively.

The black crappie community was negatively associated with temperature and found in HUC8s with a low range in elevation (Figure 3.4). The white crappie community was positively associated with temperature and had a complex (though mostly negative) relationship with range in elevation. The largemouth bass community had a unimodal relationship with temperature and a complex but generally increasing relationship with range in elevation, and the smallmouth bass community was associated with cooler temperature and high range in elevation. Of the six HUC8s with no common nonnative species, five were predicted to have largemouth bass communities and one was predicted to have a white crappie community (Figure 3.1b).

Individual species and ecosystem characteristics

Accurate RF models were developed for the two species with the greatest number of records of both establishment and failure to establish (white crappie and walleye). Models for species with fewer than ten records of establishment and ten records of failure to establish had high misclassification rates and were not reliable. Classification rates improved for white crappie and walleye after removing variables with negative importance values, but such improvements did not occur for species with smaller sample sizes. Further iterations of removing variables with negative importance did not improve classification rates; thus, final results were obtained after a single iteration of variable removal.

The status of white crappie was correctly predicted for 91% of HUC8s where the species was introduced (Table 3.5). HUC8s where white crappie established were always correctly predicted. The most important ecosystem characteristic for predicting establishment of white crappie was the number of dams (Figure 3.3b). White crappie were more likely to establish in HUC8s with fewer than 100 dams

(Figure 3.5). Of the 45 HUC8s where no records of introduction existed for white crappie, the species was predicted to establish in 62%.

The status of walleye was correctly predicted for 80% of HUC8s where the species was introduced (Table 3.5). The most important ecosystem characteristics associated with establishment of walleye were temperature and precipitation (Figure 3.3c). Walleye were more likely to establish in HUC8s with warmer temperature and higher precipitation (Figure 3.5). Of the 43 HUC8s where no records of introduction existed for walleye, the species was predicted to establish in 74%.

DISCUSSION

Defining nonnative communities

Distinct nonnative communities exist within the Mid-Atlantic region. Though certain species are ubiquitous throughout the region (e.g., common carp), my results support the hypothesis that species differ significantly among groups of drainages. No species was found in all HUC8s in one group and absent from all other HUC8s, suggesting that the environmental characteristics discussed below serve as weak filters that affect the likelihood of establishment, but are not absolute determinants of invasion success for most species. New species introduced to the region may be more likely to invade particular HUC8s, depending on their similarity to species in existing communities.

Nonnative communities and ecosystem characteristics

Nonnative communities were structured according to gradients in climate and physical characteristics, supporting the hypothesis that ecosystems with similar characteristics support comparable nonnative communities. Additionally, nonnative richness remained an important measure of ecosystem invasibility. Compared to bass communities, less speciose crappie communities were generally found in piedmont and coastal plain HUC8s, which probably had lower NNSR because of harsher abiotic conditions (e.g., high acidity, low dissolved oxygen) and lower habitat heterogeneity (Chapter 2). However, many HUC8s with similar species richness had different nonnative communities (e.g., largemouth versus smallmouth bass communities), demonstrating the importance of nonnative species identity in describing ecosystem invasibility.

Temperature was the most important determinant of nonnative community type. Temperature increased considerably from north to south, and the smallmouth bass and black crappie communities were distributed primarily in the northern half of the region. Black crappie generally have a more

northerly range than white crappie (Scott and Crossman 1979), potentially explaining the latitudinal difference between these communities. The southern distribution of the largemouth bass community seems odd because many indicator species for this community are found far north of the Mid-Atlantic region; however, many native species show similar distributional patterns in relation to latitude and range in elevation. For example, brook trout (*Salvelinus fontinalis*) are primarily distributed north of the Mid-Atlantic region but are native throughout the Appalachians south to Georgia. The smallmouth bass community was primarily distributed throughout northwestern montane HUC8s. Here, the combination of latitude and elevation likely result in lower water temperature, which may limit the distribution of many species in the largemouth bass community.

Range in elevation was also an important determinant of nonnative community type. This factor primarily separated communities along NNSR gradients; however, range in elevation was strongly correlated with actual elevation; a common determinant of fish distributions in the region. For example, both crappie species are rarely found in montane habitats, whereas smallmouth bass are much rarer on the coastal plain (Jenkins and Burkhead 1994). It is unclear whether effects of range in elevation reflected associations with particular stream gradients, preference/avoidance of the harsh physicochemical characteristics of coastal plain habitats (Smock and Gilinsky 1992), or both.

Surprisingly, variables describing anthropogenic effects and habitat availability were not important predictors of nonnative community type, though some were of minor importance in CCA results. Anthropogenic disturbance is widely considered to be a major determinant of ecosystem invasibility as measured by species richness (Facon et al. 2006; Light and Marchetti 2007; Chiron et al. 2009), but has also been shown to affect nonnative species identity. Marchetti et al. (2004a) identified a suite of nonnative fishes associated with lentic habitats created through anthropogenic watershed alterations in California, in contrast with other nonnative species found in relatively pristine watersheds. Similarly, Olden et al. (2006) showed that many nonnative fishes associated with reservoirs in the Colorado River had traits suitable for survival in warmer, lentic waters. In my study, the limited importance of anthropogenic factors and habitat availability may be a function of scale; all HUC8s were subjected to at least moderate levels of anthropogenic disturbance (e.g., all were impounded and had modified land use). Similarly, most habitats (small streams, wetlands, etc.) were available to some degree in each HUC8. Because species were considered established if a reproducing population existed anywhere in the HUC8, even a small amount of each habitat would be sufficient for species to establish and be listed in the NASD. Anthropogenic disturbance and habitat availability may be more important

determinants of nonnative communities at finer scales. For example, nonnative communities probably differ considerably between small streams and reservoirs.

The distribution of nonnative species in the Mid-Atlantic region is likely affected by both historical patterns of introductions and ecosystem characteristics. Leprieur et al. (2009b) found that nonnative fish communities across Europe were more strongly structured by geographic distance than environmental factors, and attributed this to human-mediated dispersal (i.e., that propagule pressure varied spatially for particular species or communities). They also found that environmental factors were more important in explaining patterns of NNSR than species identity. This suggests a 'human-mediated dispersal' hypothesis for the distribution of nonnative communities. My results show a different pattern in the Mid-Atlantic region, supporting what I term the 'environmental filter' hypothesis for the distribution of nonnative communities. This hypothesis postulates that the environmental characteristics of an ecosystem regulate the establishment of individual nonnative species, ultimately structuring nonnative communities along environmental gradients across landscapes. A direct test of the environmental filter hypothesis would involve a landscape where propagule pressure was held constant for multiple species, yet environmental characteristics varied. Under the environmental filter hypothesis, such a landscape would have nonnative communities that varied with environmental gradients. NASD data are not sufficiently detailed to disentangle the effects of environmental filters and human-mediated dispersal; however, both factors probably play a role in structuring nonnative communities. The fact that relationships between nonnative communities and environmental factors were ecologically sound (e.g., crappies were sparsely distributed among montane ecosystems) provides strong support for the environmental filter hypothesis.

Additional support for the environmental filter hypothesis was provided by the fact that downstream HUC8s were less speciose. HUC8s are nested within larger-scale HUC6s, and dispersal of fishes between HUC8s within a HUC6s is more likely than dispersal between HUC8s in different HUC6s. Dispersal to upstream HUC8s in a HUC6 is probably limited by the large number of dams in the Mid-Atlantic region; however, downstream dispersal through turbines and spillways is possible (Schmetterling and McFee 2006; Williams 2008). Species established in upstream HUC8s could provide a steady, if slow, stream of potential colonizers to downstream HUC8s, yet the nonnative community of may downstream HUC8s was significantly different from those found upstream and included fewer species. This pattern provides further evidence that environmental filters are more important than dispersal in structuring nonnative communities among HUC8s in the Mid-Atlantic region.

The potential nonnative distribution of transplanted species was limited by their native distribution, though no common transplanted species was native to more than 55% of HUC8s. More importantly, no species was present in all HUC8s: even widely-introduced largemouth bass were absent from >25%. Though largemouth bass were only recorded as failed in two HUC8s, they have probably been introduced into all (or nearly all) HUC8s in the region, given the popularity of this game fish to recreational anglers. Largemouth bass were established in 47 HUC8s, native in 6, and absent from 19. Such distributions suggests that native range played only a minor role in restricting the nonnative range of largemouth bass in the Mid-Atlantic region, and that other factors, including propagule pressure and environmental filters, were involved.

Individual species and ecosystem characteristics

Models of establishment success for individual species provided ambiguous support for the environmental filter hypothesis. These models had high predictive accuracy and accounted for invasion history, showing that species distributions were not based entirely on human-mediated dispersal. Temperature, precipitation and the number of dams were all important determinants of establishment; however, the direction of these relationships was questionable. For example, walleye establishment was associated with warmer temperature even though this species is more common north of the Mid-Atlantic region (Scott and Crossman 1979), and white crappie were less likely to establish in HUC8s with a large number of dams despite a known preference for lentic conditions (Jenkins and Burkhead 1994). Because of such discrepancies, the associations between individual species and particular ecosystem characteristics may be spurious, making predictions somewhat questionable despite high model accuracy.

Interpretation of patterns of establishment for individual species may be limited by detectability of failed invasions, small sample size, and a lack of data on propagule pressure. Failed invasions are particularly difficult to detect, especially when introduction attempts are not recorded (e.g., bait release). Few records of failed invasions were available, even though many species were probably introduced to virtually every HUC8 in the region. For example, several Mid-Atlantic region states continue to recommend the stocking of largemouth bass and bluegill, along with other game fishes, in small private impoundments (Dauwalter and Jackson 2005). Additionally, establishment success is largely dependent on propagule pressure (Colautti et al. 2006), yet data were not available to quantify propagule pressure for each introduction.

Despite such limitations, the methods developed here hold great potential for predicting future spread of nonnative species. Sample size, particularly for failed invasions, could be increased by widening the geographic scope (i.e., the number of HUC8s considered). Propagule pressure could be accounted for in a number of ways, including consulting historical stocking records, or using data on angler effort or pet sales. With such improvements, the methods used in this study could provide specific lists of ecosystems highly vulnerable to invasions by particular species and would complement other approaches to modeling potential distributions of nonnative species. For example, environmental niche models such as genetic algorithm for rule-set prediction (GARP) models have been used to predict the distribution of potential invaders based on environmental correlates from their native range (Herborg et al. 2007). My models provide further information by incorporating data from ecosystems where the species has been introduced and identifying environmental characteristics associated with establishment. In addition to providing clear predictions that are relevant to managers and policy makers, such information would improve understanding of the factors regulating the establishment of nonnative species.

Assuming the relationships demonstrated by individual species models are true, environmental filters limit the establishment of each species, ultimately shaping nonnative communities. Species that rarely established may be particularly dependent on environmental conditions, whereas species that usually established are probably generalists that can survive throughout the region. Such variance in the ability to establish has likely contributed to the loosely structured communities observed in the Mid-Atlantic region, with some species restricted to ecosystems with particular characteristics and others showing more ubiquitous distributions (e.g., generalists such as common carp).

Predictions

Most HUC8s with no common nonnative species were predicted to support the largemouth bass community. This is particularly worrisome given that this community was the most diverse, and suggests the risk of invasion for these HUC8s is particularly high. Prevention efforts may be particularly warranted for these HUC8s because they are relatively uninvaded, yet are susceptible to invasion by a diverse group of common nonnative species already present in the region. White crappie and walleye have not been recorded as introduced to a majority of HUC8s in the region, and my models predict they would establish in most of these HUC8s if introduced. I expect many other species currently established in the region have the potential to spread substantially within the Mid-Atlantic region, creating a large

'invasion debt' (Strayer 2010). Efforts to prevent such spread may be optimized by focusing on watersheds where each community or species is predicted to establish.

Risk assessments for future invaders in the Mid-Atlantic region should consider how environmental gradients affect the type of species likely to invade. The limited number of indicator species for each community (1-5) precluded comparisons of species traits among communities; however, assessments of the traits of successful invaders could be conducted for each group of HUC8s with a similar nonnative community by including all nonnative species found in that group. Separate predictive models for future invaders could then be made for each group of HUC8s with a similar nonnative community (e.g., following Kolar and Lodge 2002).

Conclusions

Ecosystem invasibility varies with environmental characteristics, and depends on the type of species introduced. Consideration of nonnative species identity in addition to NNSR can improve understanding of ecosystem invasibility, leading to improvements in risk assessments of future invaders and refinements of prevention efforts. I recommend additional community-level studies of ecosystem invasibility for other regions and taxa. Species identity is expected to be an important measure of ecosystem invasibility at larger scales (e.g., continents) where environmental conditions are more variable among subregions, and at finer scales where meso- or microhabitats such as riffles and pools probably support different nonnative communities. In the Mid-Atlantic region, my findings can be used to improve predictions of which species are likely to invade particular ecosystems, and inform prevention efforts including education, management and policy decisions. For example, species in the largemouth bass community may be restricted from use in private stocking in HUC8s where this community is predicted to invade.

Table 3.1 Nonnative species established in > 5% of the 78 8-digit hydrologic units (HUC8s) in the Mid-Atlantic Region of the United States. Data were obtained from the Nonindigenous Aquatic Species Database (Fuller and Benson 2009). Values represent the number of HUC8s (of the 72 HUC8s retained for community analyses) where each species is established (E), failed to establish (F), is native (N) or is not native, nor established (NE).

Code	Scientific Name	Common Name	E	F	N	NE
Lema	<i>Lepomis macrochirus</i>	bluegill	52			20
Cyca	<i>Cyprinus carpio</i>	common carp	49			23
Misa	<i>Micropterus salmoides</i>	largemouth bass	47	2	6	19
Mido	<i>Micropterus dolomieu</i>	smallmouth bass	46	1		26
Amru	<i>Ambloplites rupestris</i>	rock bass	37		1	34
Satr	<i>Salmo trutta</i>	brown trout	28	4		44
Icpu	<i>Ictalurus punctatus</i>	channel catfish	27	1		45
Lecy	<i>Lepomis cyanellus</i>	green sunfish	27	4		45
Poni	<i>Pomoxis nigromaculatus</i>	black crappie	26	5	20	26
Poan	<i>Pomoxis annularis</i>	white crappie	23	9		49
Savi	<i>Sander vitreus</i>	walleye	22	13		50
Lemi	<i>Lepomis microlophus</i>	redeer sunfish	17	4	3	52
Pino	<i>Pimephales notatus</i>	bluntnose minnow	16		24	32
Onmy	<i>Oncorhynchus mykiss</i>	rainbow trout	15	4		57
Dope	<i>Dorosoma petenense</i>	threadfin shad	9	6		63
Legu	<i>Lepomis gulosus</i>	warmouth	7	3	22	43
Moch	<i>Morone chrysops</i>	white bass	7	4		65
Etzo	<i>Etheostoma zonale</i>	banded darter	6			66
Cacy	<i>Carpionodes cyprinus</i>	quillback	5		21	46
Doce	<i>Dorosoma cepedianum</i>	gizzard shad	5		37	30
Mosa	<i>Morone saxatilis</i>	striped bass	5	3	37	30
Pipr	<i>Pimephales promelas</i>	fathead minnow	5	10	5	62
Icfu	<i>Ictalurus furcatus</i>	blue catfish	4			68
Nole	<i>Nocomis leptcephalus</i>	bluehead chub	4		20	48
Nora	<i>Nocomis raneyi</i>	bull chub	4		9	59
Thrh	<i>Thoburnia rhothoeca</i>	torrent sucker	4		9	59

Table 3.2 Summary of canonical correspondence analysis (CCA) of common established nonnative species and ecosystem characteristics of 8-digit hydrologic units in the Mid-Atlantic Region of the United States. Nonnative species data were obtained from the Nonindigenous Aquatic Species Database (Fuller and Benson 2009). Sources for ecosystem characteristic data are summarized in Table 2.1.

CCA Element	Axis 1	Axis 2
Eigenvalues	0.218	0.094
Species-environment correlations	0.890	0.689
Cumulative percentage variance		
of species data	9.5	13.6
of species-environment relations	44.9	64.2

Table 3.3 Summary of results from Indicator Species Analysis of common established nonnative species in the Mid-Atlantic region of the United States. Data on nonnative species distributions were obtained from the Nonindigenous Aquatic Species Database (Fuller and Benson 2009). The four groups of 8-digit hydrologic units with similar nonnative communities used in this analysis were previously described by hierarchical cluster analysis. Of the 26 species analyzed, only significant indicator species are shown (i.e., species that were significantly associated with a particular group relative to random permutation). “Group” shows the cluster for which each species was a significant indicator, and groups were named for the species with the greatest indicator value (I_v). Indicator values represent the percentage of a perfect indication for a given group. The proportion of HUC8s in the group where the indicator species is established is listed under “Proportion in group”, and proportion of HUC8s in other groups where the indicator species is established is listed under “Proportion in other”.

Species	Group	I_v	p-value	Proportion in group	Proportion in other
smallmouth bass	Smallmouth Bass	60.7	0.0002	1.00	0.46
rock bass	Smallmouth Bass	56.9	0.0002	0.88	0.33
brown trout	Smallmouth Bass	48.6	0.0014	0.75	0.21
banded darter	Smallmouth Bass	25	0.0198	0.25	0.00
black crappie	Black Crappie	62.2	0.0002	1.00	0.29
largemouth bass	Largemouth Bass	60.6	0.0002	0.97	0.37
bluegill	Largemouth Bass	51.2	0.0002	1.00	0.47
channel catfish	Largemouth Bass	48.2	0.0012	0.71	0.08
bluntnose minnow	Largemouth Bass	40.3	0.0066	0.44	0.03
warmouth	Largemouth Bass	20.6	0.0396	0.21	0.00
white crappie	White Crappie	53.7	0.0004	0.86	0.26

Table 3.4 Confusion matrix showing out-of-bag error estimates for random forest (RF) analysis of the relationship between nonnative communities and ecosystem characteristics for 8-digit hydrologic units (HUC8s) in the Mid-Atlantic Region of the United States. Nonnative species data were obtained from the Nonindigenous Aquatic Species Database (Fuller and Benson 2009). Sources for ecosystem characteristic data are summarized in Table 2.1. Nonnative communities were defined using hierarchical cluster analysis and described using indicator species analysis. Overall error rate was 0.19. Row headers represent the actual nonnative community by HUC8 and column headers represent the average nonnative community predicted by RF. Error is the proportion of HUC8s in each group that was misclassified. The “Community Total” column lists the actual number of HUC8s within each community.

	Black Crappie	Largemouth Bass	Smallmouth Bass	White Crappie	Error	Community Total
Black Crappie	2	4	1	0	0.71	7
Largemouth Bass	0	32	1	1	0.06	34
Smallmouth Bass	0	4	20	0	0.17	24
White Crappie	0	3	0	4	0.43	7

Table 3.5 Confusion matrices showing out-of-bag error estimates for random forest analysis of the relationship between establishment success and ecosystem characteristics for white crappie and walleye in 8-digit hydrologic units (HUC8s) in the Mid-Atlantic Region of the United States. Nonnative species data were obtained from the Nonindigenous Aquatic Species Database (Fuller and Benson 2009). Sources for ecosystem characteristic data are summarized in Table 2.1. Row headers represent the actual status of the species by HUC8 (where introduced) and column headers represent the status predicted by RF. Error is the proportion of HUC8s in each category that was misclassified.

	Established	Failed	Error
White crappie (overall error = 0.06)			
Established	23	0	0.00
Failed	2	8	0.20
Walleye (overall error = 0.20)			
Established	19	3	0.14
Failed	4	9	0.31

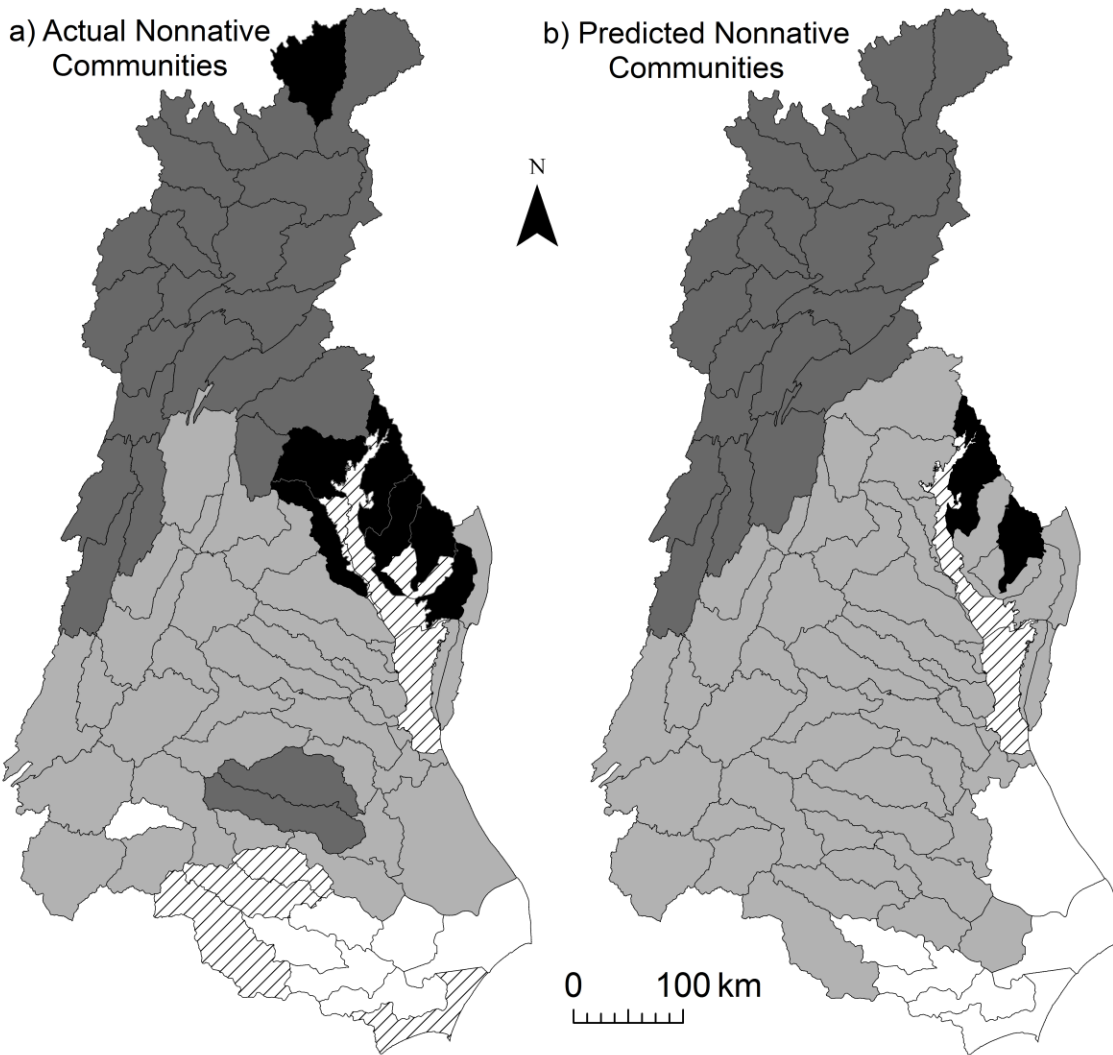


Figure 3.1 Map of the Mid-Atlantic region showing a) nonnative community by 8-digit hydrologic units (HUC8s), as defined by hierarchical cluster analysis and described by ISA and b) nonnative community predicted for each HUC8 by random forest analysis. HUC8s with no common nonnative species were excluded from a), but predictions were made for these HUC8s and are shown in b). Chesapeake Bay

HUC8s are excluded from both maps. Nonnative species data were obtained from the Nonindigenous Aquatic Species Database (Fuller and Benson 2009).

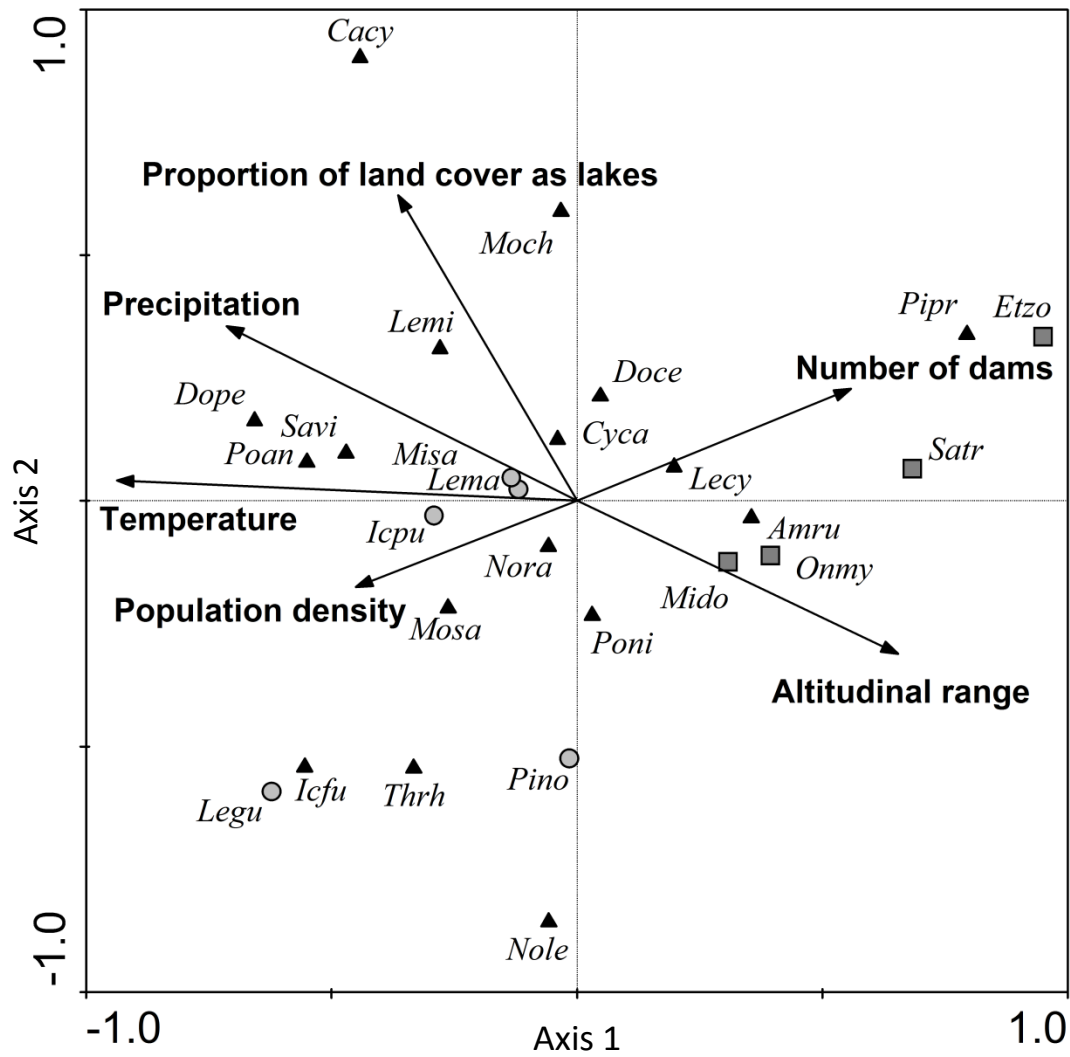
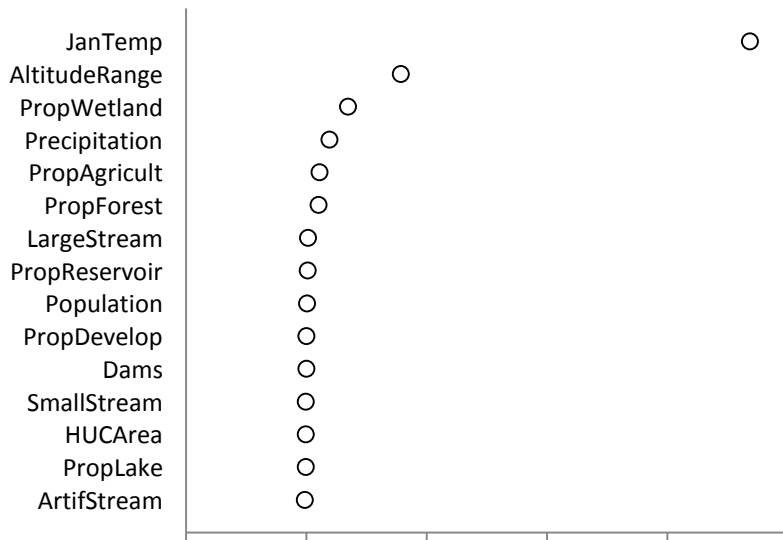


Figure 3.2 Canonical correspondence analysis biplot of nonnative species-ecosystem characteristic correlations for 8-digit hydrologic units (HUC8s) in the Mid-Atlantic Region of the United States. Nonnative species data were obtained from the Nonindigenous Aquatic Species Database (Fuller and Benson 2009). Sources for ecosystem characteristic data are summarized in Table 2.1. Species codes are defined in Table 3.1. Significant indicator species, defined by indicator species analysis, are marked by dark grey squares for the smallmouth bass community and light grey circles for the largemouth bass community. Nonnative communities were defined by hierarchical cluster analysis. All other species (including black and white crappie, which were the sole indicators for their respective communities) are marked by black triangles. Axes 1 (x-axis) and 2 are shown.

A



B



C

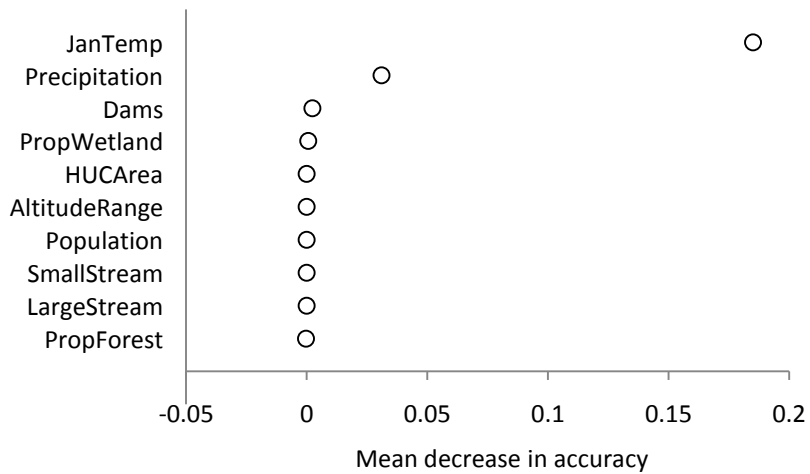


Figure 3.3 Variable importance plots from conditional variable permutation in conditional random forest analysis ($m_{\text{try}} = 8$) of A) nonnative community type, B) white crappie establishment success, and C) walleye establishment success based on ecosystem characteristics. Analyses were based on nonnative species data (obtained from the Nonindigenous Aquatic Species Database; Fuller and Benson 2009) and ecosystem characteristics of 8-digit hydrologic units (HUC8s) in the Mid-Atlantic Region of the United States. Sources for ecosystem characteristic data and variable names are summarized in Table 2.1. Nonnative communities were defined using hierarchical cluster analysis and described using indicator species analysis. Variables causing greater mean decrease in accuracy (when permuted) of the models are considered more important.

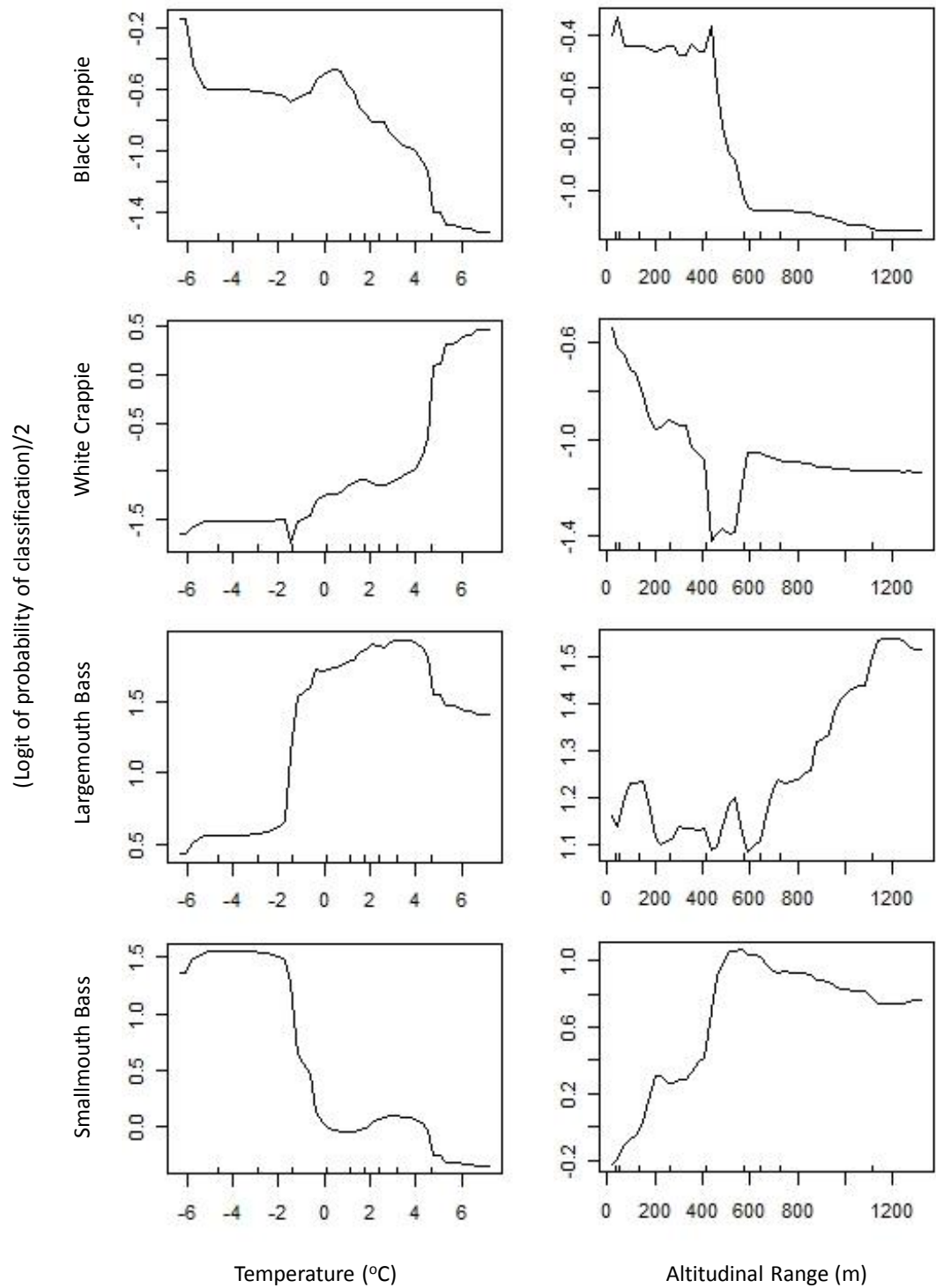


Figure 3.4 Partial dependence plots of important predictors from random forest models of nonnative community type based on ecosystem characteristics of 8-digit hydrologic units (HUC8s) in the Mid-Atlantic Region of the United States. Nonnative species data were obtained from the Nonindigenous Aquatic Species Database (Fuller and Benson 2009). Sources for ecosystem characteristic data are

summarized in Table 2.1. Nonnative communities were defined using hierarchical cluster analysis and described using indicator species analysis. Columns of graphs represent two predictor variables, and rows represent four nonnative community types. Deciles of distribution of the predictor variable are marked by dashes above the x-axes.

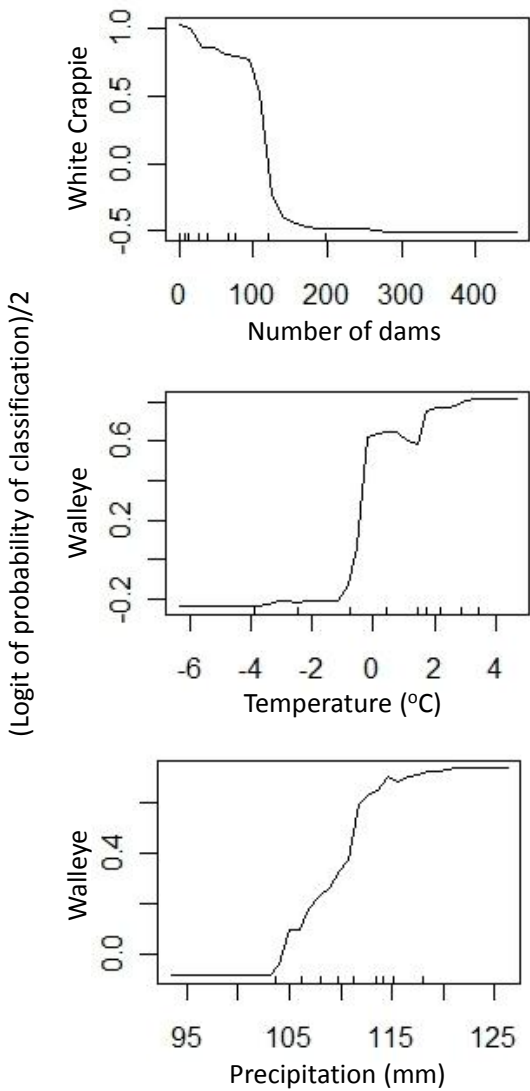


Figure 3.5 Partial dependence plots of important predictors from random forest models of individual species establishment based on ecosystem characteristics of 8-digit hydrologic units (HUC8s) in the Mid-Atlantic Region of the United States. Nonnative species data were obtained from the Nonindigenous Aquatic Species Database (Fuller and Benson 2009). Sources for ecosystem characteristic data are summarized in Table 2.1. Deciles of distribution of the predictor variable are marked by dashes above the x-axes.

Chapter 4: A comparison of approaches for quantifying impact of nonnative fishes

INTRODUCTION

The invasion process is commonly described as a series of stages or filters through which a species must pass before ecological or economic impacts occur. Stages include transport, release/introduction, establishment, spread, and impact; however, there is no consensus on the definition of the impact stage (Parker et al. 1999; Davis and Thompson 2000; Daehler 2001; Davis and Thompson 2001). The lack of a working definition contributes to difficulties in measuring and quantifying impact. In contrast to easily quantified stages with clear definitions (e.g., species that reproduce naturally after introduction are considered established), there are few studies at the impact stage (García-Berthou 2007). For example, Jeschke and Strayer (2006) included only the introduction, establishment and spread stages in their study of species transferred between Europe and North America. A clear method for measuring impact would improve predictions and management decisions regarding nonnative species likely to have the greatest impact, and allow testing of hypotheses associated with impacts of nonnative species (Parker et al. 1999; Ruesink 2003; Gherardi 2007).

Quantifying the impact of a nonnative species is difficult because socioeconomic and ecological impacts must be treated separately and a dichotomous rating (impact versus no impact) is unrealistic (Carlton 2002). Nonnative species causing ecological harm often differ from those responsible for economic losses (Shirley and Kark 2009; Gozlan et al. 2010). For example, introduced piscivores are often responsible for the extirpation of native forage fishes (Findlay et al. 2000), yet are often the basis of socioeconomically beneficial sport fisheries. Quantification of socioeconomic impact may be useful for informing management decisions but is based on cultural values, may not be scientific in nature (Andow 2005) and is likely to confound analyses of ecological patterns. Additionally, the evaluation of socioeconomic impact is a social process, and should involve feedback from a wide range of stakeholders (Davis 2009). Conversely, information on ecological impact may be limited because they are less likely to be detected and reported than economic losses (Leprieur et al. 2009a; Vilà et al. 2010). An ideal quantitative measure of impact should be objective or at least include a clear description of associated biases, and should distinguish socioeconomic and ecological impacts. To date, most classifications of species as high versus low impact have been largely subjective (Lockwood et al. 2007; Valery et al. 2008).

The study of impacts of nonnative fishes is gaining attention (Vitule et al. 2009), but lags behind analogous studies of other taxa. In their review of empirical studies of successful invaders, Hayes and Barry (2008) found that 76% of studies focused on plants and birds; only 3 of 49 studies examined freshwater fishes. Several attempts have been made to quantify the impact of nonnative fishes, including measures based on abundance, surveys of expert judgment, and reviews of documented impacts in databases (e.g., FishBase, Froese and Pauly 2010); however, the strengths, weaknesses and biases of these approaches have not been evaluated.

Impact of nonnative fishes is often quantified by reviewing descriptions of impact in databases, textbooks, and other scientific literature. Some authors have used records in FishBase or the Food and Agriculture Organization (FAO; <http://www.fao.org/fi/statist/statit.asp>) to classify species as having a high or low impact, (Ruesink 2005; Gozlan 2008). However, both of these sources likely underestimate impact, in part because impacts are not always studied and documented, and documented impacts are not necessarily entered into global databases (Leprieur et al. 2009a; Vitule et al. 2009). Continent-specific databases, including the Delivering Invasive Species Inventories for Europe database (DAISIE; <http://www.europe-aliens.org/>) in Europe and the Nonindigenous Aquatic Species Database (NASD) in the United States, may document impacts for a greater proportion of fish species than global databases, in the regions they cover (Vilà et al. 2010). Impact has also been quantified along binary or ordinal scales by reviewing scientific literature and rating invaders according to effects on native biota (Ricciardi and Atkinson 2004; Ricciardi and Cohen 2007; Ricciardi and Kipp 2008). Database and literature reviews have several limitations. Significant lag times are expected between impact occurrence, detection, and reporting (Ricciardi 2003; Leprieur et al. 2009a). Global or continental databases may not represent spatial variation in a species' impact across regions and ecosystems (Kolar and Lodge 2002).

The impact of a species in a region also can be assessed by surveying local experts and stakeholders but perception of impact by respondents depends on social values (Catford et al. 2009; Davis 2009). In a groundbreaking effort to predict potential fish invaders and their impact in the Laurentian Great Lakes, Kolar and Lodge (2002) surveyed experts, asking whether each established species was a nuisance, defined as species having undesirable ecological, economical, social, or cultural impacts. Despite the inclusion of ecological impact in the survey question, responses appeared to be based almost entirely on socioeconomic effects. For example, all large salmonids were classified as non-nuisance, even though piscivores commonly have major ecological impact (Chapleau et al. 1997; Cambray 2003; Mitchell and Knouft 2009). Concurrently, tubenose goby (*Proterorhinus marmoratus*) were classified as nuisance, despite low abundance and limited spatial distribution (Ricciardi 2003).

Attitudes toward nonnative species may differ significantly among stakeholder groups, including resource managers and scientists, with different weightings applied to ecological and social considerations (García-Llorente et al. 2008). Perception of the impact of game species (i.e., species that are commonly sought by sport fishermen and listed in recreational fishing regulations) may be particularly variable. Game fishes provide major social benefits (Pascual et al. 2002; Gozlan 2008), but also cause major ecological changes and are among the most harmful invaders (Cambray 2003). Improved understanding of the biases in perception of impact can be achieved by examining how impact ratings differ. For example, perception of impact may differ between game biologists (i.e., biologists whose work or research is primarily focused on game fishes) and non-game biologists, particularly if game and non-game fishes are regulated separately.

A third approach for assessing impact of nonnative species is to infer ecological impact from observations of proportional abundances within an assemblage. Nonnative species may have indirect effects on native species, altering food webs in ways that are not readily observed without detailed study (e.g., Vander Zanden et al. 1999; Baxter et al. 2004). Expert judgment and databases of published reports are unlikely to reflect such impacts, particularly for nonnative species with limited distributions (Leprieur et al. 2009a). However, all nonnative species likely have some effect, direct or indirect, on the receiving ecosystem (Falk-Petersen et al. 2006). This effect is correlated with abundance, though the relationship may be non-linear and per-capita effects likely vary by species (Parker et al. 1999; Ricciardi 2003; Shirley and Kark 2009). Estimates of distribution and abundance, based on regional textbooks and authors' knowledge, have been used to describe impact in regional-scale studies of successful fish invaders (Marchetti et al. 2004c; Marchetti et al. 2004b; Ribeiro et al. 2008). To refine this approach, abundance may be more accurately estimated through existing collection records or by surveying fish biologists in the region of interest.

In this study, I develop and compare five approaches for quantifying the degree of impact of nonnative fishes, which can be applied at regional to drainage basin scales. I focus on fish introductions in the Mid-Atlantic region (Figure 4.1), which has among the highest numbers of nonnative fish species in the U.S. (Nico and Fuller 1999). The five approaches include: 1) reviewing documented impacts in the NASD, surveying fish biologists regarding the 2) socioeconomic impact, 3) ecological impact, and 4) abundance of nonnative species, and 5) estimating the proportional abundance of nonnative species based on existing collection records. My goal is to compare approaches and identify strengths, weaknesses, and biases inherent in each. I describe differences by comparing average species ratings among approaches and to a global list of high-impact species. I compare variability in ratings among

approaches to evaluate consistency in estimates of impact. Here, I predict that abundance-based estimates are less variable because they are less subjective and less based on social value. Finally, I examine the bias associated with survey respondents' professional focus by comparing ratings from game and non-game biologists for game and non-game fishes. Here, I predict that game biologists (i.e., biologists whose work or research is primarily focused on game fishes) attribute smaller socioeconomic and ecological impacts to game fishes.

METHODS

Lists of nonnative freshwater fishes for each 6-digit hydrologic unit were obtained from the NASD; I considered only established species. Global lists of high-impact invaders were used as a baseline to compare estimates of species impact. Both the International Union for Conservation of Nature's (IUCN) list of 100 worst invasive species (Lowe et al. 2000) and the Global Invasive Species Database (GISD; <http://www.issg.org/database> accessed 6/30/2010) were consulted, and the presence/absence of each species on these lists was recorded. Although the use of these lists could be considered a separate approach for describing impact, I treat them as standards for comparison because of widespread agreement about impacts of the listed species. Global lists are limited as a true approach for quantifying impact because they treat impact as binary and may omit regionally important invaders.

Review approach

I reviewed impacts of nonnative fishes documented in the NASD. Species were rated as high-, medium-, or low-impact based on the severity of documented impacts (Ricciardi and Cohen 2007; Ricciardi and Kipp 2008). Ratings included: 0) no or unknown impacts, 1) mild or indirect declines in native species, and 2) major decline in one native species or moderate declines in multiple native species.

Survey approaches

A list of fish biologists as potential survey respondents was generated by contacting state and federal fisheries agencies in the study region. Websites of universities and colleges were also searched for faculty with knowledge of fish communities within the region (biologists working with fishes outside the region, or those using fish as laboratory study subjects and who wouldn't have a working knowledge of native and nonnative fish communities were excluded). Potential respondents were contacted in

October 2009 to request their participation, ask which drainages they were most familiar with, and solicit recommendations for other potential respondents (e.g., graduate students, colleagues).

A link to access the online survey was emailed to 193 potential respondents (who had either agreed or failed to respond to my initial request) on 10 November 2009, followed by three additional reminders at one week intervals. Survey responses were collected through 8 December 2009. The survey consisted of three questions for each species regarding its relative abundance and degree of socioeconomic and ecological impacts (Appendix 1). Each question represents a different approach (socioeconomic, ecological, abundance) for quantifying the impact of nonnative species. Respondents were given a definition of nuisance species and ecological impact on which to base their responses. Respondents were also asked about the primary focus of their work or research (game fishes, non-game fishes, or other). Finally, survey respondents were asked to take an additional survey for a different drainage if applicable. For analysis, impact responses were coded as: 0 (low), 1 (medium), or 2 (high).

Collection approach

Records of fish community samples were obtained from state agencies to estimate proportional abundances of species by drainage. Collection records were also obtained from the United States Geological Survey's (USGS) National Water-Quality Assessment (NAWQA) program (USGS 2008) and the U.S. Environmental Protection Agency (USEPA) Regional Environmental Monitoring and Assessment Program (REMAP; USEPA 2008). To standardize samples among data sources, only single-pass electrofishing data between 1990 and 2009 were included. Additional passes or reaches were excluded from my analysis. The West-Branch Susquehanna drainage had the fewest samples ($n = 99$); thus, 99 samples were randomly selected from each drainage to standardize sampling effort. For each sample, nonnative species were given an impact rating of: 0 (not present), 1 (present but low proportional abundance, or 2 (in the top 25% of species, ranked by proportional abundance in the sample). For samples with <4 species, nonnative species were rated "2" if they had the highest abundance.

Comparing approaches

I used correlation coefficients to describe similarity among approaches. The mean impact rating was calculated for each species, for each approach. The review approach was based on a single sample (the NASD database), so it lacked a true mean rating. Mean ratings were not normally distributed for all approaches, so Spearman's rank correlation (R) was used to test relationships. Holm's method was used

to correct for multiple tests of significance (Holm 1979). All tests were conducted at 0.05 significance within the R statistical environment (RDCT 2009).

To examine whether globally listed species were rated higher by each approach than species not listed in the GISD, samples for all species under each status (listed, unlisted) were pooled. Tests were conducted with ordinal logistic regression in the “Design” package in R (Harrell 2009). Proportional-odds ratios were calculated as a measure of effect size; ratios > 1 showed that listed species received higher ratings. Specifically, the proportional-odds ratios represent the probability, depending on listing status, of a high rating relative to a medium or low rating, and the probability of a high or medium rating relative to a low rating. The proportional-odds assumption was tested graphically (Harrell 2001) to confirm that relationships among different levels of the response variable were similar. Separate tests were conducted for the survey and collection approaches.

Differences in variability among approaches were explored to examine consistency in responses. Standard errors of the mean rating for each species were chosen for comparison because they account for sample size, which varied among species and approaches. Variability in ratings among approaches was compared with Kruskal-Wallis tests. Several species had a standard error of zero under the socioeconomic, ecological and, in particular, collection approaches, because respondents all agreed that those species had little impact, or the species was never present in a sample. This biased the original tests toward low-impact species. To remove or reduce zero-values, I separately compared the 50% of species with the greatest standard errors for each approach, using only species listed in the GISD and using only species listed as high impact in the review approach. Post-hoc comparisons were tested in the “Coin” package in R (Hothorn et al. 2008). Variability of game-fish (see below) ratings was qualitatively explored to evaluate the relationship between game status and agreement on impact ratings.

Biologist role and game versus non-game species

To examine whether game and non-game biologists gave different ratings to game and non-game species, respondents and species were categorized. A majority of respondents described the focus of their work/research as either game or non-game fishes, and were accordingly categorized as game or non-game biologists. I then categorized as game or non-game biologists some respondents that described the focus of their work/research as ‘other’ based on the specific description they provided. For example, respondents that described the focus of their work/research as “Fishing promotion and education” or “sportfish- game and panfish” were categorized as game biologists,

whereas those that described the focus of their work/research as “community surveys” or “aquatic invasive species” were categorized as non-game biologists. Respondents who I could not clearly identify as either game or non-game biologists were excluded from this analysis. For example, respondents that described the focus of their work/research as “migratory fish”, “both”, or “basic research” were excluded from this analysis. Fishing regulations and records (i.e., largest fishes caught) from each state were consulted, and species were considered game if they appeared in > 50 % of the state regulations and records. Species listed in regulations and records of fewer than three states were considered non-game species. Alewife, blueback herring (*Alosa aestivalis*), black bullhead (*Ameiurus melas*), snail bullhead (*Ameiurus brunneus*), bowfin (*Amia calva*), white sucker (*Catostomus commersonii*), green sunfish, and longear sunfish (*Lepomis megalotis*) were listed in an intermediate number of state records and regulations, and were excluded from analysis. Sockeye salmon (*Oncorhynchus nerka*) were included in only one set of regulations but were considered a game species because of widespread interest in salmon as game fish. Responses were compared using ordinal logistic regression. Tests were conducted with professional focus as the independent variable and rating as the dependent variable. Six tests were conducted to compare professional focus separately for game and non-game species, for each of the three survey approaches (socioeconomic, ecological, abundance).

RESULTS

There were 73 nonnative species established in the study area (Appendix 2). Based on the NASD database, 18 species were given a high, 17 a medium, and 38 a low impact rating. A total of 128 surveys were completed by 105 respondents, representing 54% of those to whom I sent surveys. Fifteen respondents completed surveys for two drainages, and four completed surveys for three drainages. The number of responses varied by species because species were found in 1-11 drainages and respondents were allowed to leave questions blank. The total number of responses per species, per question, ranged from 6 (brook stickleback and fourspine stickleback) to 125 (channel catfish; Appendix 2). Overall, 12 % of responses were left blank, though the number of blank responses was nearly identical among questions. Collection-record sample size depended on the number of drainages in which a species was listed and ranged from 99 (1 drainage) to 1098 (11 drainages).

Comparing approaches

The five approaches to estimating impact varied considerably in their top-ranked species (Table 4.1). Bluegill were given the highest rating by the abundance and collection approaches. Northern snakehead and channel catfish had the highest ratings under the socioeconomic and ecological approaches, respectively. Mean species ratings were significantly correlated between most approaches (Table 4.2). Only collection/ socioeconomic, and review/abundance approaches were not correlated. Strongest correlations were socioeconomic/ecological (0.77), ecological/abundance (0.62), and abundance/collection approaches (0.57).

Species listed in global (GISD) and continental (NASD) databases were not necessarily given high ratings by survey and collection approaches. Several species ranked highly by these approaches were not listed in the GISD, including blue catfish, gizzard shad, green sunfish, and rock bass, while several GISD species were given low ranks, including guppy (*Poecilia reticulata*), ide (*Leuciscus idus*), eastern mosquitofish (*Gambusia holbrooki*), and rudd (*Scardinius erythrophthalmus*). Similarly, blue tilapia, guppy, eastern mosquitofish, northern pike (*Esox lucius*), rainbow smelt (*Osmerus mordax*), redbelly tilapia and walleye were given high ratings by the NASD but not by other approaches, while blue catfish, channel catfish, common carp and gizzard shad were given high ratings by other approaches but only moderate ratings by the NASD. Only golden redhorse (*Moxostoma erythrurum*) were given moderate ratings by other approaches but a low rating by the NASD.

Each survey approach and the collection approach showed clear biases. Under the socioeconomic approach, certain game species exhibited low ratings despite high ratings under other approaches (e.g., brown and rainbow trout, largemouth and smallmouth bass), while other game species had high ratings (e.g., blue and flathead catfish, common carp). Under the ecological approach, certain species with low abundance had high ratings (e.g., blue tilapia, northern snakehead, red shiner *Cyprinella lutrensis*), while some abundant species had low ratings (e.g., bluegill, greenside darter *Etheostoma blennioides*, redear sunfish *Lepomis microlophus*).

Many species had high abundance but low ratings under other approaches, including bluegill, green sunfish, greenside darter, redear sunfish, rock bass, and yellow perch (*Perca flavescens*). Several species were not listed in any collection records despite relatively high ratings in the survey approaches (blueback herring, bull chub, eastern mosquitofish, northern snakehead, striped shiner *Luxilus chrysocephalus*, telescope shiner *Notropis telescopus*), and common carp and gizzard shad were given low ratings under the collection approach compared to survey approaches. Fourspine stickleback

(*Apeltes quadracus*) and Roanoke bass (*Ambloplites cavifrons*) were given high ratings under the collection approach compared to the survey approaches.

Approaches differed in their rating of globally listed species. Four species (brown and rainbow trouts, common carp, largemouth bass) in the study region are on the IUCN's 100 worst invasive species list (Appendix 2). All four are listed in the GISD; thus, only the GISD was used for comparisons. Fifteen species in the study region are listed, two of which (ide, rudd) did not appear in the top 18 (or 25%) ranked species by any approach. The ecological (11), review (9), and socioeconomic (8) approaches all had high numbers of GISD species as top-ranked species but the abundance and collection approaches had only three GISD species in their top-ranked species. All approaches (excluding the review approach which was not tested) gave significantly higher ratings to GISD species than non-GISD species (Table 4.3). This effect was greatest for the socioeconomic approach, followed by the ecological approach. The abundance and collection approaches showed the smallest difference in ratings between listed and unlisted species.

Standard error was significantly lowest for the collection approach in all comparisons (Figure 4.2); however, most approaches were biased by zero standard errors for low-impact species. The socioeconomic approach had the lowest standard error of the survey approaches, but the difference was not always significant. Twenty three species (including five game species) were always rated low under the socioeconomic approach and had zero standard error (Appendix 2). The top 10 species with greatest standard error under the socioeconomic approach were non-game species. Eight species were always rated "0" by the ecological approach. The top 18 species with greatest standard error under the ecological approach were non-game. No species had a standard error of zero under the abundance approach, and 21 of the 26 species with the lowest standard error were game species. The top 36 species with the greatest standard error under the abundance approach were non-game species. Thirty two species were not found in any collection sample and had a standard error of zero. Most game species had intermediate standard errors under the collection approach, but three of the top ten species with greatest standard error were game species.

Biologist role and game versus non-game species

Game and non-game biologists gave different ratings for only the ecological approach (Table 4.4). I received 52 responses from 45 game biologists, and 44 responses from 38 non-game biologists. Twenty three species were considered game and 41 non-game. Non-game biologists gave significantly higher ratings to both game and non-game species for the ecological approach. Non-game biologists

gave slightly higher ratings (but not significantly) than game biologists to non-game species under both the socioeconomic and abundance approaches.

DISCUSSION

Results varied considerably among approaches, demonstrating biases that should be considered when quantifying impact. I discuss each approach separately below.

Review approach

The review approach required relatively little effort and provided a rapid assessment of species' impact; however, impact within the region was not always accurately represented by the larger-scale NASD data. Species widely considered to be high-impact invaders such as common carp and channel catfish (Townsend and Winterbourn 1992; Koehn 2004) were given only moderate ratings based on both my criteria and impact descriptions in the continental-scale NASD, highlighting a limitation of this approach.

The impact of several species was probably overestimated for the region by the review approach. Non-native species are not likely to have equal impact in every introduced location; Ricciardi and Kipp (2008) found that high impact invaders have major impacts documented for only 19% of regions where introduced. Guppy and eastern mosquitofish were listed as high-impact in the NASD, for instance, but appeared to have little impact in the region based on other approaches. Mosquitofish are native to parts of the region, as are several species of killifish (Fundulidae; Jenkins and Burkhead 1994). Impact may be limited through competition with such ecologically similar species, or because Mid-Atlantic species have co-evolved with killifishes and may be resistant compared to other regions where guppy and eastern mosquitofish possess ecological traits unique from those in native assemblages. Regional climate may also limit the impact of species that are listed as harmful in larger-scale databases. The Mid-Atlantic region is at the southern extent of northern pike and walleye ranges (Jenkins and Burkhead 1994), and warm water temperature may limit their success, whereas conditions may be too cold for blue and redbelly tilapia to thrive.

Large-scale databases may provide useful information for risk assessments, and can lead to further understanding of the invasion process. Given that prior invasion success is associated with success at multiple stages of the invasion process (Marchetti et al. 2004b; Ribeiro et al. 2008), large-scale databases describing impact may be particularly useful when assessing species with the potential

to be introduced, or those that have recently established and whose impact has yet to be determined. However, such databases likely underestimate impact for species that have not yet been widely-introduced.

Socioeconomic approach

Attitudes toward socioeconomic nuisance status reflected social preferences for established sport fisheries and potentially media reports. More-recently introduced fishes (e.g., catfishes established for 30-50 years) were viewed as having greater impact, probably because they threaten established sport fisheries of other non-native species (e.g., largemouth bass, established for >150 years). Such attitudes may change over time (Falk-Petersen et al. 2006), as sport fisheries develop for more recently introduced game species. Species introduced from outside the region were given both high (catfishes, common carp) and low impact ratings (trouts), further reflecting particular social preferences.

Species listed in large-scale databases were given high socioeconomic impact ratings, suggesting that global/continental perception of nuisance status influenced opinions of socioeconomic impact. Northern snakehead were given the highest socioeconomic impact rating despite their recent introduction and limited distribution. This probably reflects widespread negative media reports (Dolin 2003) rather than scientific evidence of undesirable social or economic consequences of this recent introduction. Variability among socioeconomic ratings was low but increased when only GISD species (i.e., species with higher impact ratings) were considered, suggesting that widespread agreement is more common for species that have low socioeconomic impact, whereas high socioeconomic impacts tend to be more widely debated.

Popular game fish were given low socioeconomic ratings, whereas certain non-game species (e.g., mimic and telescope shiners) were given high ratings despite low abundance. This matches patterns in responses to Kolar and Lodge's (2002) survey question which combined socioeconomic and ecological impacts. When a distinction is not made between these types of impact, many survey respondents are likely to focus on socioeconomic impacts.

The socioeconomic approach may be well-suited for informing management decisions, but is unlikely to be a reliable measure of ecological patterns (Andow 2005). This approach can be further improved as a social-decision making tool by including other stakeholders, including the general public, in the survey (García-Llorente et al. 2008; Davis 2009). As an example, many anglers are quite content with the developing blue catfish fishery in the Potomac River (N. Lapointe, personal observation).

Ecological approach

Social preferences had a weaker effect on ecological impact rating but global perception of species as invaders continued to bias regional estimates. Several popular game species (e.g., largemouth bass, smallmouth bass, brown trout, and rainbow trout) were ranked considerably higher by the ecological than socioeconomic approach, suggesting that biologists acknowledge the ecologic impact of these species despite their social value. Perception was biased by social value for other species (northern snakehead, blue tilapia) that were given high ecological impact ratings despite low abundance in the region. Conversely, several species (e.g., greenside darter, bluegill) had low ecological impact rankings despite high abundance in the region, suggesting that major impacts may remain unperceived and undocumented.

I recommend the ecological approach for evaluating biological patterns and processes associated with invasions. This approach is also informative for management decisions; in addition to potential socioeconomic benefit or harm, ecological impact should be considered in decisions to introduce (or continue stocking or support/protect through regulation) nonnative species. The relative importance of ecological versus socioeconomic concerns will vary among constituencies, with both worthy of consideration (e.g., García-Llorente et al. 2008). Better information on both types of impact can inform management and policy decisions regarding species introductions. For example, Gozlan (2008) suggested that, in many cases, the socioeconomic benefits of introducing species outweigh the ecological risks, but Leprieur et al. (2009a) and Vitule et al. (2009) countered that ecological impact was not adequately considered.

Abundance approach

Data on abundance may provide the most appropriate measure of impact at regional or sub-regional scales. Differences in impact estimates between GISD and non-GISD species were weaker for the abundance approach, suggesting that more subjective approaches overestimated impact for species widely perceived as invasive. Conversely, such species may have greater per-capita effects, and disentangling the relative contributions of perception, abundance, and per-capita effects to impact ratings is difficult.

Within the region, abundance ratings for several species (e.g., smallmouth bass) differed significantly among drainages, while ecological and socioeconomic ratings did not (N. Lapointe, unpublished data). Because species (and thus per-capita effect) was held constant in this comparison,

abundance should be a reliable measure for comparing impact among drainages. The lack of spatial variation in socioeconomic and ecological ratings provides further evidence that biologists based responses on general perceptions of species as invaders rather than drainage-specific impacts.

Results did not support the prediction that estimates of abundance would be less variable than other approaches. In particular, non-game species had higher variability, suggesting their abundance was not well known. Monitoring efforts are likely to be lower for non-game species, implying that their socioeconomic and ecological impact may also be poorly understood.

Estimates of abundance may be improved as a measure of impact by modifications accounting for differences in per-capita effects among species. Parker et al. (1999) described a species' impact as a function of its range, abundance, and per-capita effects, whereas Ricciardi (2003) proposed that impact depends on a species' abundance, its ecological function, and the composition of the recipient community. I propose that modifying abundance ratings by objective criteria such as trophic level could provide a more accurate measure of impact.

Collection approach

Despite strong correlations with the abundance approach, the lack of detection of many species in the collection approach suggests that it provides unreliable estimates of impact. Cryptic species (e.g., *Notropis spp.*) may not be recorded due to identification difficulties. Additionally, capture efficiency varies among species, and several species that were never collected are not generally susceptible to backpack electrofishing (e.g., walleye). Although efficiency could be described and adjusted for (Pierce et al. 1990), such data are not readily available and would take greater effort than required for any other approach.

Existing collection records probably have limited usefulness for quantifying general impact at regional scales; however, they may be suitable for specific empirical studies of impact. When effort is constant and gear biases are accounted for, collection records can provide excellent data on community composition in relation to extrinsic factors. Impact can be estimated by the frequency of occurrence or proportional abundance of nonnative species, and potentially modified by per-capita effects as discussed above. Such records would allow for testing of hypotheses concerning determinants of impact or characteristics of successful invaders within the context of the habitats and species sampled.

Effort

The effort required to obtain data by each approach is an important consideration, particularly in relation to the quality of the data obtained. The review approach was rapid, required little effort, and was easily interpretable; however, data were incomplete, regionally significant species were excluded, and certain globally significant species were overestimated. Survey approaches required an intermediate level of effort (two to three months part-time work by a technician) to locate respondents, design the survey, collect responses, and compile data. Survey data appeared to be reliable and biases were generally apparent. Though I expected the collection approach would require less effort, similar effort to the survey approaches was required. Federal databases were easy to access but contained too few samples. Certain state agencies were helpful and provided data rapidly, whereas others required continual contact and one state did not provide data. Compiling and sorting collection records required a considerable amount of effort and there was little consistency among states in terms of effort, methods, and details provided.

Overall comparison of approaches

My comparison demonstrated major differences in species' impact ratings among approaches. I summarize the strengths, weaknesses, and biases of each approach in Table 4.5. The review, socioeconomic, and ecological approaches had the greatest similarity to the GISD; however, I interpret this as a sign that estimates of impact were less region-specific, rather than as a sign of their general superiority. No survey approach provided consistent estimates of impact for all subsets of species, though the abundance approach appeared to have slightly higher variability. The collection record approach had the lowest variability, but this was largely due to the consistent lack of detection of a large number of species.

Additionally, I found that combining ratings from the abundance and ecological approach resulted in a seemingly robust measure of impact. With this combination, the influence of global perceptions of impact appeared to be downplayed, because species such as red shiner and blue tilapia that are widely perceived as having high impacts but are not abundant in the region were given lower rankings than by the ecological approach alone. At the same time, consideration of ecological impact accounted in part for per-capita effects: species with high abundance that likely had relatively lower per-capita ecological impacts (e.g., bull chub, golden redhorse, greenside darter) were given lower rankings than by the abundance approach alone.

Biologist role and game versus non-game species

As predicted, game biologists gave lower ecological impact ratings to game fish relative to non-game biologists; however, the same pattern was observed for non-game species. I propose several possible explanations for this finding. Non-game biologists are probably more concerned about the ecological impact of introductions because nonnative species are a leading cause of species declines and extinctions (Jelks et al. 2008). Game biologists may be more focused on competition between nonnative and game species and, relative to declines in species at risk, nonnative species are not often a leading cause of sport fisheries declines. Such differences illustrate the importance of considering the characteristics of survey respondents in interpreting impact ratings. For example, the proportion of game versus non-game respondents should be accounted for if ecological impacts were compared among drainages or other units. Given that such differences existed among well-informed experts, biases among non-expert members of the public are also likely to be strong.

Contrary to my predictions, game and non-game biologists did not differ in rating socioeconomic impacts of game species. Both groups appear to have accepted the socioeconomic benefits of such species through the development of commercially and recreationally important sport fisheries (Gozlan 2008).

Conclusions

I found that species rankings differed considerably among approaches for quantifying the impact of nonnative species at ecosystem to regional scales. The consistency of responses was generally similar among survey approaches though the socioeconomic approach demonstrated slightly lower variability. Non-game biologists gave higher ecological impact ratings, but did not differ from game biologists for other approaches. I recommend different approaches for various potential applications. A combination of the ecological and abundance approaches may be ideal for studies of ecological patterns, while additional information on socioeconomic impact would be useful for informing management decisions. The review approach provides data with little effort required, but is less accurate at regional scales and should only be used when resources are not available for more intensive approaches. The collection approach was not appropriate at the regional scale, but may be useful for empirical studies of particular ecosystems. These approaches are transferrable to any region and taxa for which a reasonable amount of ecological knowledge exists. Better quantification of the impact of nonnative species will facilitate study of the invasion process, improve risk assessments, and inform management decisions.

Table 4.1 Nonnative fish species with the greatest impacts in the Mid-Atlantic Region of the United States, as estimated by several different approaches to quantifying impact. Lists of nonnative species were obtained from the Nonindigenous Aquatic Species Database (Fuller and Benson 2009). The ten highest rated species by each approach are listed. By the review approach, 18 species were equally rated 'high impact' and are listed in alphabetical order at the bottom of the table.

Rank	Socioeconomic	Ecological	Abundance	Collection
1	snakehead	blue catfish	bluegill	bluegill
2	common carp	common carp	common carp	largemouth bass
3	flathead catfish	flathead catfish	largemouth bass	brown trout
4	blue catfish	snakehead	gizzard shad	green sunfish
5	gizzard shad	brown trout	rock bass	smallmouth bass
6	alewife	red shiner	channel catfish	greenside darter
7	green sunfish	largemouth bass	smallmouth bass	rock bass
8	goldfish	gizzard shad	bull chub	fourspine stickleback
9	blue tilapia	green sunfish	golden redhorse	banded darter
10	redbelly tilapia	blue tilapia	greenside darter	striped bass
Review	blue tilapia	guppy	rainbow trout	rock bass
	brown trout	largemouth bass	red shiner	smallmouth bass
	eastern mosquitofish	muskellunge	redbelly tilapia	striped bass
	flathead catfish	northern pike	redeer sunfish	walleye
	green sunfish	rainbow smelt		

Table 4.2 Spearman rank correlations among approaches to quantifying impact (bottom-left of matrix), and Holm’s corrected p-values (top-right of matrix). Most correlations were significant; non-significant correlations and p-values shown in italics.

	Socioeconomic	Ecological	Abundance	Collection	Review
Socioeconomic		0.0000	0.0029	<i>0.3893</i>	0.0179
Ecological	0.77		0.0000	0.0179	0.0000
Abundance	0.40	0.62		0.0000	<i>0.3893</i>
Collection	<i>0.12</i>	0.33	0.57		0.0444
Review	0.34	0.51	<i>0.15</i>	0.28	

Table 4.3 Ordinal logistic regression results comparing impact ratings of species listed in the Global Invasive Species Database (GISD) to impact ratings of species not listed in this database (non-GISD). Impact ratings were given to nonnative fish species in the Mid-Atlantic Region of the United States by several different approaches to quantifying impact. Lists of nonnative species were obtained from the Nonindigenous Aquatic Species Database (Fuller and Benson 2009). The proportional odds ratio represents the odds of increasing impact rating, going from GISD to non-GISD species; >1 shows that GISD were more likely to be given higher ratings. Values closer to 1 suggest a weaker difference between GISD and non-GISD species. Significant results shown in bold.

Approach	p-value	Proportional odds ratio (GISD: non-GISD)
Socioeconomic	<0.001	4.17
Ecological	<0.001	3.71
Abundance	<0.001	1.51
Collection	<0.001	1.41

Table 4.4 Ordinal logistic regression results comparing responses to survey questions regarding the impact of nonnative species by biologists' professional focus for each approach. Separate tests were conducted on responses for game and non-game species. Responses provided several different impact ratings to nonnative fish species in the Mid-Atlantic Region of the United States. Lists of nonnative species were obtained from the Nonindigenous Aquatic Species Database (Fuller and Benson 2009). The proportional odds ratio represents the odds of increasing impact rating, going from non-game to game biologists; >1 shows that game biologists were more likely to give higher ratings, <1 shows that non-game biologists were more likely to give higher ratings. Values close to 1 suggest a weak difference between biologists' professional focus. Significant results shown in bold.

Approach	Species	p-value	Proportional odds ratio (non-game : game)
Socioeconomic	Game	0.539	1.1
	Non-game	0.128	0.69
Ecological	Game	<0.001	0.58
	non-game	0.003	0.57
Abundance	Game	0.605	1.06
	non-game	0.1	0.77

Table 4.5 Summary of the strengths, weaknesses, and biases for several approaches to quantifying impact, including recommendations for the most appropriate applications.

Strengths	Weaknesses and biases	Recommended applications
<i>Review</i>		
Required least effort, results obtained rapidly	Not useful for species with no invasion history	Predicting impact of widely-introduced species
	Not region-specific; species' impact may be over- or underestimated	When resources are not available for collecting more detailed information
<i>Socioeconomic</i>		
Data obtained with reasonable effort	Biased by global or media perceptions of impact	Informing social decisions
High agreement among respondents for low-impact species	Limited ecological relevance	
<i>Ecological</i>		
Data obtained with reasonable effort	Biased by global or media perceptions of impact	Examining ecological patterns and processes
Lower bias from social perception than socioeconomic approach	Responses for game and non-game species varied with biologist role	Informing social decisions
<i>Abundance</i>		
Data obtained with reasonable effort	Did not account for per-capita effects.	Examining ecological patterns and processes
Provided a surrogate estimate when impact was unknown	High variability among respondents, particularly for non-game species	Evaluating spatial (both scale and geography) patterns of impact
Low bias from social perception	Most GISD species given low ratings	Informing social decisions
<i>Collection</i>		

Least biased by social perception

Biased by gear efficiency, which varied with species and habitat
Many species not collected
Required considerable effort

Context-specific empirical studies

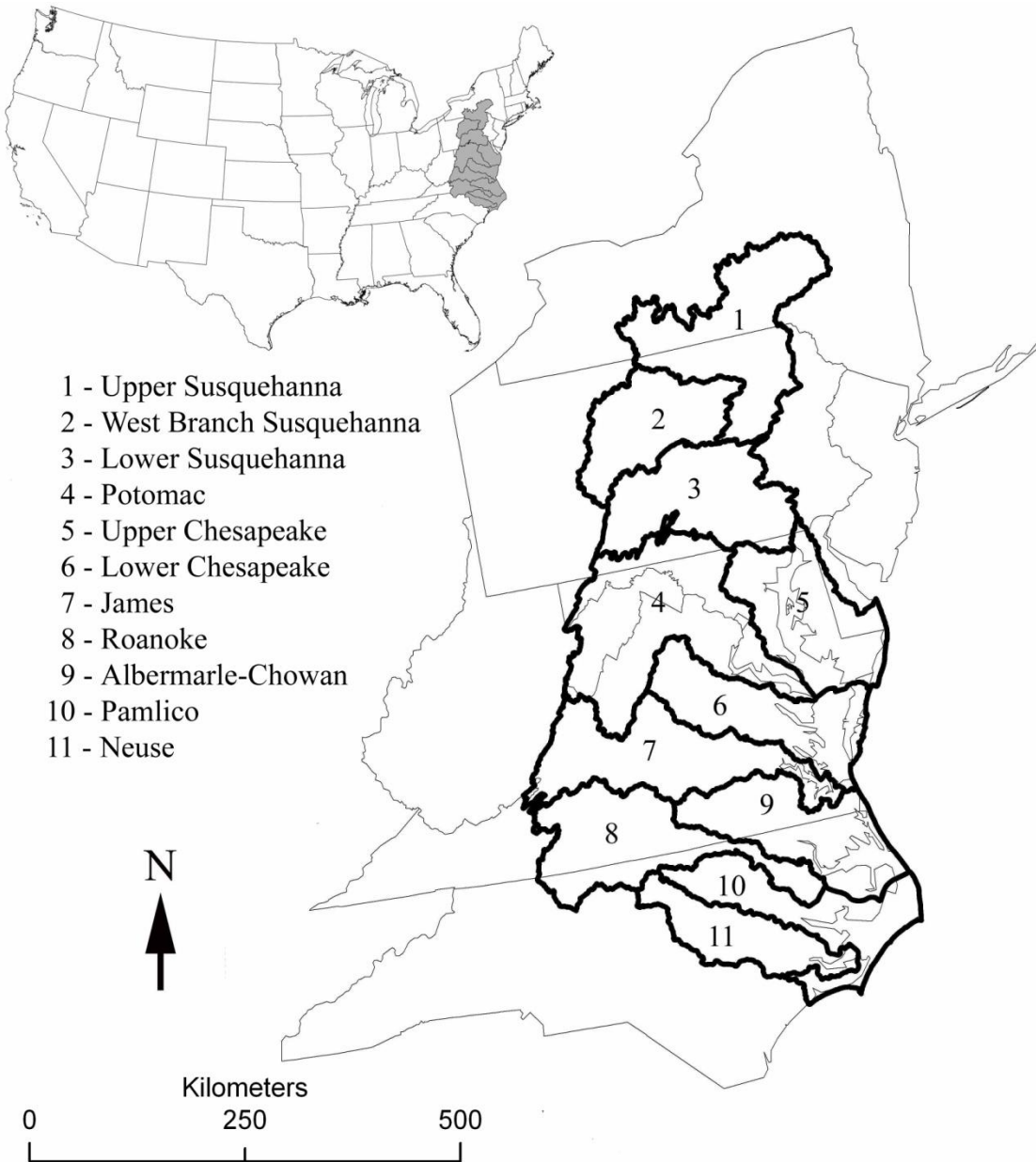


Figure 4.1 Map of six-digit hydrologic units in the Mid-Atlantic region.

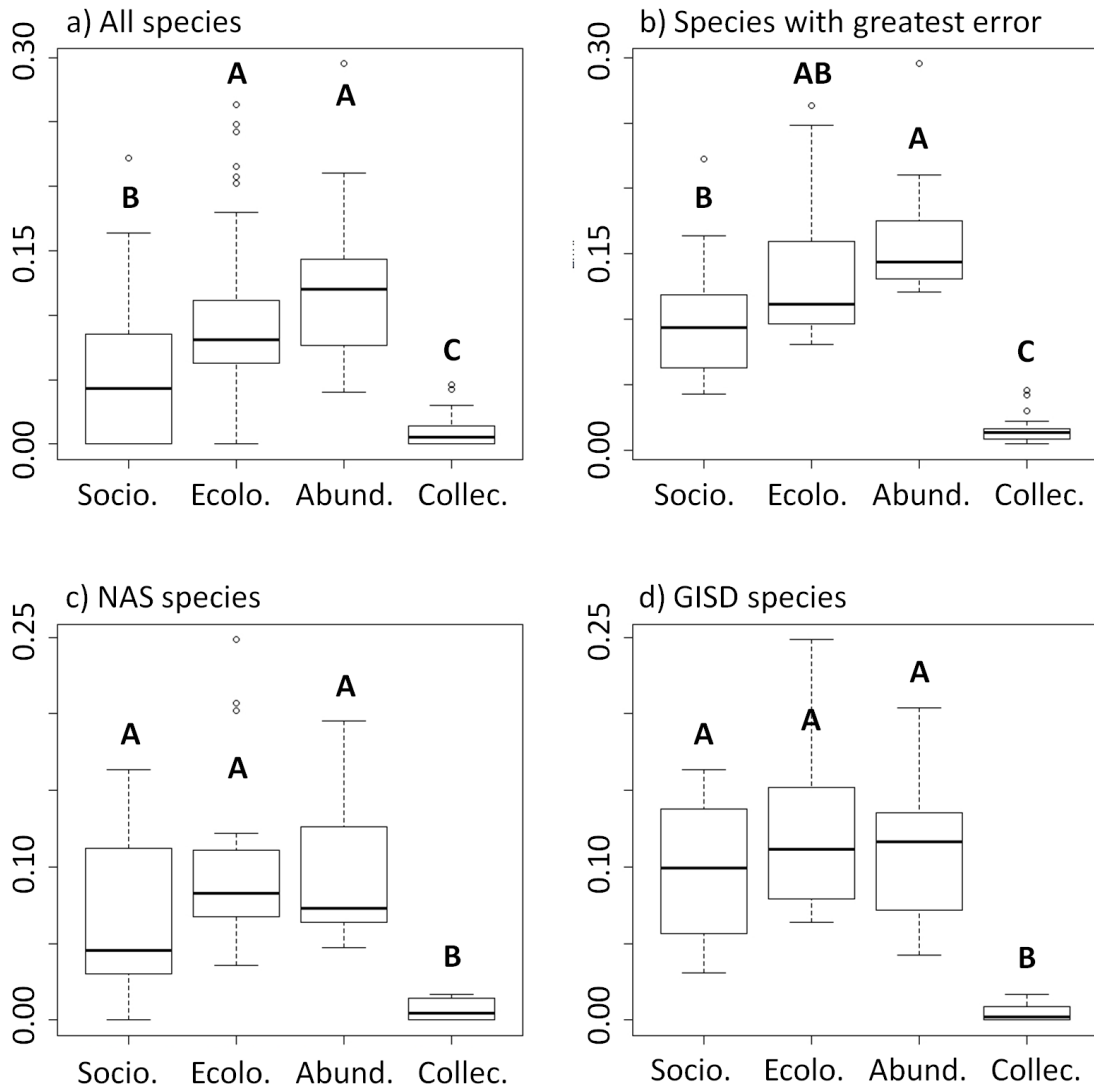


Figure 4.2 Standard errors of the mean impact rating from several approaches to quantifying impact for nonnative fish species in the Mid-Atlantic region of the United States. Plots include a) comparisons using all species, b) the 50% of species with the greatest standard error under each approach, c) species listed as high impact under the review approach, and d) species listed in the GISD. In each diagram from left to right, plots represent socioeconomic, ecological, abundance and collection approaches to quantifying impact and the y-axes show mean error by species. Significance of pair-wise comparisons is shown by capital letters in bold.

General Conclusions

How bad is it?

My results illustrate the pervasiveness of nonnative fishes in the Mid-Atlantic region. New species continue to be introduced to the region via multiple pathways, adding to an existing invasion debt resulting from the expected spread of established invaders. I expect this to contribute to an extinction debt (Sax and Gaines 2008; Jackson and Sax 2010) for many native species; the scope of the problem associated with nonnative species is probably vastly underrated. The Mid-Atlantic region is already among the most heavily invaded in the U.S. (Fuller et al. 1999), yet many invasions probably remain undetected, either because of a lack of historical data on native species distributions, or because of lags in detection and reporting. The impact of existing invaders is expected to increase with time and as each species spreads, further exacerbating the problem. The data presented here demonstrate the scope of fish invasions in the Mid-Atlantic region, and underscore the need for immediate actions to reduce the risk and impact of future invasions.

The Tens Rule

The “Tens Rule” (Williamson and Fitter 1996), which states that only one in ten introduced species will establish and only one in ten of these will become invasive, continues to be widely cited in invasion biology (e.g., Gozlan 2008). Several authors have argued that this proportion is conservatively low, particularly for freshwater fishes. My results support this assertion. Of the 98 fish species recorded as introduced to the Mid-Atlantic region, 69 (70%) established reproducing populations in at least one location. This value is similar to establishment rates for fishes in other locations, including 58% in Portugal (Ribeiro et al. 2009), 63% in Europe (García-Berthou et al. 2005), and 64% worldwide (Ruesink 2005). The proportion of species having impacts is often underestimated, particularly by global databases such as FishBase (Leprieur et al. 2009a; Vitule et al. 2009). Impacts were listed in FishBase for 13 (18%) fish species in the Mid-Atlantic region, whereas the Nonindigenous Aquatic Species Database listed impacts for 35 (48%) species and high impacts for 18 (25%). The European DAISE database listed impacts in similar proportions (1/3) for freshwater vertebrates (Vilà et al. 2010), suggesting that regional databases may be more complete than existing global databases. My other approaches, though relative, suggested that most nonnative fishes have at least some impact in the region. Similarly, Ruesink et al. (1995) reported that 50-95% of nonnative fishes had impacts on native species in California, and García Berthou et al. (2005) reported that 50-86% of common aquatic invaders had

impacts in Europe. There is overwhelming evidence that the Tens Rule is grossly conservative in estimating the impacts of nonnative freshwater fishes, leading to poor assessments of the risks posed by potential invaders.

Specific predictions and management implications

In this dissertation, I provide options for addressing nonnative species issues in the Mid-Atlantic region at each stage of the invasion process. I identify the main pathways of concern for the transport and introduction of species into the region, including exotic species, transplanted native species, and the spread of existing invaders. Exotic species are most likely to arrive through pathways associated with economic activities. The aquarium trade involves the largest number of species, but aquaculture, live-food, biological supply and shipping industries also pose risks. Related to each of these, the sale of live organisms over the internet is particularly problematic because it offers ample opportunities for the purchase of restricted species. Many native and established nonnative species are most likely to be transplanted through bait releases, which are largely unregulated and widespread. Large numbers of individuals are probably released as bait, further exacerbating the problem. Finally, canals, the stocking of private ponds and impoundments, and particularly illegal introductions by members of the public are high-risk pathway for the spread of existing invaders. In many of these cases, the complicity of state agencies in the release of live organisms is debatable. Risks can be reduced for most pathways by education and outreach programs, cooperative initiatives with industry partners, and banning the release of live organisms throughout the region. Stronger prevention efforts would further reduce the risk, but may be controversial. Such efforts would be supported by empirical research into the threats posed by each pathway and impacts of nonnative species in the region. Strong prevention efforts could include polluter-pays policies structured around clean lists of low-risk species, harsh penalties and greater enforcement effort, and inter-state and –agency policy coordination for policy and management (ELI 2007).

Limited resources can be used efficiently to prevent invasions by focusing on highly invulnerable ecosystems and high-risk species. I predicted the establishment and spread of nonnative species based on ecosystem characteristics of 8-digit hydrologic units (HUC8s) in the Mid-Atlantic region. Patterns of nonnative species richness (NNSR) revealed that coastal plain ecosystems were resistant to fish invasions because of relatively low habitat heterogeneity and harsh abiotic conditions. By further exploring ecosystem invasibility in relation to species identity, I showed that HUC8s in the south-east part of the region are susceptible to invasion by a wide range of species. Several other HUC8s within the

region were predicted to have different, usually more diverse, nonnative communities and are prime targets for prevention efforts. Additionally, I offer predictions for the spread of walleye and white crappie. The latter are included on a clean list in North Carolina, which provides blanket approval for private stocking. Managers responsible for each HUC8 can use these predictions to develop action plans for individual species, or for a suite of species likely to be found in the predicted nonnative community.

Finally, I evaluated the impacts of established nonnative species. Results provide region-specific estimates of the impact of existing invaders. Current dirty lists appear to reflect socioeconomic concerns, and my evaluation of socioeconomic impacts can be used to enhance these lists in two ways. First, most species given high socioeconomic impact ratings were rarely included on dirty lists (Table C.1). This provides a means of setting priorities for region-wide listings. Species that are not currently restricted but were listed as high-impact by multiple approaches (e.g., green sunfish) should be considered as particularly high priority. Attitudes toward species given high impact ratings by approaches other than the socioeconomic approach are also worthy of further consideration. These species likely have high socioeconomic value, yet their negative ecological effect suggests that natural resource managers should consider striking a balance between socioeconomic gain and ecological protection in their regulation. For example, native or established nonnative species with low ecological impact could be recommended or regulated as alternatives for private stocking. Additionally, impact ratings can be used for assessing the risk of future invaders, prioritizing prevention efforts, and addition of species to existing dirty lists. Species with ecological traits similar to those already having negative impacts in the region should be given the highest priority, particularly if they are present in any of the high-risk pathways identified in this study.

Advancements in invasion biology

My dissertation presents several advancements in the understanding of invasion processes and nonnative species' impacts. I provide evidence in support of the colonization pressure and research effort hypotheses for the distribution of NNSR, showing how these factors should be accounted for when analyzing NNSR patterns. After doing so, physical ecosystem characteristics were more important than anthropogenic disturbance in determining NNSR; however, human alterations have likely contributed to the higher invasibility of montane watersheds in the mid-Atlantic region. I developed and provided evidence for the environmental filter hypothesis for nonnative community identity, showing that climatic and physical characteristics determined nonnative species distributions beyond the basic effects of human-mediated dispersal. I developed simple methods for predicting nonnative

communities and species establishment based on ecosystem characteristics that can be applied to predict invasions for other regions and taxa. Finally, I developed and described straightforward approaches to quantifying the relative impacts of nonnative species, which can be used in studies of the factors explaining these impacts.

Table C.1 Evaluation of restrictions on high-impact species. Rank represents average impact rating under a specific approach, relative to all nonnative species in the Mid-Atlantic region (1 = highest impact; only the top 10 species under each approach were considered). The number of state and federal dirty lists that list each species is given under “Dirty lists”. Numbers are based on lists from New York, Pennsylvania, Delaware, Maryland, Virginia, North Carolina, and the Lacey Act. The number of other approaches that list a species as high-impact (i.e., in the top 10) is given under “Other high-impact ratings”. Species already shown under the “Socioeconomic” heading were excluded from the “Ecological” section, and so on.

Rank	Species	Dirty lists	Other high-impact ratings
Socioeconomic			
1	snakehead	7	1
2	common carp	0	2
3	flathead catfish	2	2
4	blue catfish	1	1
5	gizzard shad	0	1
6	alewife	0	0
7	green sunfish	0	3
8	goldfish	2	0
9	blue tilapia	3	2
10	redbelly tilapia	3	1
Ecological			
5	brown trout	0	2
6	red shiner	2	1
7	largemouth bass	0	3
Abundance			
1	bluegill	0	1
5	rock bass	0	2
6	channel catfish	0	0
7	smallmouth bass	0	2
8	bull chub	0	0
9	golden redhorse	0	0
10	greenside darter	0	0

Collection

8	fourspine stickleback	0	0
9	banded darter	0	0
10	striped bass	0	1

Review

N/A	eastern mosquitofish	0	0
N/A	guppy	0	0
N/A	muskellunge	0	0
N/A	northern pike	0	0
N/A	rainbow smelt	0	0
N/A	rainbow trout	0	0
N/A	redeer sunfish	0	0
N/A	walleye	0	0

Literature Cited

- Aikio, S., R. P. Duncan, and P. E. Hulme. 2010. Lag-phases in alien plant invasions: separating the facts from the artefacts. *Oikos* 119(2):370-378.
- Andow, D. A. 2005. Characterizing the ecological risks of introductions and invasions. Pages 84-103 *in* H. A. Mooney, R. N. Mack, J. A. McNeely, L. E. Neville, P. J. Schei, and J. K. Waage, editors. *Invasive alien species: a new synthesis*. Island Press, Washington, D.C.
- Angermeier, P. L., and M. R. Winston. 1998. Local vs. regional influences on local diversity in stream fish communities of Virginia. *Ecology* 79(3):911-927.
- Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology* 85(10):2656-2663.
- Blanchet, S., F. Leprieur, O. Beauchard, J. Staes, T. Oberdorff, and S. Brosse. 2009. Broad-scale determinants of non-native fish species richness are context-dependent. *Proceedings of the Royal Society B-Biological Sciences* 276(1666):2385-2394.
- Breiman, L. 2001. Random forests. *Machine Learning* 45(1):5-32.
- Cambray, J. A. 2003. Impact on indigenous species biodiversity caused by the globalization of alien recreational freshwater fisheries. *Hydrobiologia* 500(1-3):217-230.
- Carlton, J. T. 2002. Bioinvasion ecology: assessing invasion impact and scale. Pages 7-17 *in* E. Leppakoski, S. Gollasch, and S. Olenin, editors. *Invasive aquatic species of Europe: distribution, impacts and management*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Catford, J. A., R. Jansson, and C. Nilsson. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions* 15(1):22-40.
- Chang, A. L., J. D. Grossman, T. S. Spezio, H. W. Weiskel, J. C. Blum, J. W. Burt, A. A. Muir, J. Piovio-Scott, K. E. Veblen, and E. D. Grosholz. 2009. Tackling aquatic invasions: risks and opportunities for the aquarium fish industry. *Biological Invasions* 11(4):773-785.
- Chapleau, F., C. S. Findlay, and E. Szenasy. 1997. Impact of piscivorous fish introductions on fish species richness of small lakes in Gatineau Park, Quebec. *Ecoscience* 4(3):259-268.
- Chapman, F. A. 2000. Ornamental fish culture, freshwater. Pages 602-610 *in* R. R. Stickney, editor. *Encyclopedia of aquaculture*. John Wiley and Sons, New York, New York.
- Chapman, F. A., S. A. FitzCoy, E. M. Thunberg, and C. M. Adams. 1997. United States of America trade in ornamental fish. *Journal of the World Aquaculture Society* 28(1):1-10.
- Chevan, A., and M. Sutherland. 1991. Hierarchical partitioning. *American Statistician* 45(2):90-96.

- Chiron, F., S. Shirley, and S. Kark. 2009. Human-related processes drive the richness of exotic birds in Europe. *Proceedings of the Royal Society B-Biological Sciences* 276(1654):47-53.
- Chong, G. W., Y. Otsuki, T. J. Stohlgren, D. Guenther, P. Evangelista, C. Villa, and A. Waters. 2006. Evaluating plant invasions from both habitat and species perspectives. *Western North American Naturalist* 66(1):92-105.
- Chytrý, M., V. Jarošík, P. Pyšek, O. Hájek, I. Knollová, L. Tichý, and J. Danihelka. 2008. Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology* 89(6):1541-1553.
- Clarkson, R. W., P. C. Marsh, S. E. Stefferud, and J. A. Stefferud. 2005. Conflicts between native fish and nonnative sport fish management in the southwestern United States. *Fisheries* 30(9):20-27.
- Clavero, M., and E. García-Berthou. 2005. Invasive species are a leading cause of animal extinctions. *Trends in Ecology & Evolution* 20(3):110-110.
- Colautti, R. I., I. A. Grigorovich, and H. J. MacIsaac. 2006. Propagule pressure: a null model for biological invasions. *Biological Invasions* 8(5):1023-1037.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302-1310.
- Cooper, E. L. 1983. *Fishes of Pennsylvania and the northeastern United States*. Pennsylvania State University, University Park, Pennsylvania.
- Copp, G. H., K. J. Wesley, and L. Vilizzi. 2005. Pathways of ornamental and aquarium fish introductions into urban ponds of Epping Forest (London, England): the human vector. *Journal of Applied Ichthyology* 21(4):263-274.
- Courtenay, W. R. 2007. Introduced species: What species do you have and how do you know? *Transactions of the American Fisheries Society* 136(4):1160-1164.
- Courtenay, W. R. J. 1999. Aquariums and water gardens as vectors of introduction. Pages 127-128 *in* R. Claudi, and J. H. Leach, editors. *Nonindigenous freshwater organisms: vectors, biology and impacts*. Lewis Publishers, Boca Raton, Florida.
- Courtenay, W. R. J., and C. R. Robins. 1975. Exotic organisms - an unsolved, complex problem. *Bioscience* 25(5):306-313.
- Courtenay, W. R. J., and J. N. Taylor. 1986. Strategies for reducing risks from introductions of aquatic organisms - a philosophical perspective. *Fisheries* 11(2):30-33.
- Craven, P., and G. Wahba. 1979. Smoothing noisy data with spline functions: estimating the correct degree of smoothing by the method of generalized cross-validation. *Numerical Mathematics* 31:377-403.

- Crossman, E. J., and B. C. Cudmore. 1999. Summary of North American introductions of fish through the aquaculture vector and related human activities. Pages 297-303 in R. Claudi, and J. H. Leach, editors. *Nonindigenous freshwater organisms, vectors, biology and impacts*. Lewis Publishers, Boca Raton, Florida.
- Cutler, D. R., T. C. Edwards, K. H. Beard, A. Cutler, and K. T. Hess. 2007. Random forests for classification in ecology. *Ecology* 88(11):2783-2792.
- Daehler, C. C. 2001. Two ways to be an invader, but one is more suitable for ecology. *Bulletin of the Ecological Society of America*.
- Dauwalter, D. C., and J. R. Jackson. 2005. A re-evaluation of US state fish-stocking recommendations for small, private, warmwater impoundments. *Fisheries* 30(8):18-28.
- Davies, K. F., P. Chesson, S. Harrison, B. D. Inouye, B. A. Melbourne, and K. J. Rice. 2005. Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology* 86(6):1602-1610.
- Davis, M. A. 2009. *Invasion biology*. Oxford University Press, Inc., New York, New York.
- Davis, M. A., and K. Thompson. 2000. Eight ways to be a colonizer; two ways to be an invader: a proposed nomenclature scheme for invasion ecology. *Bulletin of the Ecological Society of America* 81(3):226-230.
- Davis, M. A., and K. Thompson. 2001. Invasion terminology: should ecologists define their terms differently than others? No, not if we want to be of any help! *Bulletin of the Ecological Society of America* 82(3):206.
- District Department of the Environment (DDE). 2010. Fisheries and wildlife regulated activities (webpage). <http://ddoe.dc.gov/ddoe/cwp/view,a,1209,q,494749.asp> accessed 6/30/2010.
- Delaware Department of Natural Resources and Environmental Control (DDNREC). 2010. 2010 Delaware fishing guide. <http://www.fw.delaware.gov/Fisheries/Documents/2010%20Delaware%20Fishing%20Guide.pdf> accessed 6/30/2010.
- Diez, J. M., P. A. Williams, R. P. Randall, J. J. Sullivan, P. E. Hulme, and R. P. Duncan. 2009. Learning from failures: testing broad taxonomic hypotheses about plant naturalization. *Ecology Letters* 12(11):1174-1183.
- Dolin, E. J. 2003. *Snakehead: a fish out of water*. Smithsonian Institution Press, Washington, DC.
- Duggan, I. C., C. A. M. Rixon, and H. J. MacIsaac. 2006. Popularity and propagule pressure: determinants of introduction and establishment of aquarium fish. *Biological Invasions* 8(2):377-382.

- Edwards, C., D. Hill, and J. Maxwell. 1998. Aquatic zoogeography of North America (nearctic zone). U.S.D.A. Forest Service, Rhinelander, Wisconsin.
- Environmental Law Institute (ELI). 2007. Halting the invasion in the Chesapeake Bay: preventing aquatic invasive species introduction through regional cooperation. The Environmental Law Institute.
- Ericson, J. A. 2005. The economic roots of aquatic species invasions. *Fisheries* 30(5):30-33.
- Facon, B., B. J. Genton, J. Shykoff, P. Jarne, A. Estoup, and P. David. 2006. A general eco-evolutionary framework for understanding bioinvasions. *Trends in Ecology & Evolution* 21(3):130-135.
- Falk-Petersen, J., T. Bøhn, and O. T. Sandlund. 2006. On the numerous concepts in invasion biology. *Biological Invasions* 8(6):1409-1424.
- Findlay, C. S., D. G. Bert, and L. G. Zheng. 2000. Effect of introduced piscivores on native minnow communities in Adirondack lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 57(3):570-580.
- Fridley, J. D., J. J. Stachowicz, S. Naeem, D. F. Sax, E. W. Seabloom, M. D. Smith, T. J. Stohlgren, D. Tilman, and B. Von Holle. 2007. The invasion paradox: reconciling pattern and process in species invasions. *Ecology* 88(1):3-17.
- Froese, R., and D. Pauly. Editors. 2010. FishBase. World Wide Web electronic publication. www.fishbase.org, version (05/2010) accessed 07/28/2010.
- Fuller, P. F., and A. J. Benson. 2009. Nonindigenous aquatic species database. United States Geological Survey, Gainesville, Florida <http://nas.er.usgs.gov/queries/FactSheet.asp?speciesID=2265> Accessed 6/30/2010.
- Fuller, P. F., L. G. Nico, and J. D. Williams. 1999. Nonindigenous fishes introduced into inland waters of the United States. American Fisheries Society Special Publication 27, Bethesda, Maryland.
- García-Berthou, E. 2007. The characteristics of invasive fishes: what has been learned so far? *Journal of Fish Biology* 71:33-55.
- García-Berthou, E., C. Alcaraz, Q. Pou-Rovira, L. Zamora, G. Coenders, and C. Feo. 2005. Introduction pathways and establishment rates of invasive aquatic species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences* 62(2):453-463.
- García-Llorente, M., B. Martín-López, J. A. González, P. Alcorlo, and C. Montes. 2008. Social perceptions of the impacts and benefits of invasive alien species: implications for management. *Biological Conservation* 141(12):2969-2983.

- Gassó, N., D. Sol, J. Pino, E. D. Dana, F. Lloret, M. Sanz-Elorza, E. Sobrino, and M. Vilà. 2009. Exploring species attributes and site characteristics to assess plant invasions in Spain. *Diversity and Distributions* 15(1):50-58.
- Gertzen, E., O. Familiar, and B. Leung. 2008. Quantifying invasion pathways: fish introductions from the aquarium trade. *Canadian Journal of Fisheries and Aquatic Sciences* 65(7):1265-1273.
- Gherardi, F. 2007. Understanding the impact of invasive crayfish. Pages 507-542 *in* F. Gherardi, editor. *Biological invaders in inland waters: profiles, distribution, and threats*. Springer, Dordrecht, The Netherlands.
- Gido, K. B., and J. H. Brown. 1999. Invasion of North American drainages by alien fish species. *Freshwater Biology* 42(2):387-399.
- Goldberg, C. S., and L. P. Waits. 2009. Using habitat models to determine conservation priorities for pond-breeding amphibians in a privately-owned landscape of northern Idaho, USA. *Biological Conservation* 142(5):1096-1104.
- Gozlan, R. E. 2008. Introduction of non-native freshwater fish: is it all bad? *Fish and Fisheries* 9(1):106-115.
- Gozlan, R. E., J. R. Britton, I. Cowx, and G. H. Copp. 2010. Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology* 76(4):751-786.
- Harrell, F. E. J. 2001. *Regression modeling strategies: with applications to linear models, logistic regression and survival analysis*. New York, New York.
- Harrell, F. E. J. 2009. *Design: design package*. R package version 2.3-0. <http://CRAN.R-project.org/package=Design> accessed 6-30-2010.
- Hastie, T., and R. Tibshirani. 1986. Generalized additive models. *Statistical Science* 1(3):297-318.
- Hayes, K. R., and S. C. Barry. 2008. Are there any consistent predictors of invasion success? *Biological Invasions* 10(4):483-506.
- Hellmann, J. J., J. E. Byers, B. G. Bierwagen, and J. S. Dukes. 2008. Five potential consequences of climate change for invasive species. *Conservation Biology* 22(3):534-543.
- Herborg, L. M., N. E. Mandrak, B. C. Cudmore, and H. J. MacIsaac. 2007. Comparative distribution and invasion risk of snakehead (Channidae) and Asian carp (Cyprinidae) species in North America. *Canadian Journal of Fisheries and Aquatic Sciences* 64(12):1723-1735.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6:65-70.

- Hothorn, T., P. Buehlmann, S. Dudoit, A. Molinaro, and M. Van Der Laan. 2006. Survival ensembles. *Biostatistics* 7(3):355-373.
- Hothorn, T., K. Hornik, M. A. Van de Wiel, and A. Zeileis. 2008. Implementing a class of permutation tests: the coin package. *Journal of Statistical Software* 28(8):1-23.
- Houlahan, J. E., and C. S. Findlay. 2003. The effects of adjacent land use on wetland amphibian species richness and community composition. *Canadian Journal of Fisheries and Aquatic Sciences* 60(9):1078-1094.
- Hulme, P. E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46(1):10-18.
- Hulme, P. E., S. Bacher, M. Kenis, S. Klotz, I. Kuhn, D. Minchin, W. Nentwig, S. Olenin, V. Panov, J. Pergl, P. Pyšek, A. Roques, D. Sol, W. Solarz, and M. Vilà. 2008. Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *Journal of Applied Ecology* 45(2):403-414.
- Jackson, S. T., and D. F. Sax. 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology & Evolution* 25(3):153-160.
- Jelks, H. L., S. J. Walsh, N. M. Burkhead, S. Contreras-Balderas, E. Diaz-Pardo, D. A. Hendrickson, J. Lyons, N. E. Mandrak, F. McCormick, J. S. Nelson, S. P. Platania, B. A. Porter, C. B. Renaud, J. J. Schmitter-Soto, E. B. Taylor, and M. L. Warren. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. *Fisheries* 33(8):372-407.
- Jenkins, R. E., and N. M. Burkhead. 1994. *Freshwater fishes of Virginia*. American Fisheries Society Bethesda, Maryland.
- Jeschke, J. M., and D. L. Strayer. 2006. Determinants of vertebrate invasion success in Europe and North America. *Global Change Biology* 12(9):1608-1619.
- Johnson, B. M., R. Arlinghaus, and P. J. Martinez. 2009. Are we doing all we can to stem the tide of illegal fish stocking? *Fisheries* 34(8):389-394.
- Johnson, P. T. J., J. D. Olden, and M. J. Vander Zanden. 2008. Dam invaders: impoundments facilitate biological invasions into freshwaters. *Frontiers in Ecology and the Environment* 6(7):359-365.
- Keller, R. P., P. Ergassan, and D. C. Aldridge. 2009. Vectors and Timing of Freshwater Invasions in Great Britain. *Conservation Biology* 23(6):1526-1534.
- Keller, R. P., and D. M. Lodge. 2007. Species invasions from commerce in live aquatic organisms: problems and possible solutions. *Bioscience* 57(5):428-436.

- Kerr, S. J., C. S. Brousseau, and M. Muschett. 2005. Invasive aquatic species in Ontario: a review and analysis of potential pathways for introduction. *Fisheries* 30(7):21-30.
- Koehn, J. D. 2004. Carp (*Cyprinus carpio*) as a powerful invader in Australian waterways. *Freshwater Biology* 49(7):882-894.
- Kohler, C. C., and W. R. J. Courtenay. 1986. American Fisheries Society position on introductions of aquatic species. *Fisheries* 11(2):39-42.
- Kolar, C. S., and D. M. Lodge. 2002. Ecological predictions and risk assessment for alien fishes in North America. *Science* 298(5596):1233-1236.
- Lacey Act. 2009. 50CFR, Ch.1, Sec.16.13, p. 97 Importation of live or dead fish, mollusks, and crustaceans, or their eggs. <http://frwebgate2.access.gpo.gov/cgi-bin/PDFgate.cgi?WAISdocID=1ShGiz/14/2/0&WAIAction=retrieve> accessed 6/30/2010.
- Leprieur, F., O. Beauchard, S. Blanchet, T. Oberdorff, and S. Brosse. 2008. Fish invasions in the world's river systems: when natural processes are blurred by human activities. *Plos Biology* 6(2):404-410.
- Leprieur, F., S. Brosse, E. García-Berthou, T. Oberdorff, J. D. Olden, and C. R. Townsend. 2009a. Scientific uncertainty and the assessment of risks posed by non-native freshwater fishes. *Fish and Fisheries* 10(1):88-97.
- Leprieur, F., J. D. Olden, S. Lek, and S. Brosse. 2009b. Contrasting patterns and mechanisms of spatial turnover for native and exotic freshwater fish in Europe. *Journal of Biogeography* 36(10):1899-1912.
- Levine, J. M., and C. M. D'Antonio. 2003. Forecasting biological invasions with increasing international trade. *Conservation Biology* 17(1):322-326.
- Liaw, A., and M. Wiener. 2002. Classification and regression by randomForest. *R News* 2:18-22.
- Light, T., and M. P. Marchetti. 2007. Distinguishing between invasions and habitat changes as drivers of diversity loss among California's freshwater fishes. *Conservation Biology* 21(2):434-446.
- Lindgren, C. J. 2006. Angler awareness of aquatic invasive species in Manitoba. *Journal of Aquatic Plant Management* 44:103-108.
- Litvak, M. K., and N. E. Mandrak. 1993. Ecology of fresh-water baitfish use in Canada and the United-States. *Fisheries* 18(12):6-13.
- Lockwood, J. L., P. Cassey, and T. M. Blackburn. 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions* 15(5):904-910.

- Lockwood, J. L., M. F. Hoopes, and M. P. Marchetti. 2007. *Invasion ecology*. Blackwell Publishing Ltd, Oxford, United Kingdom.
- Lodge, D. M. 1993. Biological invasions - lessons for ecology. *Trends in Ecology & Evolution* 8(4):133-137.
- Lovell, S. J., and S. F. Stone. 2005. The economic impacts of aquatic invasive species: a review of the literature. *Agricultural and resource economics review*. US Environmental Protection Agency, National Center for Environmental Economics, Washington, DC.
- Lowe, S. J., M. Browne, and S. Boudjelas. 2000. 100 of the world's worst invasive alien species. ICUN/SSC Invasive Species Specialist Group (ISSG), Auckland, New Zealand.
- Ludwig, H. R., and J. A. Leitch. 1996. Interbasin transfer of aquatic biota via anglers' bait buckets. *Fisheries* 21(7):14-18.
- Mac Nally, R. 2002. Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. *Biodiversity and Conservation* 11(8):1397-1401.
- Mac Nally, R., and C. J. Walsh. 2004. Hierarchical partitioning public-domain software. *Biodiversity and Conservation* 13(3):659-660.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10(3):689-710.
- Magnuson, J. J. 1976. Managing with exotics - game of chance. *Transactions of the American Fisheries Society* 105(1):1-9.
- Mandrak, N. E. 1989. Potential invasion of the Great Lakes by fish species associated with climatic warming. *Journal of Great Lakes Research* 15(2):306-316.
- Marchetti, M. P., T. Light, P. B. Moyle, and J. H. Viers. 2004a. Fish invasions in California watersheds: testing hypotheses using landscape patterns. *Ecological Applications* 14(5):1507-1525.
- Marchetti, M. P., P. B. Moyle, and R. Levine. 2004b. Alien fishes in California watersheds: characteristics of successful and failed invaders. *Ecological Applications* 14(2):587-596.
- Marchetti, M. P., P. B. Moyle, and R. Levine. 2004c. Invasive species profiling? exploring the characteristics of non-native fishes across invasion stages in California. *Freshwater Biology* 49(5):646-661.
- McCune, B., and J. B. Grace. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, Oregon.
- McCune, B., and M. J. Mefford. 2006. *PC-OORD. Multivariate analysis of ecological data version 5.20*. MjM Software, Gleneden Beach, Oregon.

- Maryland Department of Natural Resources (MDNR). 2010. 2010 Maryland fishing guide.
http://www.dnr.state.md.us/fisheries/fishing_guide/2010_MD_Fishing_Guide_Final_LowRes.pdf
f accessed 6/30/2010.
- Menhinick, E. F. 1991. The freshwater fishes of North Carolina. North Carolina Wildlife Resources Commission, Raleigh, North Carolina.
- Meronek, T. G., F. A. Copes, and D. W. Coble. 1995. A summary of bait regulations in the north-central United States. *Fisheries* 20(11):16-23.
- Miller, R. R., J. D. Williams, and J. E. Williams. 1989. Extinctions of North American fishes during the past century. *Fisheries* 14(6):22-38.
- Minchin, D. 2007. Aquaculture and transport in a changing environment: overlap and links in the spread of alien biota. *Marine Pollution Bulletin* 55(7-9):302-313.
- Mitchell, A. L., and J. H. Knouft. 2009. Non-native fishes and native species diversity in freshwater fish assemblages across the United States. *Biological Invasions* 11(6):1441-1450.
- Moerke, A. H., and G. A. Lamberti. 2003. Responses in fish community structure to restoration of two Indiana streams. *North American Journal of Fisheries Management* 23(3):748-759.
- Moerman, D. E., and G. F. Estabrook. 2006. The botanist effect: counties with maximal species richness tend to be home to universities and botanists. *Journal of Biogeography* 33(11):1969-1974.
- Moyle, P. B., and T. Light. 1996. Biological invasions of fresh water: empirical rules and assembly theory. *Biological Conservation* 78(1-2):149-161.
- Moyle, P. B., and M. P. Marchetti. 2006. Predicting invasion success: freshwater fishes in California as a model. *Bioscience* 56(6):515-524.
- Naylor, R. L., S. L. Williams, and D. R. Strong. 2001. Ecology - aquaculture - a gateway for exotic species. *Science* 294(5547):1655-1656.
- North Carolina Department of Agriculture and Consumer Services. 2010. Article 63 Aquaculture Development Act.
<http://ncagr.gov/markets/aquaculture/documents/NCAQUACULTURESTATUTES.pdf> accessed 6/30/2010.
- North Carolina Wildlife Resources Commission (NCWRC). 2009. North Carolina inland fishing, hunting and trapping regulations digest 2009-2010.
http://www.ncwildlife.org/Regs/2009_10/2009_10_RegsDigest.pdf accessed 6/30/2010.

- Nelson, J. S., E. J. Crossman, H. Espinosa-Peréz, L. T. Findley, C. R. Gilberd, R. N. Lea, and J. D. Williams. 2004. Common and scientific names of fishes from the United States, Canada and Mexico, 6th ed. American Fisheries Society Special Publication 29, Bethesda, Maryland.
- Nelson, K. C., M. A. Palmer, J. E. Pizzuto, G. E. Moglen, P. L. Angermeier, R. H. Hilderbrand, M. Dettinger, and K. Hayhoe. 2009. Forecasting the combined effects of urbanization and climate change on stream ecosystems: from impacts to management options. *Journal of Applied Ecology* 46(1):154-163.
- Nico, L. G., and P. L. Fuller. 1999. Spatial and temporal patterns of nonindigenous fish introductions in the United States. *Fisheries* 24(1):16-27.
- New York Invasive Species Council (NYISC). 2010. Final report: a regulatory system for non-native species. http://www.dec.ny.gov/docs/lands_forests_pdf/invasive062910.pdf accessed 6/30/2010.
- New York State Department of Environmental Conservation (NYS DEC). 2010a. Baitfish of New York State: how to identify and legally use them in our freshwaters and the Hudson http://www.dec.ny.gov/docs/fish_marine_pdf/baitfishofny.pdf accessed 6/30/2010.
- New York State Department of Environmental Conservation (NYSDEC). 2010b. Regulation 180.9 fish dangerous to indigenous fish populations. <http://www.dec.ny.gov/regs/3934.html#13350> accessed 6/30/2010.
- Olden, J. D., M. K. Kennard, F. Leprieur, P. A. Tedesco, K. O. Winemiller, and E. García-Berthou. 2010. Conservation biogeography of freshwater fishes: recent progress and future challenges. *Diversity and Distributions* 16(3):496-513.
- Olden, J. D., N. L. Poff, and K. R. Bestgen. 2006. Life-history strategies predict fish invasions and extirpations in the Colorado River basin. *Ecological Monographs* 76(1):25-40.
- Padilla, D. K., and S. L. Williams. 2004. Beyond ballast water: aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. *Frontiers in Ecology and the Environment* 2(3):131-138.
- Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers, and L. Goldwasser. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1:3-19.
- Pascual, M., P. Macchi, J. Urbanski, F. Marcos, C. Riva Rossi, M. Novara, and P. Dell'Arciprete. 2002. Evaluating potential effects of exotic freshwater fish from incomplete species presence-absence data. *Biological Invasions* 4(1):101-113.

- Pautasso, M., and M. L. McKinney. 2007. The botanist effect revisited: Plant species richness, county area, and human population size in the United States. *Conservation Biology* 21(5):1333-1340.
- Perrings, C. 2002. Biological invasions in aquatic systems: the economic problem. *Bulletin of Marine Science* 70(2):541-552.
- Peters, J. A., and D. M. Lodge. 2009. Invasive species policy at the regional level: a multiple weak links problem. *Fisheries* 34(8):373-381.
- Pennsylvania Fish and Boat Commission (PFBC). 2010. Pennsylvania fishing summary: summary of fishing regulations and laws. <http://www.fish.state.pa.us/fishpub/summary/z00complete.pdf> accessed 6/30/2010.
- Pierce, C. L., J. B. Rasmussen, and W. C. Leggett. 1990. Sampling littoral fish with a seine - corrections for variable capture efficiency. *Canadian Journal of Fisheries and Aquatic Sciences* 47(5):1004-1010.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and t. R. C. Team. 2009. nlme: linear and nonlinear mixed effects models.
- Pont, D., B. Hugueny, and T. Oberdorff. 2005. Modelling habitat requirement of European fishes: do species have similar responses to local and regional environmental constraints? *Canadian Journal of Fisheries and Aquatic Sciences* 62(1):163-173.
- Prasad, A. M., L. R. Iverson, and A. Liaw. 2006. Newer classification and regression tree techniques: Bagging and random forests for ecological prediction. *Ecosystems* 9(2):181-199.
- Preisser, E. L., J. S. Elkinton, and K. Abell. 2008. Evolution of increased cold tolerance during range expansion of the elongate hemlock scale *Fiorinia externa* Ferris (Hemiptera: Diaspididae). *Ecological Entomology* 33(6):709-715.
- Puth, L. M., and D. M. Post. 2005. Studying invasion: have we missed the boat? *Ecology Letters* 8(7):715-721.
- Pyšek, P., D. M. Richardson, J. Pergl, V. Jarošík, Z. Sixtová, and E. Weber. 2008. Geographical and taxonomic biases in invasion ecology. *Trends in Ecology & Evolution* 23(5):237-244.
- Rahel, F. J., and J. D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. *Conservation Biology* 22(3):521-533.
- R Development Core Team (RDCT). 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, ISBN 3-900051-07-0, <http://www.R-project.org>. accessed 6/30/2010, Vienna, Austria.

- Reichard, S., D. C. Schmitz, D. Simberloff, D. Morrison, P. P. Lehtonen, P. N. Windle, G. Chavarria, and R. W. Mezitt. 2005. The tragedy of the commons revisited: invasive species. *Frontiers in Ecology and the Environment* 3(2):109-115.
- Ribeiro, F., M. J. Collares-Pereira, and P. B. Moyle. 2009. Non-native fish in the fresh waters of Portugal, Azores and Madeira Islands: a growing threat to aquatic biodiversity. *Fisheries Management and Ecology* 16(4):255-264.
- Ribeiro, F., B. Elvira, M. J. Collares-Pereira, and P. B. Moyle. 2008. Life-history traits of non-native fishes in Iberian watersheds across several invasion stages: a first approach. *Biological Invasions* 10(1):89-102.
- Ricciardi, A. 2001. Facilitative interactions among aquatic invaders: is an "invasional meltdown" occurring in the Great Lakes? *Canadian Journal of Fisheries and Aquatic Sciences* 58(12):2513-2525.
- Ricciardi, A. 2003. Predicting the impacts of an introduced species from its invasion history: an empirical approach applied to zebra mussel invasions. *Freshwater Biology* 48(6):972-981.
- Ricciardi, A., and S. K. Atkinson. 2004. Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. *Ecology Letters* 7(9):781-784.
- Ricciardi, A., and J. Cohen. 2007. The invasiveness of an introduced species does not predict its impact. *Biological Invasions* 9(3):309-315.
- Ricciardi, A., and R. Kipp. 2008. Predicting the number of ecologically harmful exotic species in an aquatic system. *Diversity and Distributions* 14(2):374-380.
- Richardson, D. M., and P. Pyšek. 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography* 30(3):409-431.
- Richardson, D. M., and P. Pyšek. 2008. Fifty years of invasion ecology - the legacy of Charles Elton. *Diversity and Distributions* 14(2):161-168.
- Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6(2):93-107.
- Rixon, C. A. M., I. C. Duggan, N. M. N. Bergeron, A. Ricciardi, and H. J. Macisaac. 2005. Invasion risks posed by the aquarium trade and live fish markets on the Laurentian Great Lakes. *Biodiversity and Conservation* 14(6):1365-1381.
- Rose, C. A. 2005. Economic growth as a threat to fish conservation in Canada. *Fisheries* 30(8):36-38.

- Rothlisberger, J. D., W. L. Chadderton, J. McNulty, and D. M. Lodge. 2010. Aquatic invasive species transport via trailered boats: what is being moved, who is moving it, and what can be done. *Fisheries* 35(3):121-132.
- Ruesink, J. L. 2003. One fish, two fish, old fish, new fish: which invasions matter? P. Kareiva, and S. A. Levin, editors. *The importance of species; perspectives on expendability and triage*. Princeton University Press, Princeton, New Jersey.
- Ruesink, J. L. 2005. Global analysis of factors affecting the outcome of freshwater fish introductions. *Conservation Biology* 19(6):1883-1893.
- Ruesink, J. L., I. M. Parker, M. J. Groom, and P. M. Kareiva. 1995. Reducing the risks of nonindigenous species introductions - guilty until proven innocent. *Bioscience* 45(7):465-477.
- Sales, J., and G. P. J. Janssens. 2003. Nutrient requirements of ornamental fish. *Aquatic Living Resources* 16(6):533-540.
- Sax, D. F., and S. D. Gaines. 2008. Species invasions and extinction: the future of native biodiversity on islands. *Proceedings of the National Academy of Sciences of the United States of America* 105:11490-11497.
- Sax, D. F., J. J. Stachowicz, J. H. Brown, J. F. Bruno, M. N. Dawson, S. D. Gaines, R. K. Grosberg, A. Hastings, R. D. Holt, M. M. Mayfield, M. I. O'Connor, and W. R. Rice. 2007. Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution* 22(9):465-471.
- Schmetterling, D. A., and J. A. McFee. 2006. Migrations by fluvial largescale suckers (*Catostomus macrocheilus*) after transport upstream of Milltown Dam, Montana. *Northwest Science* 80(1):18-25.
- Scott, M. C., and G. S. Helfman. 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. *Fisheries* 26(11):6-15.
- Scott, W. B., and E. J. Crossman. 1979. *Freshwater fishes of Canada*. Bulletin of the Fisheries Research Board of Canada 184, Ottawa, Ontario.
- Seaber, P. R., F. P. Kapinos, and G. L. Knapp. 1987. Hydrologic unit maps.
- Shafland, P. L., K. B. Gestring, and M. S. Stanford. 2008. Categorizing introduced fishes collected from public waters. *Southeastern Naturalist* 7(4):627-636.
- Shirley, S. M., and S. Kark. 2009. The role of species traits and taxonomic patterns in alien bird impacts. *Global Ecology and Biogeography* 18(4):450-459.
- Shiu, H., and L. Stokes. 2008. Buddhist animal release practices: historic, environmental, public health and economic concerns. *Contemporary Buddhism* 9(2):181-196.

- Simberloff, D. 2003. How much information on population biology is needed to manage introduced species? *Conservation Biology* 17(1):83-92.
- Smock, L. A., and E. Gilinsky. 1992. Coastal Plain blackwater streams. Pages 271-313 in C. T. Hackney, S. M. Adams, and W. H. Martin, editors. *Biodiversity of the southeastern United States: Aquatic Communities*. Wiley, New York, New York.
- Sol, D., M. Vilà, and I. Kuhn. 2008. The comparative analysis of historical alien introductions. *Biological Invasions* 10(7):1119-1129.
- Starnes, W. C. 2002. Current diversity, historical analysis, and biotic integrity of fishes in the lower Potomac basin in the vicinity of Plummers Island, Maryland-Contribution to the natural history of Plummers Island, Maryland XXVIIx. *Proceedings of the Biological Society of Washington* 115(2):273-320.
- Starnes, W. C., J. Odenkirk, and M. J. Ashton. in press. Update and analysis of fish occurrences in the lower Potomac River drainage in the vicinity of Plummers Island, Maryland. *Proceedings of the Biological Society of Washington*.
- Stokstad, E. 2010. Biologists rush to protect Great Lakes from onslaught of carp. *Science* 327:932.
- Strayer, D. L. 2010. Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology* 55(s1):152-174.
- Strobl, C., A. L. Boulesteix, T. Kneib, T. Augustin, and A. Zeileis. 2008. Conditional variable importance for random forests. *Bmc Bioinformatics* 9.
- Strobl, C., A. L. Boulesteix, A. Zeileis, and T. Hothorn. 2007. Bias in random forest variable importance measures: illustrations, sources and a solution. *Bmc Bioinformatics* 8.
- ter Braak, C. J. F., and P. Smilauer. 1998. *Canoco reference manual and user's guide to Canoco for Windows: software for canonical community ordination (version 4)*. Microcomputer Power, Ithaca, New York.
- ter Braak, C. J. F., and P. Smilauer. 2004. *Canoco for Windows version 4.53*. Biometris - Plant Research International, Wageningen, The Netherlands.
- Thomas, V. G., C. Vasarhelyi, and A. J. Niimi. 2009. Legislation and the capacity for rapid-response management of nonindigenous species of fish in contiguous waters of Canada and the USA. *Aquatic Conservation-Marine and Freshwater Ecosystems* 19(3):354-364.
- Tlusty, M. 2002. The benefits and risks of aquacultural production for the aquarium trade. *Aquaculture* 205(3-4):203-219.

- Townsend, C. R., and M. J. Winterbourn. 1992. Assessment of the environmental risk posed by an exotic fish - the proposed introduction of channel catfish (*Ictalurus punctatus*) to New Zealand. *Conservation Biology* 6(2):273-282.
- United States Environmental Protection Agency (USEPA). 2008. Surface waters data and metadata files. USEPA Region 3 <http://www.epa.gov/emap/remap/html/three/data/index.html> accessed 12/01/2009, Philadelphia, Pennsylvania.
- United States Geological Survey (USGS). 2008. Ecology data. <http://water.usgs.gov/nawqa/ecology/> accessed 12/01/2009, Reston, Virginia.
- Valery, L., H. Fritz, J. C. Lefeuvre, and D. Simberloff. 2008. In search of a real definition of the biological invasion phenomenon itself. *Biological Invasions* 10(8):1345-1351.
- Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* 401(6752):464-467.
- Vander Zanden, M. J., and J. D. Olden. 2008. A management framework for preventing the secondary spread of aquatic invasive species. *Canadian Journal of Fisheries and Aquatic Sciences* 65(7):1512-1522.
- Virginia Department of Game and Inland Fisheries (VDGIF). 2010. 2010 freshwater fishing in Virginia. <http://www.epaperflip.com/aglaia/viewer.aspx?docid=73e54b76c85043caaa8f9e855307b477> accessed 6/30/2010.
- Venables, W. N., and B. D. Ripley. 2002. *Modern applied statistics with S*. 4th ed. Springer, New York, New York.
- Vilà, M., C. Basnou, P. Pyšek, M. Josefsson, P. Genovesi, S. Gollasch, W. Nentwig, S. Olenin, A. Roques, D. Roy, and P. E. Hulme. 2010. How well do we understand the impacts of alien species on ecosystem services? a pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment* 8(3):135-144.
- Vitousek, P. M., C. M. D'Antonio, L. L. Loope, M. Rejmánek, and R. Westbrooks. 1997. Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* 21(1):1-16.
- Vitule, J. R. S., C. A. Freire, and D. Simberloff. 2009. Introduction of non-native freshwater fish can certainly be bad. *Fish and Fisheries* 10(1):98-108.
- Walsh, C., and R. Mac Nally. 2008. *heir.part: hierarchical partitioning*. R package version 1.0-3.
- Westphal, M. I., M. Browne, K. MacKinnon, and I. Noble. 2008. The link between international trade and the global distribution of invasive alien species. *Biological Invasions* 10(4):391-398.

- Whitney, K. D., and C. A. Gabler. 2008. Rapid evolution in introduced species, 'invasive traits' and recipient communities: challenges for predicting invasive potential. *Diversity and Distributions* 14(4):569-580.
- Whittaker, R. J., M. B. Araujo, J. Paul, R. J. Ladle, J. E. M. Watson, and K. J. Willis. 2005. Conservation biogeography: assessment and prospect. *Diversity and Distributions* 11(1):3-23.
- Whittier, T. R., and T. M. Kincaid. 1999. Introduced fish in northeastern USA lakes: regional extent, dominance, and effect on native species richness. *Transactions of the American Fisheries Society* 128(5):769-783.
- Williams, J. G. 2008. Mitigating the effects of high-head dams on the Columbia River, USA: experience from the trenches. *Hydrobiologia* 609:241-251.
- Williamson, M., and A. Fitter. 1996. The varying success of invaders. *Ecology* 77(6):1661-1666.
- Wood, S. N. 2008. Fast stable direct fitting and smoothness selection for generalized additive models. *Journal of the Royal Statistical Society Series B-Statistical Methodology* 70:495-518.
- West Virginia Department of Natural Resources (WVDNR). 2010. Fishing 2010 regulations summary. <http://www.wvdnr.gov/Fishing/Regs10/fishRegs2010%20final.pdf> accessed 6/30/2010.

Appendix A: Example of the survey administered to obtain estimates of nonnative species impact. Questions one to three were repeated for each species. Question four was given at the end of the survey.

- 1) The relative abundance of the species in suitable habitats in the drainage is:
 - a. generally abundant throughout the drainage
 - b. locally abundant somewhere in the drainage
 - c. not abundant anywhere in the drainage

- 2) Nuisance fishes are those species whose establishment has led to undesirable economical, social, or cultural impacts. Based on this definition, the species is a:
 - a. major nuisance.
 - b. moderate nuisance.
 - c. minor nuisance or not a nuisance.

- 3) Fishes having an ecological impact are those that have noticeably, negatively affected native species (including non-fishes), either directly or indirectly. Based on this definition, the species has had a:
 - a. major ecological impact.
 - b. moderate ecological impact.
 - c. minor or no ecological impact.

- 4) Please state the focus of your work/research
 - a. Game fishes
 - b. Non-game fishes
 - c. Other _____

Appendix B: Nonnative fishes in the study region. Column headings are defined as follows: “HUCs” is the total number of drainages in which a species is established; “Game” lists game species as “Yes”; “GISD” lists species found in the GISD as “Yes”; and, for collection approaches with more than one sample, “N” is the sample size, “R” is the species’ rank based on mean rating, and “E” is the species’ rank based on standard error of the mean rating. Highest ranking species (i.e., 1) had the highest mean rating or standard error.

Scientific Name	Common Name	HUCs	Game	GISD	Review	Socioeconomic			Ecological			Abundance			Collection		
					Rating	N	R	E	N	R	E	N	R	E	N	R	E
<i>Alosa pseudoharengus</i>	alewife	3	N/A	Yes	1	47	6	18	47	11	25	47	28	54	297	25	22
<i>Alosa aestivalis</i>	blueback herring	1	N/A	No	0	18	16	16	18	25	16	19	15	29	99	42	42
<i>Ambloplites cavifrons</i>	Roanoke bass	3	Yes	No	0	32	51	51	32	60	47	31	51	49	297	15	15
<i>Ambloplites rupestris</i>	rock bass	8	Yes	No	2	88	24	39	87	15	46	85	5	65	792	7	10
<i>Ameiurus melas</i>	black bullhead	2	N/A	No	1	21	43	30	21	59	51	21	63	43	198	42	42
<i>Ameiurus brunneus</i>	snail bullhead	1	N/A	No	0	14	51	51	14	63	45	14	52	22	99	24	5
<i>Amia calva</i>	bowfin	3	N/A	No	0	38	33	27	38	58	55	37	60	42	297	42	42
<i>Apeltes quadracus</i>	fourspine stickleback	1	No	No	1	6	51	51	6	66	66	6	69	11	99	8	2
<i>Carassius auratus</i>	goldfish	2	No	Yes	1	29	8	17	29	16	17	29	37	24	198	38	36
<i>Carpoides cyprinus</i>	quillback	2	No	No	0	24	37	29	24	52	48	23	48	35	198	31	33
<i>Catostomus commersonii</i>	white sucker	1	N/A	No	1	16	51	51	16	66	66	15	46	27	99	20	7
<i>Channa argus</i>	snakehead	1	No	Yes	1	16	1	6	16	4	7	16	21	16	99	42	42
<i>Culaea inconstans</i>	brook stickleback	1	No	No	0	6	51	51	6	66	66	6	69	11	99	42	42
<i>Cyprinella lutrensis</i>	red shiner	1	No	Yes	2	12	11	9	12	6	5	13	39	26	99	42	42
<i>Cyprinella spiloptera</i>	spotfin shiner	1	No	No	0	12	51	51	12	61	34	12	21	33	99	31	23
<i>Cyprinus carpio</i>	common carp	11	Yes	Yes*	1	118	2	25	118	2	54	117	2	72	1089	17	31
<i>Dorosoma cepedianum</i>	gizzard shad	3	No	No	1	40	5	14	40	8	24	39	4	44	297	15	8
<i>Dorosoma petenense</i>	threadfin shad	7	No	No	0	74	27	35	74	34	60	75	29	66	693	30	34
<i>Enneacanthus gloriosus</i>	bluespotted sunfish	1	No	No	0	7	51	51	7	66	66	7	72	21	99	42	42

<i>Esox masquinongy</i>	muskellunge	3	Yes	No	2	39	34	28	40	19	29	40	50	50	297	42	42
<i>Esox lucius</i>	northern pike	4	Yes	No	2	51	30	33	51	27	33	50	58	55	396	37	40
<i>Etheostoma zonale</i>	banded darter	3	No	No	1	31	28	22	30	21	14	30	24	39	297	9	4
<i>Etheostoma blennioides</i>	greenside darter	1	No	No	0	14	51	51	14	49	26	14	10	6	99	6	1
<i>Gambusia holbrooki</i>	eastern mosquitofish	1	No	Yes	2	13	25	15	13	40	15	14	18	4	99	42	42
<i>Ictalurus furcatus</i>	blue catfish	4	Yes	No	1	43	4	10	43	1	21	43	16	46	396	13	12
<i>Ictalurus punctatus</i>	channel catfish	11	Yes	No	1	125	22	41	125	14	62	124	6	70	1089	14	29
<i>Ictiobus bubalus</i>	smallmouth buffalo	1	No	No	0	12	37	20	12	61	34	12	69	38	99	42	42
<i>Lepomis macrochirus</i>	bluegill	11	Yes	No	1	117	36	48	117	24	56	115	1	73	1089	1	6
<i>Lepomis cyanellus</i>	green sunfish	11	N/A	No	2	115	7	34	115	9	61	114	20	68	1089	4	20
<i>Lepomis megalotis</i>	longear sunfish	1	N/A	No	0	15	51	51	15	30	10	16	31	25	99	19	3
<i>Lepomis microlophus</i>	redecor sunfish	11	Yes	No	2	115	48	50	114	55	65	114	26	62	1089	11	28
<i>Lepomis gulosus</i>	warmouth	3	Yes	No	1	31	50	44	31	41	41	30	46	48	297	25	26
<i>Leuciscus idus</i>	ide	1	No	Yes	0	16	29	19	16	37	18	16	52	3	99	42	42
<i>Lota lota</i>	burbot	1	No	No	0	8	51	51	8	52	13	9	59	9	99	42	42
<i>Luxilus cerasinus</i>	crescent shiner	2	No	No	0	19	51	51	18	56	42	18	44	20	198	38	36
<i>Luxilus chrysocephalus</i>	striped shiner	1	No	No	0	13	51	51	13	22	4	13	17	2	99	42	42
<i>Micropterus salmoides</i>	largemouth bass	11	Yes	Yes*	2	117	34	45	118	7	53	116	3	71	1089	2	13
<i>Micropterus dolomieu</i>	smallmouth bass	10	Yes	No	2	112	40	46	112	13	52	112	7	61	990	5	16
<i>Micropterus punctulatus</i>	spotted bass	3	Yes	No	1	34	15	23	34	20	27	33	41	52	297	31	32
<i>Morone saxatilis</i>	striped bass	6	Yes	No	2	60	51	51	60	30	36	62	14	59	594	10	19
<i>Morone chrysops</i>	white bass	2	Yes	No	1	26	31	26	26	29	28	24	33	37	198	38	36
<i>Moxostoma cervinum</i>	blacktip jumprock	1	No	No	0	9	16	1	8	26	1	8	43	7	99	31	23
<i>Moxostoma erythrurum</i>	golden redhorse	1	No	No	0	14	19	11	14	17	12	14	9	5	99	27	17
<i>Nocomis leptocephalus</i>	bluehead chub	2	No	No	0	23	45	36	23	44	37	23	25	15	198	20	14

<i>Nocomis raneyi</i>	bull chub	1	No	No	0	9	16	1	9	23	3	8	8	7	99	42	42
<i>Nocomis biguttatus</i>	hornyhead chub	1	No	No	0	15	51	51	15	66	66	15	62	27	99	42	42
<i>Notropis atherinoides</i>	emerald shiner	2	No	No	0	29	49	42	28	49	32	30	38	41	198	42	42
<i>Notropis volucellus</i>	mimic shiner	2	No	No	0	20	11	8	20	33	11	21	40	19	198	42	42
<i>Notropis buccatus</i>	silverjaw minnow	1	No	No	0	9	51	51	9	66	66	9	49	9	99	42	42
<i>Notropis telescopus</i>	telescope shiner	1	No	No	0	8	11	3	8	37	9	8	13	1	99	42	42
<i>Noturus gilberti</i>	orange-fin madtom	1	No	No	0	9	32	13	9	56	20	9	63	13	99	42	42
<i>Oncorhynchus clarkii</i>	cutthroat trout	1	Yes	No	1	15	51	51	15	43	22	16	67	40	99	42	42
<i>Oncorhynchus mykiss</i>	rainbow trout	5	Yes	Yes*	2	68	21	32	67	12	40	67	32	67	495	23	27
<i>Oncorhynchus nerka</i>	sockeye salmon	1	Yes	No	0	15	51	51	15	64	50	15	73	60	99	42	42
<i>Oreochromis aureus</i>	blue tilapia	1	No	Yes	2	14	9	4	14	10	2	15	63	31	99	42	42
<i>Osmerus mordax</i>	rainbow smelt	1	No	No	2	16	51	51	16	52	31	16	52	30	99	42	42
<i>Perca flavescens</i>	yellow perch	5	Yes	No	0	56	26	31	56	37	59	55	12	57	495	18	21
<i>Percina roanoka</i>	Roanoke darter	1	No	No	0	9	51	51	9	30	8	9	35	17	99	42	42
<i>Percina notogramma</i>	stripeback darter	1	No	No	0	17	51	51	17	66	66	17	61	34	99	42	42
<i>Phoxinus oreas</i>	mountain redbelly dace	2	No	No	0	22	51	51	22	65	63	22	36	14	198	42	42
<i>Pimephales notatus</i>	bluntnose minnow	4	No	No	0	42	43	43	42	42	39	40	19	47	396	12	11
<i>Pimephales promelas</i>	fathead minnow	5	No	No	0	66	14	24	64	28	44	63	30	58	495	29	35
<i>Poecilia reticulata</i>	guppy	1	No	Yes	2	15	20	7	15	51	30	15	63	31	99	42	42
<i>Pomoxis nigromaculatus</i>	black crappie	6	Yes	No	0	67	41	47	67	36	58	66	11	56	594	20	30
<i>Pomoxis annularis</i>	white crappie	9	Yes	No	0	96	47	49	96	48	64	96	42	69	891	41	41
<i>Pylodictis olivaris</i>	flathead catfish	5	Yes	Yes	2	58	3	12	57	3	19	57	27	51	495	31	39
<i>Rhinichthys cataractae</i>	longnose dace	1	No	No	1	14	51	51	14	66	66	13	57	18	99	31	23
<i>Salmo trutta</i>	brown trout	8	Yes	Yes*	2	93	23	38	93	5	43	93	23	63	792	3	9
<i>Sander vitreus</i>	walleye	6	Yes	No	2	60	51	51	60	35	49	59	45	64	594	42	42

<i>Scardinius erythrophthalmus</i>	rudd	2	No	Yes	0	23	45	36	23	44	37	24	68	53	198	42	42
<i>Semotilus corporalis</i>	fallfish	1	No	No	0	13	39	21	13	47	23	14	52	22	99	27	17
<i>Thoburnia rhotroeca</i>	torrent sucker	4	No	No	0	38	42	40	38	46	57	37	34	45	396	42	42
<i>Tilapia zillii</i>	redbelly tilapia	1	No	Yes	2	18	10	5	18	17	6	18	52	36	99	42	42

*Also found in the IUCN's top 100 invasive species list.