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Invasion note

Popularity and propagule pressure: determinants of introduction and establishment of aquarium fish

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Abstract

Propagule pressure is frequently cited as an important determinant of invasion success for terrestrial taxa, but its importance for aquatic species is unclear. Using data on aquarium fishes in stores and historical records of fish introduced and established in Canadian and United States waters, we show clear relationships exist between frequency of occurrence in shops and likelihood of introduction and of establishment. Introduced and established taxa are also typically larger than those available from stores, consistent with the propagule pressure hypothesis in that larger fish may be released more frequently due to outgrowing their aquaria. Attempts to reduce the numbers of introductions may be the most practical mechanism to reduce the number of new successful invasions.

Introduction

Invasions are sequential, multi-phase processes, involving transportation, introduction, establishment and spread. Understanding invasions may best be achieved by examining each component phase separately, although most literature to date has focused only on later phases (Carlton 1996; Kolar and Lodge 2001). The number and/or frequency of propagules released at introduction, known as propagule pressure, is emerging as an important determinant of invasion success. Likelihood of extinction presumably is greater at small population sizes due both to demographic and environmental stochasticity (Sax and Brown 2000; Duncan et al. 2003). Larger and/or more frequent introductions are thus expected to have greater probabilities of successful establishment. This pattern has been observed for a variety of terrestrial taxa (e.g., Forsyth and Duncan 2001; Lounibos 2002). Propagule pressure has rarely been documented for aquatic, and in particular for freshwater, organisms (e.g., Wonham et al. 2000; MacIsaac et al. 2002). In particular, it has rarely been examined for fish, despite frequent invasions of this group worldwide (Fuller et al. 1999; Wonham et al. 2000).

The aquarium trade imports hundreds of fish species into North America annually (Ramsay 1985; Chapman et al. 1997). A number have subsequently been introduced into freshwater habitats by home aquarists, and many of these have established persistent, self-reproducing populations (e.g., Crossman and Cudmore 1999; Fuller et al. 1999). Aquarium fishes are introduced into recipient waters as a disposal method apparently perceived as more humane than various euthanasia options (Courtenay and Taylor 1986). The most commonly cited reasons for release of healthy fishes are that owners tire of them, or that fish become too large or prolific for their aquaria (e.g., Courtenay 1999; Crossman and Cudmore 1999).

Using data of fish occurrence in aquarium stores and from United States and Canadian waters that presumably originated from private aquaria, we test the hypothesis that propagule pressure is a major determinant of introduction and establishment via the aquarium hobby. In addition, we assess other introduction characteristics that may influence establishment success: taxonomic identity and ability to attain large size in aquaria. Recognition of such patterns may improve our ability to predict and reduce the probability of future invasions (Duncan et al. 2003).

Data collection, analyses and results

Introduction and establishment records of aquarium fish into freshwaters of Canada and the USA were obtained primarily using Fuller et al. (1999), Nelson and Paetz (1992) and the United States Geological Survey (USGS) nonindigenous aquatic species database (http://nas.er.usgs.gov/). We considered records only for deliberate releases from home aquaria. Taxa were considered established even if populations were later eradicated. We found 94 fish species reported as introduced, including 34 established.

We surveyed freshwater fish occurrence from 20 aquarium and pet stores between October 2002 and July 2003. Stores ranged from small, privately owned retailers to large, North American chains, located between Toronto, Ontario, Canada and Macomb County, Michigan, USA. We recorded 308 fish taxa (see Rixon et al. in press), including 54 reported as introduced. Occurrence frequency was calculated for each taxon as the proportion of stores in which that taxon was present, and was used as a proxy measure of propagule pressure. This may provide a better proxy of ‘frequency’ than of ‘numbers’ released, although fishes introduced more often have greater chances of occasional release in high numbers. The area we surveyed was smaller than for the introduction data, and popularity of some species may change over time. However, our most frequently occurring taxa are similar to the most popular fish listed from importation records surveyed in 1971 and 1992 from a broad array of United States ports (Ramsay 1985; Chapman et al. 1997). We thus have confidence that our data represent broader scale spatial and temporal patterns of popularity.

To determine if introduction and establishment is related to propagule supply from private aquaria, we compared occurrences of fishes in Canadian and USA waters with their occurrence frequency in stores. Fishes were grouped into categories of 50 based on store occurrence frequency (i.e., the 50 most frequently occurring, 51–100th most frequently occurring, etc). Because occurrence frequencies overlapped categories (e.g., fishes in 5% of stores could be assigned to the 201–250th or 251–300th most frequently occurring category), species order was randomized within occurrence frequencies; fishes were then assigned to each category based on order listed. Relationships were examined using linear regression (Systat 7.0), with dependent variables $\log_{10}$ transformed for analyses. A strong negative relationship was observed between store frequency and both recorded introduction ($R^2 = 0.936$, $P < 0.01$) and establishment ($R^2 = 0.674$, $P < 0.05$) into freshwater habitats (Figure 1).

To examine whether different taxonomic groups are under or over-represented at each

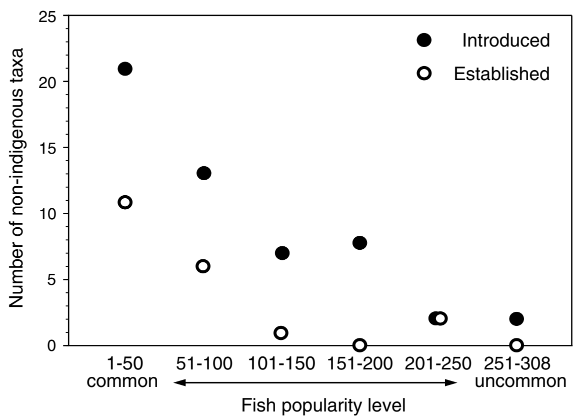

Figure 1. Number of aquarium fish introduced and established in Canadian and United States waters. Fishes were ranked based on frequency of occurrence in stores from most frequently occurring (ranked 1) to least frequently occurring (ranked 308). Fishes are grouped into categories of 50.

invasion phase, we determined: (1) if composition of fish families recorded as introduced correspond to those in stores; and (2) if established taxa are similar in composition to those introduced. These were tested using χ^2 goodness of fit tests, using the restrictions outlined by Zar (1996). In the introduction phase, for example, the numbers of species introduced for each family were the observed variables, whereas expected frequencies were calculated based on occurrence frequencies in the stores. Where analyses detected differences between frequencies, the family with the greatest contribution to the χ^2 value was removed, and the remaining families reanalysed to see if these conformed (Zar 1996). Six families had relatively high numbers of introductions (>5 species) and were used in analyses (Figure 2). Differences were found between frequencies of families in stores and introduced ($\chi^2 = 37.67$, $df = 5$, $P < 0.001$), and between introduction and establishment ($\chi^2 = 9.27$, $df = 3$, $P < 0.05$). Poeciliidae, the second most commonly introduced taxon, was relatively unimportant in store surveys and contributed most to the χ^2 value (36.68); frequencies of other taxa conformed after its removal. Between introduction and establishment phases, poeciliids also contributed most to the χ^2 value (8.44); other taxa conformed after its removal. Belodontiidae and Loricariidae were not used in this analysis as they did not meet the requirements for χ^2 (expected frequencies <2). Characidiae were highly speciose in stores, and the third most introduced, but had no established species.

To test if introduction and establishment is related to taxa outgrowing tanks, we compared maximum obtainable fish lengths between each invasion phase. Maximum lengths for introduced and 287 store fish taxa were obtained from the Fishbase database (Froese and Pauly 2002); others were identifiable only to genera, were hybrids, or are apparently undescribed species. Species were divided into five length classes, each typically twice the length of the previous class, providing similar numbers of introductions in each. Analyses were performed as for taxonomic groupings. An additional comparison was made between length ranges of all store species and the most common 94 species (equal to the number reported as introduced) to determine if length differences exist based on popularity. Most fishes in stores are small, and become less common with increasing length (Figure 3). Comparing all species from stores to the top 94, higher proportions of more common fishes are smaller in length, and less frequent taxa tend to be larger. Chi-square analysis indicated differences between fishes in stores (all 287) and introduced ($\chi^2 = 35.62$, $df = 4$, $P < 0.001$). Differences were greatest at the extremes, with the $>$ 80 cm length range contributing most to the χ^2 value ($\chi^2 = 16.57$; higher frequency of fishes introduced

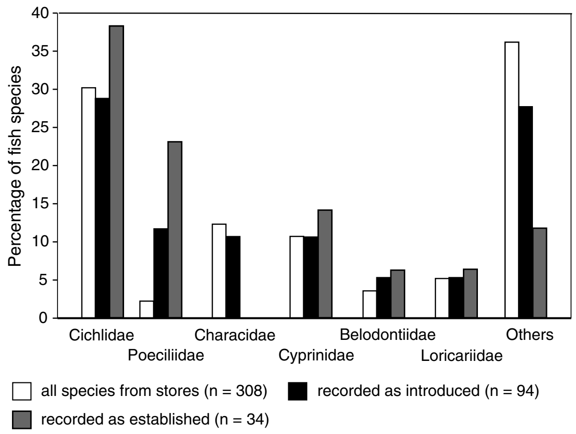

Figure 2. Relative proportions of fish families recorded from stores, as introduced and established. Families were included in the plot if they had greater than five species introductions, and are ordered by number of introductions.

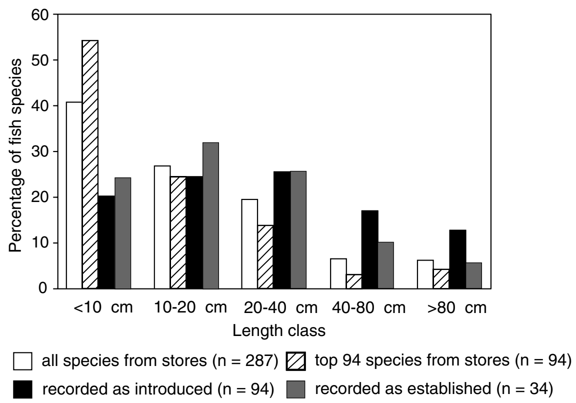

Figure 3. Relative proportions of different length classes of fishes recorded from stores, as introduced and established. For stores, plots are made for all species from which length data could be obtained, and for the 94 most frequently occurring species.

in this length range) followed by < 10 cm ($\chi^2 = 9.74$; lower frequencies introduced). Length distributions between introduced and established fishes differed ($\chi^2 = 10.45$, $df = 4$, $P < 0.05$) without removal of the 10–20 cm length class ($\chi^2 = 8.44$). Overall, maximum fish lengths were greater for those introduced (median length = 24.2 cm) or established (15.5 cm) than for those most common (top 94 species; 8.9 cm) or present (all species; 12 cm) in stores.

Discussion

Our study shows clear relationships between occurrence frequency of fish in aquarium stores and their introduction and establishment in freshwater habitats. This suggests that species more readily available to hobbyists are introduced more frequently and in greater numbers than rare species. 'Popularity' therefore appears to be an important determinant of invasions from aquarium release. Introduction effort through high propagule release sizes and/or frequencies, known collectively as propagule pressure, is increasingly recognised as one of the best correlates of establishment success (e.g., Forsyth and Duncan 2001; Lounibos 2002). Our results are among the first to document similar trends for freshwater organisms. However, we acknowledge our measure of propagule supply, popularity in stores, is removed from actual introduction efforts. From stores, a subset will first be kept in home aquaria, and only a proportion of these will be released. Nevertheless, our results indicate that attempts to reduce the numbers of aquarium fish released may well be the most practical method for reducing the invasion rate by this vector. It also strengthens the importance of using a measure of propagule supply in predictive models of aquarium fish invasion threats (e.g., Rixon et al. in press). With human population growth, and associated growth of the aquarium hobby, inoculation frequency and subsequent establishment by this vector is likely to increase with time.

Occurrence frequency in stores explained much of the variation in the introduction and establishment data. However, 40 introduced species were not found in our stores. Firstly, our aim was not to visit stores until all introduced fish species were found, but rather it was to assess the relative popularities of the common species. Secondly, in compiling our dataset of introductions we employed a liberal approach, including species listed as released by aquarists even if alternative vectors were listed; this was the case for most of those fishes not found (e.g., Fuller et al. 1999). Others may not be present in the aquarium trade or are rare taxa. Thousands of fishes are estimated to be part of this industry, with most being uncommon (Ramsay 1985). Based on importation records, Chapman et al. (1997) recorded 730 aquarium fish species entering the USA in October 1992; thus, if we obtained a more elaborate dataset, potentially recording more introduced species, the relationship would likely not remain linear, but instead form a strong exponential decay curve. Not having recorded some introduced species in stores therefore does not undermine the patterns we observed.

The importance of store occurrence frequency to species' introductions was reflected in the family data at each invasion phase. However, an over-representation of poeciliid introductions was found relative to that in stores. This may reflect the high number established relative to introduced, as species will more likely be recorded if their populations persist. Some poeciliids are among the most popular aquarium fishes, largely as they are hardy and easy to breed (Axelrod et al. 1995). Such characteristics may be advantageous for establishment. Our occurrence frequency from stores may also underestimate poeciliid importance, as common species are sold in many varieties (e.g., mollies, guppies, swordtails and platies). Some species were perhaps not recognised due to taxonomic difficulties, e.g., the introduced *Poecilia mexicana* and *P. peterensis* are members of the *P. sphenops* and *P. latipinna* species complexes, respectively. These may thus have been present but were not distinguished from their congeners. Characidae were common in stores and introduced, although none have established. A likely reason is small release sizes, as many introductions are reported as single individuals, e.g., black pacu, red piranha. This may reflect their keeping in small numbers due to large size and aggressive nature.

Introduced and established taxa typically had larger maximum lengths than those from stores, consistent with the hypothesis that larger fish are released more frequently. However, alternative reasons confounding this are that larger fish, although perhaps less commonly introduced due to lower store occurrences, survive longer and are caught more easily than smaller fish, e.g., common fishing methods capture larger fish more efficiently (e.g., Vaux et al. 1995). That greater proportions of smaller fish were found established than introduced provides evidence that smaller fish may be introduced more frequently than is observed, with smaller, short lived, species that do not establish less likely to be found.

Most aquarium fishes recorded as introduced have not established populations. Besides propagule supply, environmental factors relating to growth and reproductive success are critical. For releases into temperate regions, climatic mismatch is undoubtedly important as most aquarium species are native to the tropics (Chapman 2000). More tropical latitudes (e.g., Florida) and geothermal areas thus have disproportionately high numbers both introduced and established. Because of such large-scale variability in habitat, and of regional importation regulations, factors responsible for invasion success beyond propagule supply require regional assessment. However, any observed trends should be considered secondary determinants of the invasion process.

In conclusion, popularity is apparently an important factor associated with invasion success of fishes from private aquaria. Courtenay and Stauffer (1990) stated any aquarium fish has the potential to be released at some time. Indeed, we believe that most popular species have already been released into Canadian or USA waters. Many likely go unrecorded, failing to establish populations due to inadequate propagule sizes or subsequent factors affecting survival and reproduction. The relationships between popularity and introduction or establishment likely apply to other taxa in the aquarium trade (e.g., molluscs, plants), and also to other vectors where organisms are commercially purchased (e.g., live fish from food markets, bait fish). In order to prevent future invasions by such industries, strategies to reduce propagule supplies such as education of possible ecological and legal consequences of release, or an ability to return unwanted organisms to stores, must be utilized (e.g., Courtenay and Taylor 1986).

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