Life history strategies differentiate established from failed non-native freshwater fish in peninsular Florida

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Abstract

Aim: Non-native fishes threaten native biodiversity worldwide. Life history traits have been used to predict the risk of establishment for non-native fish in several regions of the world and parts of the United States, but not yet for Florida despite the elevated risk of establishment in the state due to many invasion pathways and favourable climate. Our goal was to identify which life history traits may be useful for predicting which non-native freshwater fishes might successfully establish populations in Peninsular Florida.

Location: Peninsular Florida, USA.

Methods: We conducted a factor analysis to evaluate 21 life history traits for 125 fishes in three different groups: native fishes, non-native fish species currently established in Florida and introduced fishes that failed to establish in Florida. We also modelled overall life history traits of those fishes according to the triangular model by Winemiller and Rose to compare overall strategies among the three different groups and tested for significant trait differences between failed and established fishes.

Results: Our analyses of life history traits showed that successful species have a high investment in their offspring and tend to be larger bodied. Parental care was particularly important, with only one of the established species lacking parental care. Triangular life history model results showed that most successfully established species such as those in the family Cichlidae are equilibrium strategists with a high degree of parental care, low-to-intermediate fecundity and a larger maturation size.

Main conclusions: Understanding the life history strategies and traits that aid in the prediction of non-native fish invasiveness is key for effective risk assessment and management. Further analysis of these traits as predictors of establishment and invasion success is needed, and regional risk assessments of non-native fishes will benefit from inclusion of several traits highlighted in this study.

Keywords: exotic, invasive, K-selected, risk assessment, r-selected, triangular model
1 | INTRODUCTION

Life history theory provides a strong framework for making inferences about non-native species invasion success (Capellini et al., 2015; Fournier et al., 2019). However, the use of biological traits to predict or describe invasion by non-native species is debated in the recent invasion ecology literature (Capellini et al., 2015; Garcia-Berthou, 2007; Sakai et al., 2001). Criticism primarily stems from the fact that there are no biological traits that consistently predict invasion across taxa and regions (Garcia-Berthou, 2007; Hayes & Barry, 2008). Across taxa and regions, only three factors seem to provide consistent predictive ability – propagule pressure, climate match and invasion history (Hayes & Barry, 2008). These factors alone, however, are not reliable at separating non-native fish species that establish versus those that fail to establish self-sustaining populations in peninsular Florida. Most of the non-native fishes that have failed to establish self-sustaining populations have similar propagule pressure and climate match to those that have successfully established. Invasion history is perhaps more useful, however, several established non-native fish species in Florida have little to no prior invasion history (e.g. Pike Killifish Belonesox belizanus), and some non-natives that have failed to establish are well-known invaders across the globe (e.g. Goldfish Carassius auratus, and Silver Carp Hypophthalmichthys molitrix).

There has also been a recent trend towards more general risk assessments that can be applied to any taxonomic group at a variety of spatial scales, rendering life history traits and strategies less relevant to risk assessment. This is evidenced by the recent development of the Aquatic Species Invasiveness Screening Kit (AS-ISK; Copp et al., 2016), a generalized risk screening tool based on the more taxonomically specialized Fish Invasiveness Screening Kit (FISK; Copp et al., 2009; Lawson et al., 2013). Another generic risk screening tool in use in the United States is the Ecological Risk Screening Summary (ERSS) developed by the U.S. Fish and Wildlife Service (USFWS, 2020). Tools like the AS-ISK and FISK utilize a wide variety of factors related to risk, including some life history traits, but focus more on the three most predictive factors across taxa and regions, propagule pressure, climate matching and invasion history (Hayes & Barry, 2008). The ERSS focuses solely on climate matching and invasion history. Although these methods can be successful in hazard identification and the provision of initial risk estimates, more specialized, taxon- and region-specific data and tools are necessary to assess risk of invasion in a comprehensive manner (Verbrugge et al., 2012). For example, FISK identifies several globally invasive fishes (e.g. Goldfish and Common Carp Cyprinus carpio) as potential hazards to peninsular Florida, yet these species have proven to be of low risk overall despite high propagule pressure and climate match (Lawson et al., 2015), suggesting that other factors such as life history traits and strategies might be critical.

At the regional scale, life history traits may be relevant predictors of successful establishment or invasion potential (Forsyth et al., 2004; Goodwin et al., 1999; Kolar & Lodge, 2002). For freshwater fish, life-history traits have been found to explain success or failure of non-natives in several regional studies (Allen et al., 2013; Howeth et al., 2016; Kolar & Lodge, 2002; Marchetti et al., 2004a, 2004b; Olden et al., 2006; Vila-Gispert et al., 2005); however, no specific life history traits consistently predict success across regions (Garcia-Berthou, 2007). This is perhaps not surprising given the considerable differences in climate, habitat and fish fauna (native and introduced) of the major regions within the United States with current analyses – Great Lakes (Howeth et al., 2016; Kolar & Lodge, 2002), California (Marchetti et al., 2004a, 2004b) and the Colorado River (Olden et al., 2006). In particular, few analyses of introduced fishes in warm climate regions are completed. Moreover, the wide variety of analytical approaches used in the studies further suggests a potential for variation in outcomes. The elusiveness of universal predictors and the success of regional analyses suggest more focus on the testing and comparison of life history traits on a regional basis. Increased spatial coverage of regional studies is needed to better understand the potential commonalities across regions of similar characteristics such as climate and habitat.

Florida (USA) is a hub of travel and commerce, has a large human population and encompasses most major pathways of freshwater fish introduction (Hill, 2002). In peninsular Florida, approximately 40 species of non-native freshwater fish have established populations, while at least 100 more have been observed in the environment (USGS, 2021). With thousands of fish species in trade (imported and domestically produced; Chapman et al., 1997; Smith et al., 2008; Tuckett et al., 2017), Florida continues to accumulate fish introductions, some of which fail, whereas others establish (see USGS, 2021). State agencies tasked with management of non-native fishes have embraced science-based risk screening and comprehensive risk assessments as critical tools used to inform decision making (e.g. Hardin & Hill, 2012; Hill & Lawson, 2015). A key knowledge gap impeding risk assessment in Florida and many warm climate regions is the influence of life history traits and strategies on success and failure of introduced fishes.

Despite the importance of Florida as a global hotspot for invasion, there has been no study of the relationship between life history traits and establishment success for non-native fishes in the region (Schofield & Loftus, 2015). To address this knowledge gap, our goal was to evaluate the importance of life history to establishment success of non-native freshwater fishes in peninsular Florida. We consider non-native fish to be those with a native range completely outside the study region of peninsular Florida. We consider non-native fish to be those with a native range completely outside the study region of peninsular Florida. Specifically, our objectives were to (1) visualize associations of native and non-native fish species with specific life history traits, (2) compare traits of successful and failed species and (3) use the triangular life history model of Winemiller and Rose (1992) to test the importance of life history strategies to establishment success. Peninsular Florida’s combination of tropical and hot summer temperate climates (Koppen-Geiger climate classification zones Af, Am, Aw, and Cfa; Beck et al., 2018; Peel et al., 2007) is unique in the United States and we expected to find a different set of traits relating to successful establishment of non-native fishes here compared to other regions. Thus, risk prediction factors and
their importance in Florida may differ from temperate or cold regions (e.g. Lawson et al., 2013) where most regional analyses have occurred. This research is among the largest regional analyses to date and is an important first step towards developing a risk assessment tool specifically for non-native fishes in peninsular Florida as well as more generally evaluating invasion success in warm climate regions.

2 | METHODS

2.1 | Data collection

Fish species, which occur in the fresh waters of peninsular Florida south of the Suwannee River basin, were divided into three groups: non-natives that have successfully established populations, non-natives that have failed to establish and fish species that are native to peninsular Florida. García-Berthou (2007) discusses the importance of clarity and consistency when assigning species to groups such as these because incorrect classification can bias results. The status of each non-native species listed by Shafland (1996), Shafland et al. (2008) and the USGS NAS (USGS, 2021) was considered when assigning non-native fishes to the appropriate group. Current knowledge and unpublished information gained from local experts also played a role in determining the group to which each species would belong. Ultimately, species that were classified as successfully established are non-natives that have self-sustaining, reproducing populations at the time of this study. Forty species that have successfully established populations in peninsular Florida were initially considered for the analyses. However, nine of those established species were excluded because of insufficient life history data (5 cichlid, 2 loricariid), or status as a hybrid (1 cichlid, 1 poeciliid), which left 31 successfully established non-natives for analysis (Appendix S2). Removal of these species should not bias our analyses because numerous cichlid, poeciliid and loricariid congeners were included in our analyses. Our list of failed species was composed of those considered to be either formerly reproducing where their populations have declined or collapsed, or were reported as collected in the waters of Florida with no evidence of a reproducing or stable population (Shafland et al., 2008). Species were only included in this list if they failed on their own and were not intentionally eradicated, and if there was evidence of enough propagule pressure for reproduction to be possible (e.g. no singletons were included in the analysis). We started with a list of 57 non-native species that have been collected with no evidence of reproduction, which was paired down to 33 after removing species with three or fewer records in the region, indicating low propagule pressure (Appendix S3). We do not believe this biased the results as many of the fish removed from the list of failed species were from families well represented among the 33 species included in the analyses (Cichlidae, Cyprinidae, Callichthyidae, Osphronemidae and Poeciliidae; see Appendix S3). Furthermore, CLIMATCH analyses (Crombie et al., 2008) revealed that several of the failed species not included had a low climate match with Florida (Climate 6 score, USFWS, 2020), and a moderate-high climate match was a pre-requisite for inclusion in analyses. A list of 63 species native to peninsular Florida that live in or require freshwater habitats south of the Suwannee River was also compiled using distributions found in Page and Burr (2011). Predominantly marine fishes which may spend time in brackish freshwaters in Florida were excluded from all three groups (e.g. Striped Mullet Mugil cephalus and Common Snook Centropomus undecimalis), although one anadromous species (American Shad Alosa sapidissima) and one catadromous species (American Eel Anguilla rostrata) were included because they require freshwater habitats to complete their life cycle. Two native fundulid species were removed because there was insufficient life history data available, leaving a total of 61 species that were included in the analyses (Appendix S4).

The selection of traits to include in descriptive or predictive studies of invasion is variable. Some studies, such as Olden et al. (2006), use a large number of biological traits \( n = 22 \) in an attempt to thoroughly relate species to their environment, whereas others such as Marchetti et al. (2004a) considered fewer, more widely used variables \( n = 10 \) in their models. Relevant literature was referenced to develop a comprehensive list of life history traits to consider for use in the analyses for this study (Table 1). Several traits, such as chronic lower lethal temperature, were originally considered but later eliminated due to a lack of data for many of the species. A total of 21 life history traits remained, for which information was gathered for all species in the three groups (Table 1). Many researchers include other types of variables which relate to human use, climate and invasion history. While these are useful for risk assessment, the focus of this paper is on life history traits specifically and their ability to explain non-native species establishment success. Adequate propagule pressure (3 or more collections in the state), and climate match with all or part of peninsular Florida were pre-requisites to inclusion of species in the non-native species lists for analysis.

Following the selection of traits and fish species included in these analyses, a literature review was conducted to gather traits data for all 21 variables for each species (Appendix S1 – Data sources). Multiple searches for each species using both common name and scientific name, both with and without “life history” included in the search bar, were conducted using Google Scholar and the Web of Science. Primary literature was used whenever possible, but databases, including Fishbase (Froese & Pauly, 2021), FishTraits (Frimpong & Angermeier, 2009) and grey literature, were used to fill in any data gaps. For some species, data for specific traits were not available, in which case regional biologist expertise and congener data for species with similar or overlapping geographic ranges and similar life histories were used to fill in data gaps following the methods of Olden et al. (2006). As noted above, species lacking data that could not be determined using biologist expertise or congener data were removed from the lists and not included in analyses.
2.2 Statistical analyses

To determine which traits differ most significantly between successful and failed non-native species, continuous and ordinal traits were tested independently using the Mann–Whitney rank sum test. This non-parametric test was chosen because none of the data fit a normal distribution. Categorical traits were tested using a Chi-square test. Raw data for all traits were used, except for fecundity which was log10 transformed. For each trait, data for successfully established species were compared to data for failed species and level of significance was determined. Bar charts were constructed for traits that had a significant difference \( (p < 0.05) \) between the two groups to better visualize the data and identify differences among the two groups.

The variables with significant differences between the two groups of non-natives were then compared using Spearman rank correlations to identify any significant correlations. Two pairs of variables, parental care and reproductive guild, and time to hatch and egg diameter, had a correlation of 0.6 or higher. We removed reproductive guild and time to hatch, which left five traits for inclusion in a factor analysis. Factor analysis was used because one of the five traits was categorical, and factor analysis is suitable for quantifying trait space with mixed data types. Ordination plots were created using the R packages “FactoMineR” and “factoextra” using R version 4.0.3 (R Core Team, 2020) and RStudio version 1.3.1093 (RStudio Team, 2020). A permutational MANOVA using the adonis function in the R package “vegan” tested whether group (native, non-native failed and non-native established) explains trait variations among freshwater fishes in Florida.

Overall life history strategies of all 125 fishes were determined using a subset of the traits data that were applied to the triangular life history model proposed by Winemiller and Rose (1992). The Winemiller and Rose (1992) model is a reworking of the r- and K-selected life history strategies set forth by MacArthur and Wilson (1967) and presents three endpoint strategies. The r-selected strategy was split to create the periodic and opportunistic strategies with K-selected species reclassified as equilibrium strategists (Winemiller, 1995; Winemiller & Rose, 1992). All fishes, both marine and freshwater, fall somewhere within the triangular model. Some fish may be closely associated with a specific strategy, although most will fall within the space between endpoint strategies (Winemiller & Rose, 1992). Periodic strategists can be characterized by a long lifespan, large body size, high fecundity, small eggs and high recruitment variability (Logez et al., 2016; Vila-Gispert et al., 2005; Winemiller & Rose, 1992). Opportunistic strategists typically live in highly disturbed systems and are characterized by small body size, small eggs, short lifespan and high demographic resilience (Logez et al., 2016;
Mims et al., 2010; Vila-Gispert et al., 2005; Winemiller & Rose, 1992). Equilibrium strategists are characterized by delayed maturity, low fecundity, large egg size and moderate-to-high parental care (Logez et al., 2016; Mims et al., 2010; Winemiller & Rose, 1992). The three life history axes used in the model followed the methods of Olden et al. (2006) and were (1) maturation size; (2) mean fecundity and (3) investment per progeny (calculated as the sum of egg diameter and parental care). The natural logarithm of the values for these variables were calculated for each of the 125 species and the data were added to a three-dimensional graph, with its two-dimensional parts also displayed. Each of the three groups was assigned a unique symbol and species were plotted accordingly in the graph and results were visually assessed and interpreted.

3 | RESULTS

Tests comparing successful and failed non-native species for each trait revealed a significant difference (p < 0.05) between the two groups for 7 of the 21 traits examined (Figure 1). A significant difference for body size (p < 0.05) and parental care (p < 0.001) supports our hypothesis that these two traits could be predictive of establishment success for fishes introduced to Florida. Successfully established species tend to have a larger body size, larger egg diameter, higher levels of parental care, longer time to hatch, larger swim factor and no fluvial dependence than species that have failed to establish (Figure 2).

Native, non-native failed and non-native established fish groups differed significantly in their trait diversity (PERMANOVA, R^2 = 0.148, p < 0.001). The first two dimensions of the factor analysis explained 55% of the total variation, and reproductive traits largely influenced both axes. Dimension 1 was most influenced by maximum length and egg diameter, whereas Dimension 2 was most influenced by parental care and fluvial dependence. Most of the successful non-natives were concentrated in or near the top right quadrant, which describes an association with higher levels of parental care, larger egg diameter, larger maximum length and no fluvial dependence (Figure 2). Three successfully established non-natives
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of the family Poeciliidae, Pike Killifish, Green Swordtail _Xiphophorus hellerii_ and Southern Platytai _Xiphophorus maculatus_ were most highly associated with these traits given their live-bearing reproductive strategy. Successfully established cichlid species, which have moderate-to-high parental care via nest guarding or mouth-brooding, a more moderate maximum body length and larger egg diameter also fell in or along the top-right quadrant. Other successfully established non-natives, such as the Asian Swamp Eel _Monopterus albus_ and Bullseye Snakehead _Channa marulius_, were more strongly associated with maximum length. Oriental Weather Loach _Misgurnus anguillicaudatus_ and Croaking Gourami _Trichopsis vittata_ were more separated from the rest of the successfully established non-native species because they are smaller bodied and have lower levels of parental care than other successfully established non-native fishes in Florida.

The distribution of successfully established non-native fish species within the triangular life history model supported the hypothesis that parental care and high investment in offspring are important (Figure 3). Most of these species (n = 27) were clustered within the equilibrium strategy portion of the triangular life history model and are characterized by moderate-to-low fecundity, delayed maturation and moderate-to-high investment per progeny. Four of the 31 successful species fell outside the equilibrium group, two of which are in between the equilibrium and opportunistic endpoint strategies. Those two species were Green Swordtail and Southern Platytai, live-bearing fish in the family Poeciliidae. The other two species, Weather Loach and Croaking Gourami, fell in between the periodic and opportunistic endpoint strategies. Non-native species that have failed to establish in peninsular Florida were somewhat evenly distributed among strategies, however, only 15% fell within the cluster of successful non-native equilibrium strategists and approximately 50% fell within the opportunistic strategy. Those native equilibrium strategists include Channel Catfish _Ictalurus punctatus_, White Catfish _Ameiurus catus_, Yellow Bullhead _Ameiurus natalis_, Tadpole Madtom _Noturus gyrinurus_, Largemouth Bass _Micropterus salmoides_ and Redbreast Sunfish _Lepomis auritus_.

**FIGURE 2** Ordination plots resulting from factor analysis of five trait variables for 125 fish species. The first plot shows all species with symbols and colors differentiating those that are non-native established, non-natives that failed to establish or native along with marginal density plots on the first two axes (a), and the second is an eigenvector plot of the traits where “yes” and “no” correspond to fluvial dependence, which is categorical (b).

4 | DISCUSSION

Successfully established non-native fish in Florida tend to have a longer maximum length, larger egg diameter, and higher degree of parental care compared to unsuccessful species. Nearly all successful species were equilibrium strategists which tend to be moderate to large in size but have relatively large eggs and a high degree of parental care (Winemiller & Rose, 1992). Parental care in particular seemed important to success, along with correlated reproductive traits. The biparental care exhibited by many cichlid species, which is a strong equilibrium strategy, is not found in any species native to the United States except for the single cichlid native to the country, the Rio Grande Cichlid _Herichthys cyanoguttatus_. Opportunistic and periodic strategists have proven largely unsuccessful as invaders of peninsular Florida’s freshwaters.

Body length is thought to be an important trait of successful non-native fishes in Florida as the majority of non-native fish species established in the state reach a maximum length of ≥16 cm total length (Lawson et al., 2013). Furthermore, Su et al. (2020) found that non-native established fish species have more extreme morphological
traits compared to those that have failed to establish. In the present study, established species were found to have a significantly higher swim factor than those that failed to establish. Body size of successful species was also longer than that of unsuccessful species, however, our results suggest that reproductive traits such as parental care and egg diameter may be stronger predictors of success for non-native fishes in Florida. Equilibrium strategists display a wide range of maturation size and fishes within this strategy are variable with respect to maximum length. This endpoint strategy is mostly driven by its low-to-moderate fecundity and high investment per progeny, whereas maturation size and large body size tend to be more important for periodic and opportunistic strategists (Mims et al., 2010; Winemiller & Rose, 1992). This suggests that as a predictor variable, maximum length may not be reliable for predicting successful establishment of non-natives for Florida, even with 27 of 31 successful species having maximum lengths exceeding 15 cm, because about half of unsuccessful species also exceeded this length (Figure 1). Maximum length may be a useful predictor of spread or impact, or may be more useful for predicting failure rather than success (Lawson, 2018).

The distribution of established non-native fishes across life history strategies differed considerably from the distribution of native fish across strategies. Florida's native fish fauna is dominated by opportunistic strategists (Mims et al., 2010; present study), whereas the established non-native fish fauna is dominated by equilibrium strategists. Native opportunistic species, mainly cyprinid and cyprinodontiform fishes, were characterized by small body size, low investment per progeny and early maturation. The success of this strategy for native species suggests that other factors likely impede establishment of opportunistic fishes in peninsular Florida. About 30% of Florida's native fishes, including ictalurids and centrarchids, are equilibrium strategists (Mims et al., 2010; present study). Few native fishes exhibited a true periodic life history strategy, and this was expected because most long-lived, highly fecund freshwater fish species are large-bodied riverine fishes that most of peninsular Florida's hydrological characteristics and habitats do not support (Winemiller et al., 2010; present study).
The relatively few periodic strategists that do inhabit Florida’s water bodies include the Florida Gar *Lepisosteus platyrynchus*, Longnose Gar *Lepisosteus osseus*, American Eel *Anguilla rostrata*, American Shad *Alosa sapidissima*, Gizzard Shad *Dorosoma cepedianum* and Striped Bass *Morone saxatilis*. Of these species, American Shad and Striped Bass are confined to a single river system within peninsular Florida, both species and the American Eel are diadromous fishes and Gizzard Shad is cryptogenic in peninsular Florida.

Most of the successfully established non-natives form a tight cluster in the triangular model; however, there are a few exceptions. The Oriental Weatherfish is unusual among successful non-natives in Florida because it does not exhibit any parental care. It is also a temperate species with physiological tolerances unlike any of the other non-native species examined (van Kessel et al., 2013). Specific factors related to its success are unknown, although we speculate that its typical occurrence in ditches and ephemeral marshes and ponds and its habit of burying in sediments reduces its contact with native fishes important in biotic resistance. Croaking Gourami is also different from other successful non-natives because of its small body size, tiny eggs, and lower degree of parental care (Leingpornsap et al., 2006; Schofield & Schulte, 2016). It is, however, one of the less successful species because it was known only from a small, localized population from the 1970s through 1990s and was considered extirpated by the 2000s following surveys at the known sites (Shafland et al., 2008; USGS, 2021). In 2012, Croaking Gourami was found in a complex of canals, ditches and wetlands nearby, suggesting undetected persistence of the original population (Schofield & Pecora, 2013; Schofield & Schulte, 2016). The African Jewelfish *Hemichromis letoumeuxi*, although embedded in the cluster of equilibrium strategists, is unique because of its small body size and rapid spread throughout south and central regions of Florida (Hill, 2016; Langston et al., 2010; Lopez et al., 2012). Its success may be partially due to its ability to survive the harsh conditions of its native range (Langston et al., 2010; Schofield et al., 2007). This species has been able to survive low-water conditions in the Everglades by taking refuge in solution holes and its aggressive behaviour facilitates its survival (Hill, 2016; Lopez et al., 2012; Porter-Whitaker et al., 2012; Schofield et al., 2014).

Although several traits are clearly associated with successful establishment, numerous species with these traits have failed in Florida. Several of the failed cichlids such as the Firemouth Cichlid and Banded Tilapia are ecologically similar and closely related to successful species, yet they have not established stable populations (Shafland et al., 2008). Some cichlids seemed on their way to successful establishment when unexplained population declines occurred. For example, the Eartheater, a previously expanding species yet which are frequently associated with warm thermal refuges in the region (e.g. Nico et al., 2012). The panhandle has a more diverse native freshwater fish fauna than the remainder of the state (Gilbert, 1987) and has a different history of invasion that warrants its own analysis. The Florida panhandle has considerably different non-native fishes such as the cold-tolerant Common Carp and native transplants from nearby river basins such as Rough Shinier *Notropis baileyi* (USGS, 2021).

Biotic resistance further influences the establishment success of non-native species (Beaury et al., 2020; Jeschke, 2014). After a fish is introduced, it must pass through a variety of barriers or filters to become established and will be exposed to numerous predators and competitors (Blackburn et al., 2011). Peninsular Florida remained under water until its mid-Oligocene emergence approximately 29 million years ago, and therefore its native species are largely opportunistic colonizers, a subset of species from Florida’s more
faunally diverse bordering states, Alabama and Georgia (Gilbert, 1987; Mims et al., 2010; Nico, 2005). A depauperate fauna might be predicted to offer less resistance to invasion than would a more diverse fauna (Elton, 1958; Lodge, 1993). Larger-bodied fishes seemingly face low biotic resistance in Florida; nevertheless, smaller-bodied fishes may be limited by native species such as the aggressive Eastern Mosquitofish Gambusia holbrooki (Schofield et al., 2021; Thompson et al., 2012; Tuckett, Deacon, et al., 2021), and large predatory fishes such as Florida Bass Micropterus floridanus (Hill, 2016; Hill et al., 2011; Hill & Tuckett, 2018) and Bowfin Amia calva. The equilibrium strategy which is exhibited by all but two species of successfully established non-native fishes in Florida, increases juvenile survivorship if the habitat is stable (Winemiller & Rose, 1992). Parental care, especially the biparental care exhibited by most of the established cichlids in Florida, reduces mortality of eggs and juveniles by native predators which are common in Florida waters (Gross & Sargent, 1985). Many of the non-native species that have failed to establish in Florida are small-bodied ornamental fishes, cultured to be brightly coloured, which may further reduce their survival by making them more vulnerable to predation (Hill et al., 2011; Tuckett et al., 2017; Tuckett, Ressell, et al., 2021).

Other factors can provide additional insights into the success and failure of non-natives. The focus of the present study was on life history traits specifically, so variables related to human use, climate and invasion history were not included, although they are known to play a role in establishment success across a variety of taxa and regions (Hayes & Barry, 2008; Howeth et al., 2016). Many species have had numerous opportunities to establish in Florida waters due to their popularity and long occurrence in the aquarium trade and aquaculture, known factors increasing propagule pressure (Padilla & Williams, 2004). Florida’s warm climate, including tropical regions in south Florida (Beck et al., 2018), provides favourable conditions somewhere in the peninsula for most temperate and tropical fishes. Another factor that limited which variables and species were included was data availability, particularly for introduced species that have failed to establish (Garcia-Berthou, 2007; Marchetti et al., 2004a). Despite this limitation, the inclusion of additional species that have been collected in peninsular Florida would not likely change the pattern observed. The few established species that were not included would fall within the equilibrium strategy and failed species with too few collection records for inclusion would reinforce the diverse array of strategies observed for that group. More research investigating the basic life history traits of species, particularly those in trade, will help with the precision of these types of analyses in the future.

The results of this study largely contrast with other analyses, both global and regional. A global analysis of fish invasions revealed that small body size, omnivory and rapid reproduction were predictive of successful establishment (Ruesink, 2005). However, the predictive value of those traits was also much lower than in the present study or in other regional studies (Moyle & Marchetti, 2006; Ruesink, 2005). Another global study found that parental investment and fecundity were significantly associated with establishment success of non-native fishes, however, they did not include other traits except for body mass and brain size in their analysis (Drake, 2007). Interestingly, reproductive traits did not appear to be as important for establishment in regional studies from temperate regions. The variety of traits found to be important for fish establishment in the previous regional studies differ considerably (Table 2) from the Colorado River Basin (Olden et al., 2006), Mediterranean streams (Vila-Gispert et al., 2005), Iberian Peninsula (Ribeiro et al., 2008), Great Lakes (Kolar & Lodge, 2002) and California (Marchetti et al., 2004a, 2004b). This suggests that trait importance may vary by region and invasion stage (Garcia-Berthou, 2007), possibly making

| Publication                  | Region                      | Number of species studied | Major predictors                                                                                                                                                                                                 |
|------------------------------|-----------------------------|---------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Kolar and Lodge (2002)       | Great Lakes (USA)           | 45                        | Relative growth, diet breadth, temperature tolerance, salinity tolerance, history of invasion                                                                                                                          |
| Marchetti et al. (2004a)     | California (USA)            | 87                        | Maximum size, size of native range, physiological tolerance, adult trophic status, propagule pressure, distance to native source, parental care, prior invasion success                                      |
| Marchetti et al. (2004b)     | California (USA)            | 87                        | Maximum life span, physiological tolerance, smaller size of native range, propagule pressure, parental care, prior invasion success                                                                                   |
| Vila-Gispert et al. (2005)   | Catalonia                   | 30                        | Large body size, long longevity, late maturity, high fecundity, few spawns per year, short reproductive span                                                                                                           |
| Olden et al. (2006)          | Colorado River (USA)        | 47                        | No fluvial dependency, slow flow preference, variable spawning substrate requirements, early maturation, small egg size, short time to hatch, larger swim factor                                                                 |
| Ribeiro et al. (2008)        | Iberian Peninsula           | 35                        | Prior invasion success, small adult size, small distance from native range                                                                                                                                       |
| Present Study                | Peninsular Florida (USA)    | 64                        | Larger body size, larger egg diameter, higher levels of parental care, longer time to hatch, larger swim factor, no fluvial dependency and greater salinity tolerance                                                 |
regional analyses more useful for predicting success (Hayes & Barry, 2008), particularly in countries with diverse climates and habitats.

The differences between our results for Florida and those from other regions of the United States (Howeth et al., 2016; Kolar & Lodge, 2002; Marchetti et al., 2004a; Ruesink et al., 2006) provide evidence that taxon-specific risk assessments at smaller (regional) spatial scales may be the most appropriate for effective risk screening, particularly for countries with diverse climates and habitats (Garcia-Berthou, 2007; Marchetti et al., 2004a; Ruesink, 2005). Most of the United States is temperate or cold in climate and the non-native fish fauna in most states is almost entirely comprised of transplanted species from other parts of the country or temperate invaders from Eurasia (Hill, 2002; Nico & Fuller, 1999). In contrast, Florida’s warm climate, geography and history have led to the establishment of many tropical species that for the most part cannot establish elsewhere in the conterminous United States (Hill, 2002; Nico & Fuller, 1999). This makes Florida more similar to other warm regions such as parts of Mexico and Central America, South America, southern Africa, south and Southeast Asia and Australia than to the more well-studied temperate and cold regions of the United States such as the Laurentian Great Lakes, the Colorado River and California. Future research will involve creating models using biological traits to predict success of non-native fish in Florida at different stages of the invasion process: reproduction, establishment, spread and impact. More studies like this can inform the development of risk screening tools for regions that have elevated non-native species concerns. It will further contribute to our rather limited knowledge of the dynamics of species invasions in warmer climate regions.

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CONFLICT OF INTEREST
The authors do not declare any conflict of interest.

PEER REVIEW
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DATA AVAILABILITY STATEMENT
The life history trait data for all species included in this study are available on Dryad at the following link: https://doi.org/10.5061/dryad.3n5tb2rj. The sources from which data were gathered are compiled in Appendix S1.

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**BIOSKETCH**

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**SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of the article at the publisher’s website.

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