Predicting successful reproduction and establishment of non-native freshwater fish in peninsular Florida using life history traits

Authors: Lawson, Katelyn M., and Hill, Jeffrey E.

Source: Journal of Vertebrate Biology, 70(4)

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/jvb.21041

Journal of Vertebrate Biology

Open Access

J. Vertebr. Biol. 2021, 70(4): 21041

DOI: 10.25225/jvb.21041

SPECIAL ISSUE: INVASIVE FISHES
RESEARCH PAPER

Predicting successful reproduction and establishment of non-native freshwater fish in peninsular Florida using life history traits

Katelyn M. LAWSON[1,2*] and Jeffrey E. HILL[1]

[1] *School of Forest, Fisheries and Geomatics Sciences, Program in Fisheries and Aquatic Sciences, Tropical Aquaculture Laboratory, University of Florida, Ruskin, Florida, USA; e-mail: jeffhill@ufl.edu*

[2] *Department of Biological Sciences, 101 Rouse Life Sciences, Auburn University, Auburn, Alabama, USA; e-mail: dowlika@auburn.edu*

Received 1 June 2020; Accepted 10 August 2021; Published online 30 September 2021

Abstract. Identification of factors that facilitate successful completion of invasion process stages by non-native species is a major priority among invasion biologists. Stage-based analyses of non-native fish species traits have been conducted for several regions, but not for a subtropical non-native species hotspot like peninsular Florida. Typically, establishment is the first stage of analysis but Florida is home to many non-native fish species that have successfully reproduced, yet failed to establish. Therefore, we used life history traits and three model types (categorical and regression trees, logistic regression, and discriminant analysis) to predict successful reproduction and establishment by non-native fishes in peninsular Florida. Statistical models for predicting both successful reproduction and establishment suggested parental care was the most important variable, but other traits included in the best models differ between the two stages. The high level of parental care in successful non-native fishes of Florida is unique among non-native freshwater fish faunas across the United States. Other studies also found that suites of traits used to predict various stages of the invasion process differ, suggesting that stage-based analyses provide a good foundation for better understanding invasion processes. Our results may be applied to stage-based risk screening tools for non-native fishes in Florida.

Key words: life history, invasive species, quantitative risk assessment

Introduction

The identification of factors contributing to successful establishment and invasion by non-native species is an important objective for invasion biologists (Leung et al. 2012). In support of this objective, numerous studies examining the life history traits of introduced non-native species have been conducted for a variety of taxonomic groups. The results of these studies, even within one taxonomic group such as fishes, are highly variable and dependent on numerous factors such as regional characteristics, phylogenetic constraints, and stage of the invasion process examined (Garcia-Berthou 2007). The most heavily investigated stage of the invasion process is establishment (Garcia-Berthou 2007, Hayes & Barry 2008), however there are several steps that non-native organisms must complete prior to successfully establishing a stable population (Kolar & Lodge 2001, 2002, Hill 2008).

* *Corresponding Author*

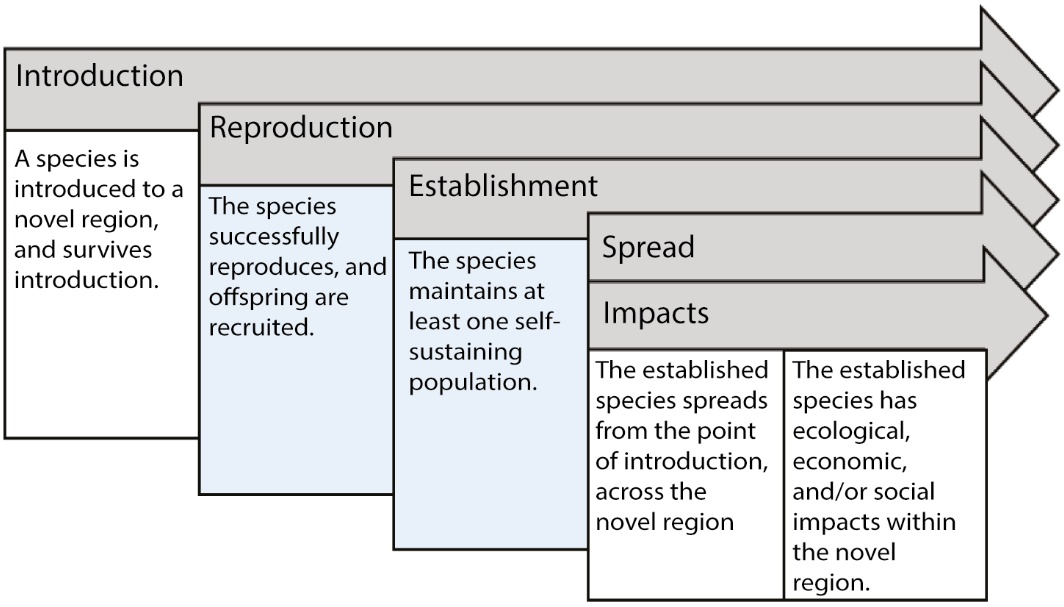

Fig. 1. The five stages of the invasion process described in the present study. The two stages examined in the present study, reproduction and establishment, are shaded.

Many different stages and definitions of the invasion process have been published (Kolar & Lodge 2001, Lockwood et al. 2005, Blackburn et al. 2011, Leung et al. 2012) therefore explicitly defining terminology is important (Richardson et al. 2000, Catford et al. 2009). One common aspect of invasion process models is that they are based on conditional probabilities; a species must successfully complete one stage before it can progress to the next (Hill 2008, Leung et al. 2012). We developed a linear, stage-based invasion model based on the literature to inform an investigation into the importance of life history traits in invasion science (Fig. 1). The stages that are included in this model are 1) transport/introduction into novel environment and survival, 2) successful reproduction and recruitment, 3) establishment of a self-sustaining population, 4) spatial spread of the population beyond the initial point of establishment, and 5) ecological and/or socio-economic impacts to the region where it is established (Fig. 1).

Survival following initial introduction is difficult to document because existing data underestimate failed introductions due to insufficient spatial and temporal coverage of sampling, low detectability of some species, and under-reporting of captures (Kolar & Lodge 2001, Garcia-Berthou 2007, Lawson et al. 2017). In Florida, there are likely hundreds of non-native fish species that have been introduced and gone undetected (Tuckett et al. 2016). Still, many non-native fish species have been collected multiple times in Florida yet failed to reproduce and recruit (United States Geological Survey 2021). The availability of this information makes it feasible to model successful reproduction among a select group of non-native fishes within the study region of peninsular Florida. Further, there are many non-native fish species in Florida for which reproduction has been documented, but not establishment of self-sustaining populations. An introduced species' ability to successfully reproduce is dependent on many factors such as high enough propagule pressure for availability of mates (Lockwood et al. 2005, Colautti et al. 2006, Simberloff et al. 2009) and cues for reproduction. Other requirements include suitable habitat for egg deposition and survival (Ortega et al. 2007), availability of food, and protection from predators to ensure juvenile survivorship and recruitment to the population (Baltz & Moyle 1993, Moyle & Light 1996).

When an introduced species is able to recruit offspring, the population can then grow in size which leads to establishment of a self-sustaining population. In contrast, population declines can also occur if reproduction requirements are not consistently met; this has been observed for several non-native fish species in Florida (Shafland et al. 2008, Hill 2016). In the literature, the reproduction stage is often considered to be a barrier or filter to establishment that must be overcome (Copp et al. 2005, Colautti et al. 2006, Blackburn et al. 2011) rather than a distinct stage of the invasion process.

There are likely many reasons for this such as lower propagule pressure, harsher receiving environment, climate mismatch and other filters that prohibit the detection of introduced species that fail to reproduce and reproducing species that fail to establish. Consequently, this stage has not received much attention in previous studies predicting invasion success. Florida's warm climate, diverse water bodies, large human population, and ornamental aquaculture industry have facilitated the introduction of many species that are able to survive and reproduce yet fail to establish. This unique combination of factors allows us to study the reproduction stage of the invasion process, a novel first step for examining non-native fish success in Florida.

A quantitative approach was taken to identify traits associated with successful reproduction and those associated with establishment success given that reproduction occurs in non-native freshwater fishes in peninsular Florida (USA). Florida, with its large human population, strong introduction pathways, and favourable climate (Hill 2002) has more reported sightings of foreign non-native freshwater fish species than any other US state (Shafland et al. 2008). Since this number is continuing to increase (Shafland et al. 2008), developing methods to profile non-native fishes that are likely to become invasive in Florida is critical to improving management. A variety of quantitative techniques have been used to examine successful completion of invasion process stages across a range of taxa (Hayes & Barry 2008). The most common are classification and regression trees, discriminant analysis (DA), and logistic or multiple linear regression (Garcia-Berthou 2007, Hayes & Barry 2008), particularly for fishes (Kolar & Lodge 2002, Marchetti et al. 2004a, b, Ruesink et al. 2005, Ribeiro et al. 2008, Allen et al. 2013, Howeth et al. 2016). These statistical techniques are all suitable for our dataset, because classification trees are well-suited for the analysis of complex ecological datasets (Howeth et al. 2016), and logistic regression is useful for datasets where the number of subjects is small with respect to the number of variables (Ribeiro et al. 2008). All have been used in similar studies for other regions and most studies have used two or more techniques, however no consensus has been reached on the best approaches. Therefore, we used classification trees, DA, and logistic regression to identify traits that likely facilitate successful reproduction and establishment of non-native freshwater fishes in Florida and compared the results. Our objectives for this study were to 1) determine which traits were most important in predicting whether introduced species would successfully reproduce, 2) identify traits that may facilitate reproducing non-native fish species to establish self-sustaining populations, and 3) compare the effectiveness of logistic regression, classification trees, and DA for predicting each of the two stages of the invasion process (Fig. 1).

Material and Methods

Data collection

A list of non-native taxa (hereafter, "species") that have been detected in peninsular Florida was first compiled and any species with fewer than three collection records was removed to ensure that species included have been introduced several times. Sources used to create this list and determine status were the US geological survey's nonindigenous aquatic species database (United States Geological Survey 2021), and Shafland et al. (2008). Species for which there was little published information were also removed. The list of remaining species was then divided into those that have reproduced successfully at any point in time somewhere in peninsular Florida, and those that have never been observed reproducing in the environment for inclusion in reproduction models. Species that have successfully reproduced were then split into two groups: those that have successfully established and those that have failed to establish populations for inclusion in establishment models. A literature review was conducted to collect data for 21 life history variables for potential use as predictors in the analyses (Table 1). 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 congener data were used following the methods of Olden et al. (2006). Categorical variables were numerically coded, and all continuous variables were left in their original state, except for fecundity which was log10 transformed.

Table 1. Traits that were used in the analyses for the present study based on six references with descriptions for measurement of each trait. Traits with an asterisk (*) were included in the analyses.

Trait (abbreviation)	References	Notes
*Maximum body length (ML)	2, 3, 4, 5	measured in cm
*Shape factor (ShpF)	5	ratio of TL to max body depth
*Swim factor (SwmF)	5	ratio of min depth caudal peduncle to max depth caudal fin
*Substrate preference (Spref)	5	rubble (cobble & gravel, 3), sand (2), silt/mud (1), or general (0)
*Fluvial dependence (FDep)	5	yes (1) or no (0); reliant on flowing water to complete life cycle
*Water velocity preference (WVel)	5	slow (0), slow-moderate (1), moderate (2), moderate-fast (3), or fast (4)
*Vertical position (Vpos)	5	benthic (0) or non-benthic (1) based on physiology and behaviour
*Trophic guild (TrG)	2, 3, 4, 5, 6	adult stage: detritivore (0), herbivore (1), invertivore (2), omnivore (3), or piscivore (4)
*Diet breadth (DietBr)	1, 5	range 1-7 (algae, macrophytes, detritus, zooplankton, aquatic insects, macroinverts, fish)
Length at maturation (Lmat)	5	female: measured in cm
Fecundity (Fecund)	2, 3, 5, 6	average # eggs or offspring per breeding season; log10 scale
*Egg size (EggDi)	4, 5	mean diameter of mature oocytes in mm
*Spawning temperature (SpTemp)	5	temperature at which spawning is initiated (Celsius)
*Parental care (PC)	2, 4, 5, 6	energetic contribution; calculated following Winemiller 1989
Reproductive guild (RepGuild)	3, 5	nonguarders (0), guarders (1), or bearers (2)
*Spawning substrate (SpSub)	5	mineral (3), vegetation (2), pelagic (1), or various (0)
Time to hatch (TTHatch)	5	mean time to egg hatch post-spawn (hours)
*Salinity tolerance (SalTol)	1, 3	none (0-4 ppt; 0), low(5-10 ppt; 1), moderate(10-20 ppt; 2), high(> 20 ppt; 3)
*Length spawning season (SpSeas)	3, 4	# of months
Migratory (Mig)	-	yes (1), no (0)
*Air breathing (AirBr)	-	yes (1), no (0)

1) Kolar & Lodge (2002), 2) Marchetti et al. (2004a), 3) Alcaraz et al. (2005), 4) Vila-Gispert et al. (2005), 5) Olden et al. (2006), 6) Ribeiro et al. (2008).

Statistical analyses

Mann-Whitney rank sum tests were used to determine significant trait differences between species that have succeeded or failed to pass through the reproduction and establishment invasion filters (Lester 2005). Life history variables were compared using Spearman rank correlations to detect significant correlations among variables; data for both groups of fishes were used in this analysis. Variables with a correlation of 0.60 or greater were identified and one variable was retained as a surrogate for both correlated variables to avoid unnecessary complexity (Marchetti et al. 2004a). When two variables were highly correlated, the trait with the highest significance according to the Mann-Whitney rank sum test for reproduction was retained. Variables that were removed from the dataset include length at maturation, fecundity, migratory, time to hatch, and reproductive guild, reducing the number of variables considered in

Table 2. Observed status *vs.* predicted status for all three reproduction models: Log Reg = logistic regression model chosen from bootstrap analysis, Class Tree = classification tree, and DA = discriminant analysis. The values are: 1 = successful reproduction, and 0 = fail to reproduce.

Taxa	Common name	Observed	Log Reg	Class Tree	DFA
Amphilophus citrinellus	Midas cichlid	1	1	1	1
Anabas testudineus	Climbing perch	1	1	1	1
Ancistrus sp.	Bristlenose catfish	1	1	1	1
Archocentrus nigrofasciatus	Convict cichlid	1	1	1	1
Astatotilapia callipterus	Eastern happy	1	1	1	1
Astronotus ocellatus	Oscar	1	1	1	1
Belonesox belizanus	Pike killifish	1	1	1	1
Betta splendens	Betta	1	1	1	0
Channa marulius	Bullseye snakehead	1	1	1	1
Chitala ornata	Clown knifefish	1	1	1	1
Cichla ocellaris	Butterfly peacock bass	1	1	1	1
Cichlasoma bimaculatum	Black acara	1	1	1	1
Cichlasoma salvini	Yellowbelly cichlid	1	1	1	1
Cichlasoma trimaculatum	Threespot cichlid	1	1	1	1
Clarias batrachus	Walking catfish	1	1	1	1
Ctenopoma nigropannosum	Twospot climbing perch	1	1	1	0
Geophagus sp.	Eartheater	1	1	1	1
Hemichromis letourneuxi	African jewel cichlid	1	1	1	1
Herichthys cyanoguttatus	Rio grande cichlid	1	1	1	1
Heros severus	Banded cichlid	1	1	1	1
Hoplias malabaricus	Trahira	1	1	1	0
Hoplosternum littorale	Brown hoplo	1	1	1	1
Hypostomus sp.	Suckermouth catfish	1	1	1	1
Macrognathus siamensis	Spotfin spiny eel	1	1	1	1
Mayaheros urophthalmus	Mayan cichlid	1	1	1	1
Metynnis hypsauchen	Silver dollar	1	1	0	0
Misgurnus anguillicaudatus	Weather loach	1	1	1	0
Monopterus albus	Asian swamp eel	1	1	1	1
Oreochromis aureus	Blue tilapia	1	1	1	1
Oreochromis mossambicus	Mozambique tilapia	1	1	1	1
Oreochromis niloticus	Nile tilapia	1	1	1	1
Parachromis managuensis	Jaguar guapote	1	1	1	1
Poecilia reticulata	Guppy	1	1	1	1
Pterygoplichthys spp.	Armored sailfin catfish	1	1	1	1
Rocio octofasciatum	Jack dempsey	1	1	1	1
Sarotherodon melanotheron	Blackchin tilapia	1	1	1	1
Thorichthys meeki	Firemouth cichlid	1	1	1	1
Tilapia mariae	Spotted tilapia	1	1	1	1
Tilapia zillii	Redbelly tilapia	1	1	1	1
Trichopsis vittata	Croaking gourami	1	1	1	1
Xiphophorus hellerii	Green swordtail	1	1	1	1
Xiphophorus maculatus	Southern platyfish	1	1	1	1

Table 2. continued.

Xiphophorus variatus	Variable platyfish	1	1	1	1
Andinoacara pulcher	Blue acara	0	0	1	1
Aphyocharax anisitsi	Bloodfin tetra	0	0	1	0
Carassius auratus	Goldfish	0	0	0	0
Cichla temensis	Speckled pavon	0	0	1	1
Colossoma macropomum	Tambaqui	0	0	0	0
Corydoras aeneus	Bronze cory	0	0	0	0
Cyprinus carpio	Common carp	0	0	0	0
Danio rerio	Zebra danio	0	0	0	0
Devario malabaricus	Malabar danio	0	0	0	0
Gymnocorymbus ternetzi	Black tetra	0	0	0	0
Helostoma temminckii	Kissing gourami	0	0	0	0
Hyphessobrycon eques	Serpae tetra	0	0	0	0
Hypophthalmichthys molitrix	Silver carp	0	0	0	0
Hypophthalmichthys nobilis	Bighead carp	0	0	0	0
Moenkhausia sanctaefilomenae	Red eye tetra	0	0	0	0
Piaractus brachypomus	Red-bellied pacu	0	0	0	0
Pimephales promelas	Fathead minnow	0	0	0	0
Polypterus delhezi	Barred bichir	0	0	0	0
Puntigrus tetrazona	Tiger barb	0	0	1	0
Tilapia sparrmani	Banded tilapia	0	0	1	1
Trichogaster labiosa	Thick-lipped gourami	0	0	0	0
Trichogaster lalius	Dwarf gourami	0	0	0	0
Trichopodus leerii	Pearl gourami	0	0	0	0
Trichopodus trichopterus	Blue gourami	0	0	1	0

the models to 16. These non-parametric tests were used because the traits' data were not normally distributed.

The remaining variables were then used to develop logistic regression models to predict successful reproduction, and to predict successful establishment of non-native fishes that have reproduced in Florida. All categorical variables were characterized as factors prior to running models. A full model with all 16 remaining variables was produced for each stage, and a backward selection procedure was used to reduce the models. A bootstrap analysis was then applied to the full models with 50 model iterations, to identify the best model for each stage and to assess predictor importance. The best model was then applied to the dataset to identify any misclassified species. In order to better assess model classification accuracy, a leave-one out cross-validation procedure was applied to each model. These analyses were completed using the R packages "stats", "MASS", "bootstepAIC", and "boot" in R version 4.0.3 (R Core Team 2020) and RStudio 1.3.1093 (RStudio Team 2020).

A second method, classification tree analysis was used to predict successful reproduction, and successful establishment. Classification trees are models developed through partitioning independent variables to predict a categorical outcome. Classification trees were used instead of regression trees because the response variable was binary (success = 1, failure = 0) rather than continuous. Due to a small sample size, we used the ten-fold cross-validation procedure to choose the best classification trees. We followed the methods of Howeth et al. (2016) and selected the smallest tree within one standard error of the misclassification rate. The R package "rpart" was used to complete these analyses in R version 4.0.3 (R Core Team 2020) and RStudio 1.3.1093 (RStudio Team 2020).

Table 3. Observed status *vs.* predicted status for all three establishment models: Log Reg = logistic regression model chosen from bootstrap analysis, Class Tree = classification tree, and DA = discriminant analysis. The values are: 1 = successful establishment, and 0 = fail to establish.

Taxa	Common name	Observed	Log Reg	Class Tree	DFA
Amphilophus citrinellus	Midas cichlid	1	1	1	1
Astatotilapia callipterus	Eastern happy	1	1	1	0
Astronotus ocellatus	Oscar	1	1	1	1
Belonesox belizanus	Pike killifish	1	1	1	1
Channa marulius	Bullseye snakehead	1	1	1	1
Chitala ornata	Clown knifefish	1	1	1	0
Cichla ocellaris	Butterfly peacock bass	1	1	1	1
Cichlasoma bimaculatum	Black acara	1	1	1	1
Cichlasoma salvini	Yellowbelly cichlid	1	1	1	1
Clarias batrachus	Walking catfish	1	1	1	1
Hemichromis letourneauxi	African jewel cichlid	1	1	1	1
Herichthys cyanoguttatus	Rio grande cichlid	1	1	1	1
Heros severus	Banded cichlid	1	1	1	1
Hoplosternum littorale	Brown hoplo	1	1	1	1
Hypostomus sp.	Suckermouth catfish	1	1	1	1
Macrognathus siamensis	Spotfin spiny eel	1	1	1	1
Mayaheros urophthalmus	Mayan cichlid	1	1	1	1
Misgurnus anguillicaudatus	Weather loach	1	1	0	0
Monopterus albus	Asian swamp eel	1	1	1	1
Oreochromis aureus	Blue tilapia	1	1	1	1
Oreochromis mossambicus	Mozambique tilapia	1	1	1	1
Oreochromis niloticus	Nile tilapia	1	1	1	1
Parachromis managuensis	Jaguar guapote	1	1	1	1
Pterygoplichthys disjunctivus	Vermiculated sailfin catfish	1	1	1	1
Pterygoplichthys multiradiatus	Orinoco sailfin catfish	1	1	1	1
Rocio octofasciatum	Jack dempsey	1	1	1	1
Sarotherodon melanotheron	Blackchin tilapia	1	1	1	1
Tilapia mariae	Spotted tilapia	1	1	1	1
Trichopsis vittata	Croaking gourami	1	1	0	0
Xiphophorus hellerii	Green swordtail	1	1	1	1
Xiphophorus maculatus	Southern platyfish	1	1	1	1
Anabas testudineus	Climbing perch	0	0	0	0
Ancistrus sp.	Bristlenose catfish	0	0	0	0
Betta splendens	Betta	0	0	0	1
Ctenopoma nigropannosum	Twospot climbing perch	0	0	0	0
Geophagus sp.	Eartheater	0	0	1	0
Hoplias malabaricus	Trahira	0	0	0	0
Metynnis sp.	Silver dollar	0	0	0	0
Poecilia reticulata	Guppy	0	0	0	1
Thorichthys meeki	Firemouth cichlid	0	0	1	1

Canonical discriminant analysis, a multivariate method that determines the relationship between a categorical variable and independent variables of mixed data types, was also used. Canonical scores and structure coefficients for the discriminant function were plotted. These analyses were completed using the R package "candisc" in RStudio R version 4.0.3 (R Core Team 2020) and RStudio 1.3.1093 (RStudio Team 2020). For each of the two stages predicted, the best logistic regression model identified in the bootstrap procedure was used to classify each species from the original dataset, and the classification results were compared with the results from the classification tree and discriminant function.

Results

Of the 67 non-native fish species selected, 24 species have never been observed reproducing in peninsular Florida (Table 2). Of the 43 species that have successfully reproduced, three were unable to establish potentially due to human intervention; however, it is unknown whether they would have established had they not been eradicated. Those three species, convict cichlid *Archocentrus nigrofasciatus* Gunther, 1867 (Hill & Cichra 2005), three spot cichlid *Cichlasoma trimaculatum* Gunther, 1867 (Courtenay & Stauffer 1990), and redbelly tilapia *Tilapia zillii* Gervais, 1848 (Hogg 1976, Courtenay et al. 1984, 1986, Taylor et al. 1986) were not included in the dataset used to create models predicting successful establishment. The variable platyfish *Xiphophorus variatus* Meek, 1904 was also removed due to fluctuating populations and unknown status in many areas where it has previously been observed (United States Geological Survey 2021). Although four species of *Pterygoplichthys* were combined in the analyses for reproduction (*Pterygoplichthys* sp.), the two species most commonly found in Florida, the vermiculated sailfin catfish *Pterygoplichthys disjunctivus* Weber, 1991 and the Orinoco sailfin catfish *Pterygoplichthys multiradiatus* Hancock, 1828 were included in the analyses for successful establishment resulting in 40 species for analysis. Of those 40 species, 31 successfully established and nine failed to establish (Table 3).

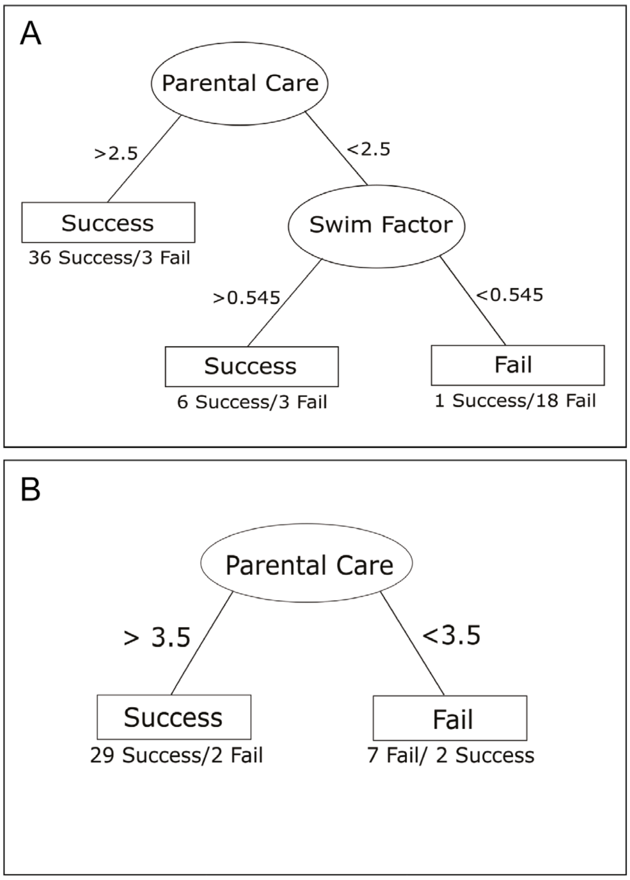

Fig. 2. Classification tree predicting successful reproduction and establishment of non-native fish in peninsular Florida. A) Successful reproduction of non-native fish. B) Successful establishment of non-native fish that have reproduced in peninsular Florida. These classification trees could be used as a rapid screen or hazard identification of non-native fishes with potential for introduction in Florida.

Reproduction

The statistical models supported parental care as the most important variable, with larger egg diameter strongly supported in two of the three methods. The final model identified in the logistic regression bootstrap analysis included the following predictors: maximum body length, swim factor, substrate preference, fluvial dependence, trophic guild, diet breadth, egg diameter, spawning temperature, parental care, salinity tolerance, and spawning season. The predictors selected most frequently for models in the bootstrap analysis, indicating a higher level of importance, include egg diameter and parental care (Table 4). As the model was developed using all the data, classification was completed with 100% accuracy, however leave-one-out cross-validation resulted in a 78% classification accuracy.

The classification tree that was selected (Fig. 2) used parental care and swim factor to classify successful and failed species with 90% accuracy (87% upon ten-fold cross-validation). The resultant tree shows that species likely to reproduce successfully have parental care greater than 2.5 and those likely to fail have parental care less than 2.5 and

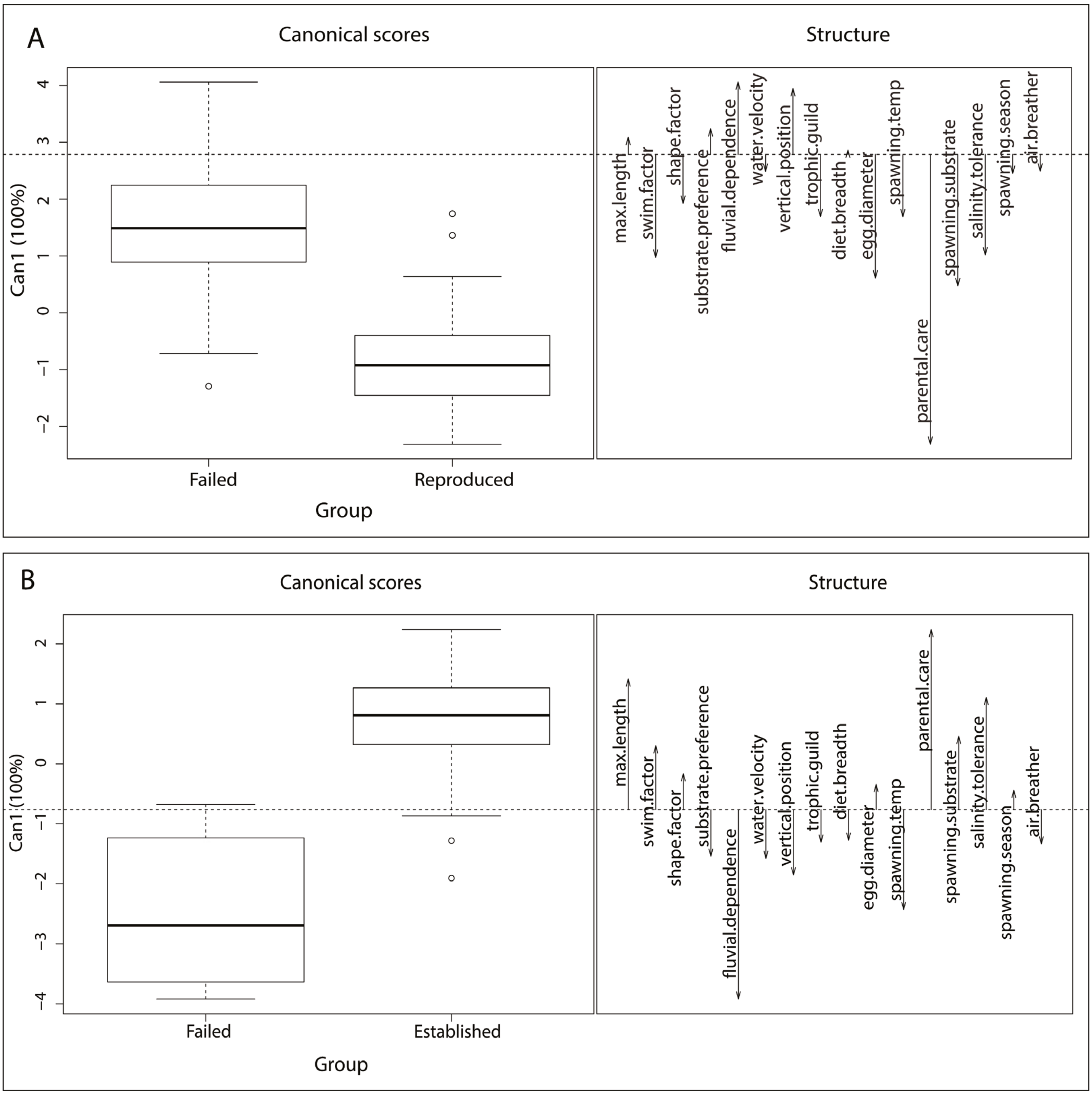

Fig. 3. Canonical discriminant analysis results for predicting successful reproduction among fishes introduced into peninsular Florida (A) and successful establishment by fishes that reproduced (B). The boxplots summarize canonical scores by displaying the median, first and third quartiles, minimum, maximum and outliers for each group. Variable contribution to the models is displayed as vectors with longer arrows indicating greater contribution.

a swim factor less than 0.545 (relative cost = 0.29, AUROC = 0.91). The discriminant function that best predicted successful reproduction indicates that high parental care, larger egg diameter, and spawning substrate are correlated with successful reproduction (Fig. 3). The misclassification rate for the model was 0.134 (0.223 in jackknife validation) and the discriminant function classified species with 87% accuracy (78% in jackknife validation). Table 2 contains the prediction results for all species by model. Among the models predicting successful reproduction, the classification tree model performed the best, and misidentified only one species with successful reproduction, the silver dollar *Metynnis* sp., as failed. Of the species that failed to reproduce, the classification tree predicted six would successfully reproduce, which was less than the nine misclassifications by canonical discriminant analysis.

Establishment

For establishment, given that reproduction occurs, parental care was a consistent variable across models. The models also suggested that reproducing species that established were not fluvial dependent and were relatively benthic

Table 4. The percentage of logistic regression models each predictor variable was included in during bootstrap analysis for each of the invasion stages.

Reproduction		Establishment	
Predictor	% Selected	Predictor	% Selected
egg diameter	92	parental care	67
parental care	82	egg diameter	64
spawning temperature	68	maximum length	53
spawning season	62	swim factor	51
air breather	58	fluvial dependence	47
diet breadth	56	shape factor	44
maximum length	56	spawning season	42
swim factor	56	diet breadth	38
shape factor	54	spawning temperature	29
vertical position	52	vertical position	29
substrate preference	42	air breather	24
Fluvial dependence	38	spawning substrate	16
water velocity	38	salinity tolerance	11
salinity tolerance	34	water velocity	7
spawning substrate	26	substrate preference	2
trophic guild	2	trophic guild	0

in vertical position in the water column. The final model identified in the logistic regression bootstrap analysis included the following predictors: swim factor, fluvial dependence, diet breadth, egg diameter, care, salinity tolerance, and air breathing. The predictors selected most frequently for models in the bootstrap analysis, indicating a higher level of importance, also include egg diameter and parental care (Table 4). As the model was developed using all the data, classification was completed with 100% accuracy, however leave-one-out cross-validation resulted in a 80% classification accuracy.

The classification tree that was selected (Fig. 2) used only parental care to classify successful and failed species with 90% accuracy (79% upon ten-fold cross-validation). Species with parental care greater than 3.5 were more likely to successfully establish than those with parental care lower than 3.5 (relative cost = 0.44, AUROC = 0.86). The discriminant function that best predicted successful establishment among species that have reproduced indicates species that have established have high levels of parental care, no fluvial dependence, larger maximum length, and greater salinity tolerance (Fig. 3). The misclassification rate for the model was 0.125 (0.175 in jackknife validation) and the discriminant function classified species with 88% accuracy (83% in jackknife validation). For predicting successful establishment, both the classification tree and discriminant analysis misclassified the croaking gourami *Trichopsis vittata* Cuvier, 1831 as failed. Although it has established a self-sustaining population, its range in Florida is extremely small when compared to most other established species (Schofield & Schulte 2016, United States Geological Survey 2021). The classification tree only misclassified the established oriental weatherfish *Misgurnus anguillicaudatus* Cantor, 1842 as failed. Overall, we found that all three modelling techniques performed similarly (87-78% after cross-validation).

Discussion

Parental care is the most important variable for predicting both reproduction and establishment, and is the only trait included in every model reported in the present study. Other variables, particularly reproductive traits, were important predictors of reproduction and establishment but to a lesser degree. All models developed in the present study were comparable with similar predictions and accuracies for each stage. The models performed well, with percent accuracies ranging from 78-87% for predicting reproduction, and 79-83% for predicting establishment. These accuracies are consistent with similar analyses for other regions (e.g. Kolar & Lodge 2002).

Table 5. Summary of non-native fishes and corresponding parental care strategies by family for the present study and three previous studies in different parts of the United States. The number of species represents the number of species in each family present in the study area. Parental care ranges indicated the strategies employed by the species in that family. Parental care values range from 0 to 6, with higher numbers equating to greater levels of parental care (Olden et al. 2006). References are as follows: (1) Olden et al. (2006), (2) Marchetti et al. (2004b), and (3) Kolar & Lodge (2002).

	Present Study (Florida)		the River Colorado (1)		California (2)		Great Lakes (3)	
Family	# species	P-care range	# species	P-care range	# species	P-care range	# species	P-care range
Petromyzontidae							1	3
Lepisosteidae							1	1
Notopteridae	1	4						
Clupeidae			2	1	2	1	3	1
Catostomidae			7	1				
Cobitidae	1	0					1	0
Cyprinidae			12	1, 3	7	1	4	1
Callichthyidae	1	4						
Clariidae	1	4						
Ictaluridae			5	3, 4	6	3		
Loricariidae	3	4						
Atherinidae					1	1		
Esocidae			1	1	1	1		
Gasterosteidae			1	3	1	3	2	4
Osmeridae					1	1	1	1
Salmonidae			7	2	4	2	5	3, 4
Gobiidae					1	3	2	4
Synbranchidae	1	4						
Mastacembelidae	1	4						
Channidae	1	6						
Osphronemidae	1	2						
Cichlidae	17	4, 6	5	4	3	3		
Poeciliidae	3	4	4	2	4	4	1	4
Fundulidae			2	1	1	3		
Moronidae			3	1	2	1	1	1
Centrarchidae			11	3, 4	10	3	1	5
Percidae			2	1	1	3	1	1

Parental care was the most important predictor for reproduction, and for establishment because most of the species for which there is evidence of reproduction went on to establish self-sustaining populations. Of the 31 species included in this analysis that have successfully established, only the oriental weatherfish lacks parental care and the croaking gourami has relatively low levels of parental care (Lawson 2018). Each of the 29 remaining established species have higher levels of parental care with strategies including livebearing (Poeciliidae), mouthbrooding (Cichlidae), and paternal or biparental nest guarding (Lawson 2018). The high level of parental care displayed by many of the successfully established non-native fishes in Florida is unique among non-native freshwater fish faunas across the United States (Table 5; Kolar & Lodge 2002, Marchetti et al. 2004b, Olden et al. 2006).

The cichlid family in particular is a diverse group with high levels of parental care (Turner 2007) that is well-represented among successfully established non-native species in Florida. Many cichlids that are successfully established in Florida exhibit biparental care, which is a unique strategy among teleost fishes (Teresa & Goncalves-de-Freitas 2011). All Neotropical cichlid species established in Florida exhibit this biparental care strategy. Gross & Sargent (1985) theorized that biparental care resulted from the coevolution of paternal care increasing with larger egg sizes, necessitating a longer guarding period and teamwork to successfully guard mobile fry. This biparental care strategy has not evolved in native North American fish families, being present in North America only in the members of the family Cichlidae that spread north from South America into Mexico and the Rio Grande River basin of Texas. The family Centrachidae which possesses life history strategies similar to the family Cichlidae only exhibits nest guarding by males (Blumer 1982, Gross & Sargent 1985). Of the many African cichlid species that have likely been introduced to Florida, the tilapiine species have been the most successful (United States Geological Survey 2021). These species also have a high degree of parental care; members of the genus *Oreochromis* are maternal mouthbrooders, *Tilapia* spp. are nest guarders, and blackchin tilapia *Sarotherodon melanotheron* Ruppell, 1852 is a paternal (occasionally biparental) mouthbrooder (Trewavas 1983).

Although parental care is the best predictor of both successful reproduction and establishment, other traits included in the best models differ between the two stages. Egg diameter and swim factor seem to be important predictors of successful reproduction, whereas fluvial dependence and vertical position in the water column are more important predictors of establishment. Other studies have found that suites of traits used to predict various stages of the invasion process differ, which suggests that stage-based analyses provide a good foundation for a better understanding of invasion processes (Kolar & Lodge 2002, Marchetti et al. 2004b, Howeth et al. 2016). Parental care, along with physiological tolerance, were the two strongest predictors of establishment for non-native fishes in California according to Marchetti et al. (2004b). The reason behind its importance, that parental care increases juvenile survival and minimizes their dispersal into poor environments (Marchetti et al. 2004b), is likely the same for Florida. Similar to the present study, they also found parental care to be an important predictor of the other stages they examined with otherwise different suites of traits as predictors for each stage.

In addition to parental care, traits that appear to be important for predicting successful reproduction of non-native fishes in Florida include egg diameter, air breathing, swim factor, and to a lesser degree diet breadth, maximum length, fluvial dependence, and spawning season. Larger egg diameters among species that have successfully reproduced indicate a higher level of parental investment in offspring, consistent with the equilibrium life history strategy (Winemiller & Rose 1992, Winemiller 1995, Lawson 2018). Egg diameter has also been shown to positively correlate with the duration of parental care in ectothermic animals (Sargent et al. 1987, Kolm et al. 2006). Of the introduced fishes examined, many that have successfully reproduced in Florida are facultative air breathers and have larger swim factors which indicates less frequent or slower swimming, and no fluvial dependency (Olden et al. 2006). Fishes possessing all four major traits (parental care, air-breathing, larger swim factors, no fluvial dependency) indicating successful reproduction include clown knifefish *Chitala ornata* Gray, 1831, brown hoplo *Hoplosternum littorale* Hancock, 1828, suckermouth catfish *Hypostomus* sp., armoured sailfin catfish *Pterygoplichthys* spp., walking catfish *Clarias batrachus* Linnaeus, 1758, spotfin spiny eel *Macrognathus siamensis* Gunther, 1861, Asian swamp eel *Monopterus albus* Zuiew, 1793, and bullseye snakehead *Channa marulius* Hamilton, 1822.

The suite of traits that best predict successful establishment differs from those predicting reproduction. Parental care is still the single best predictor, however fluvial dependence, maximum length, and vertical position in the water column are of secondary importance. It should be noted that there are no successfully established non-native fishes in Florida with fluvial dependence. Many of the introduced benthic species have also successfully established, and this strategy seems particularly successful when combined with parental care, air breathing, and lack of fluvial dependence, as demonstrated by brown hoplo, suckermouth catfish, armoured sailfin catfish, walking catfish, spotfin spiny eel, and Asian swamp eel. These species are especially suited to the soft substrate and generally low to no flow aquatic habitats in Florida. The brown hoplo, armoured sailfin catfishes, and walking catfish have done especially well and can be found in a variety of habitats across much of peninsular Florida (Lawson 2018, United States Geological Survey 2021). Many other species that have successfully established in Florida are not benthic or air breathing, but pelagic species with similarly high levels of parental care and lack of fluvial dependence such as those in the family Cichlidae. Successfully established species also have a larger maximum body length.

Despite numerous opportunities presented by the introduction of fishes of varying geographic origin and body size, observations of reproduction in peninsular Florida by opportunistic or periodic strategists (Winemiller & Rose 1992) are almost completely lacking (Table 2). The lack of reproduction in opportunistic non-native fishes is especially surprising given the large proportion of native fishes that fall within or near this category (Lawson 2018). The inability to reproduce or establish could be due to unsuitable environmental conditions or biotic resistance, however specific causes of failure remain unknown. Abiotic and biotic factors have been shown to influence the failure of small-bodied fish invaders (Hill & Tuckett 2018) which are often opportunistic strategists. Aggression (Thompson et al. 2012), predation (Hill 2016), and asymmetric intraguild predation (Tuckett et al. 2021) from native species are known mechanisms of biotic resistance in the region. Periodic strategists may have more difficulty reproducing in Florida habitats due to their often exacting requirements for flowing waters or other habitat features that may not be present or conditions that may be temporally mismatched for reproduction. Research into the specific mechanisms of failure in reproduction and recruitment, whether abiotically or biotically driven, is warranted.

Peninsular Florida possesses a variety of unique attributes that make it particularly susceptible to non-native fish introductions. These attributes include a subtropical climate, large human population, numerous importation locations, and a robust ornamental aquaculture industry (Hill & Yanong 2002). The pet trade and ornamental aquaculture industries have facilitated the importation and culture of hundreds of non-native fish species into Florida (Chapman et al. 1997, Hill & Yanong 2002). The diversity and number of donor regions of these non-native fishes are unparalleled when compared to other regions of the United States. Fishes that have successfully established in Florida come from tropical regions of Central America, South America, Africa, and Asia, whereas most established non-natives in California, the Great Lakes, and the River Colorado are native transplants, or temperate species from Eurasia. This leads to relatively little overlap in Florida's introduced fauna and that of other studied regions of the US (Table 5). These differences in non-native fauna are largely a product of the types of introduction pathways that are most common for each region, and the receiving environments. The fact that peninsular Florida imports so many non-native tropical fish species which have a strong climate match to the state presents a need for the development of a region-specific risk screening tool for fishes.

In terms of accurately predicting the success of species included in the training dataset, there is some variation among the models. Logistic regression provides the best understanding of variable importance, but the models are not as user-friendly for predicting success of a large number of species. Classification trees combine a high degree of accuracy with a simple model that can be applied easily, allowing the user to quickly screen a large number of species. In a study comparing the performance of three model types applied to mixed ecological data, Olden & Jackson (2002) found that of the three, classification trees outperformed multiple linear regression and discriminant analysis. We similarly found that the classification trees misidentified fewer species than both the best logistic regression model, and the best discriminant function.

The results of the present study may be applied toward the creation of stage-based risk screening tools for non-native fishes for Florida. Region-specific analyses using traits to predict success are growing in popularity and are useful for regions with elevated risk (e.g. Kolar & Lodge 2002). The results of the classification tree analysis in particular can be used for hazard identification or as a simple, coarse screen for Florida (Fig. 2). Species with parental care scores > 2.5 are likely to reproduce (92%) and those with score < 2.5 still have a 67% chance of reproduction if their swim factor is > 0.545. Given successful reproduction, 94% of species with parental care scores > 3.5 have successfully established. This simple tool can augment more detailed and complex risk screening tools such as the fish invasiveness screening kit (FISK: Copp et al. 2009, Lawson et al. 2013, Vilizzi et al. 2019) and aquatic species invasiveness screening kit (AS-ISK: Copp et al. 2016, Vilizzi et al. 2021). The development of more regional risk screening tools can assist managers by improving accuracy and saving time. Future research will address characteristics that can be used to predict spread and determine the magnitude and probability of impacts by non-native fishes in Florida. The spread of non-native fishes in Florida has not been specifically investigated and new methods for measuring spread may be needed for this region. Similarly, few analyses address the impacts of non-native fishes in Florida (Schofield & Loftus 2015), a critical need for additional research to improve risk assessment.

Acknowledgements

We thank the University of Florida, College of Agricultural and Life Sciences for Graduate Student Fellowship funding, the School of Forest Resources and Conservation, and the faculty, staff and students of the Tropical Aquaculture Laboratory (Craig Watson, Director) for their assistance. We also thank Drs. Michael Allen, Charles Cichra, Daryl Parkyn, and Steven Johnson (University of Florida) for their valuable suggestions for the improvement of this manuscript and Kelly Gestring (Florida Fish and Wildlife Conservation Commission) for helpful discussions about the lists of successful and failed non-native species. Author contributions: K. Lawson and J. Hill designed the study and K. Lawson collected the data, conducted analyses, and drafted the manuscript. Both authors contributed to the final version of the manuscript.

Literature

Alcaraz C., Vila-Gispert A. & Garcia-Berthou E. 2005: Profiling invasive fish species: the importance of phylogeny and human use. *Divers. Distrib. 11: 289–298.*

Allen C.R., Nemec K.T., Wardwell D.A. et al. 2013: Predictors of regional establishment success and spread of introduced non-indigenous vertebrates. *Glob. Ecol. Biogeogr. 22: 889–899.*

Baltz D.M. & Moyle P.B. 1993: Invasion resistance to introduced species by a native assemblage of stream fishes. *Ecol. Appl. 3: 246–255.*

Blackburn T.M., Pyšek P., Bacher S. et al. 2011: A proposed unified framework for biological invasions. *Trends Ecol. Evol. 26: 333–339.*

Blumer L.S. 1982: A bibliography and categorization of bony fishes exhibiting parental care. *Zool. J. Linn. Soc. 76: 1–22.*

Catford C.A., Jansson R. & Nilsson C. 2009: Reducing redundancy in invasion ecology by integration hypotheses into a single theoretical framework. *Divers. Distrib. 15: 22–40.*

Chapman F.A., Fitz-Coy S.A., Thunberg E.M. & Adams C.M. 1997: United States of America trade in ornamental fish. *J. World Aquacult. Soc. 28: 1–10.*

Colautti R.I., Grigorovich I.A. & MacIsaac H.J. 2006: Propagule pressure: a null model for biological invasions. *Biol. Invasions 8: 1023–1037.*

Copp G.H., Bianco P.G., Bogutskaya N.G. et al. 2005: To be, or not to be, a non-native freshwater fish? *J. Appl. Ichthyol. 21: 242–262.*

Copp G.H., Vilizzi L., Mumford J. et al. 2009: Calibration of FISK, an invasiveness screening tool for nonnative freshwater fishes. *Risk Anal. 29: 457–467.*

Copp G.H., Vilizzi L., Tilbury H. & Stebbing P. 2016: Development of a generic decision-support tool for identifying potentially invasive aquatic taxa: AS-ISK. *Manag. Biol. Invasions 7: 343–350.*

Courtenay W.R., Jr., Hensley D.A., Taylor J.N. & McCann J.A. 1984: Distribution of exotic fishes in the continental United States. In: Courtenay W.R., Jr. & Stauffer J.R., Jr (eds.), Distribution, biology and management of exotic fishes. *John Hopkins University Press, Baltimore, USA: 41–77.*

Courtenay W.R., Jr., Hensley D.A., Taylor J.N. & McCann J.A. 1986: Distribution of exotic fishes in North America. In: Hocutt C.H. & Wiley E.O. (eds.), The zoogeography of North American freshwater fishes. *John Wiley and Sons, New York, USA: 675–698.*

Courtenay W.R., Jr. & Stauffer J.R., Jr. 1990: The introduced fish problem and the aquarium fish industry. *J. World Aquacult. Soc. 21: 145–159.*

Frimpong E.A. & Angermeier P.L. 2009: FishTraits: a database of ecological and life-history traits of freshwater fishes of the United States. *Fisheries 34: 487–495.*

Froese R. & Pauly D. 2019: FishBase. Downloaded on May 2021. *www.fishbase.org*

Garcia-Berthou E. 2007: The characteristics of invasive fishes: what has been learned so far? *J. Fish Biol. 71: 33–55.*

Gross M.R. & Sargent R.C. 1985: The evolution of male and female parental care in fishes. *Am. Zool. 25: 807–822.*

Hayes K.R. & Barry S.C. 2008: Are there any consistent predictors of invasion success? *Biol. Invasions 10: 483–506.*

Hill J.E. 2002: Exotic fishes in Florida. *LakeLines 22: 39–43.*

Hill J.E. 2008: Non-native species in aquaculture: terminology, potential impacts, and the invasion process. *Southern Regional Aquaculture Center, Stoneville, USA.*

Hill J.E. 2016: Collapse of a reproducing population of non-native African jewelfish (*Hemichromis letourneuxi*) in a Florida lake. *NeoBiota 29: 35–52.*

Hill J.E. & Cichra C.E. 2005: Eradication of a reproducing population of convict cichlids, *Cichlasoma nigrofasciatum* (Cichlidae), in north-central Florida. *Fla. Sci. 68: 65–74.*

Hill J.E. & Tuckett Q.M. 2018: Abiotic and biotic contributions to invasion resistance for ornamental fish in west-central Florida, USA. *Hydrobiologia 817: 363–377.*

Hill J.E. & Yanong R.P. 2002: Freshwater ornamental fish commonly cultured in Florida. *EDIS Circular 54, University of Florida, Gainesville, USA.*

Hogg R.G. 1976: Established exotic cichlid fishes in Dade County, Florida. *Fla. Sci. 39: 97–103.*

Howeth J.G., Gantz C.A., Angermeier P.L. et al. 2016: Predicting invasiveness of species in trade: climate match, trophic guild and fecundity influence establishment and impact of non-native freshwater fishes. *Divers. Distrib. 22: 148–160.*

Kolar C.S. & Lodge D.M. 2001: Progress in invasion biology: predicting invaders. *Trends Ecol. Evol. 16: 199–204.*

Kolar C.S. & Lodge D.M. 2002: Ecological predictions and risk assessment for alien fishes in North America. *Science 298: 1233–1236.*

Kolm N., Goodwin N.B., Balshine S. & Reynolds J.D. 2006: Life history evolution in cichlids 1: revisiting the evolution of life histories in relation to parental care. *J. Evol. Biol. 19: 66–75.*

Lawson K.M. 2018: Use of life history traits to predict invasion success of non-native fishes in Peninsular Florida. *PhD thesis, University of Florida, Gainesville, USA.*

Lawson K.M., Tuckett Q.M., Ritch J.L. et al. 2017: Distribution and status of five non-native fish species in the Tampa Bay drainage (USA), a hot spot for fish introductions. *BioInvasions Rec. 6: 393–406.*

Lawson L.L., Vilizzi L., Hill J.E. et al. 2013: Revisions of the fish invasiveness screening kit (FISK) for its application in warmer climatic zones, with particular reference to peninsular Florida. *Risk Anal. 33: 1414–1431.*

Lester P.J. 2005: Determinants for the successful establishment of exotic ants in New Zealand. *Divers. Distrib. 11: 279–288.*

Leung B., Roura-Pascual N., Bacher S. et al. 2012: TEASIng apart alien species risk assessments: a framework for best practices. *Ecol. Lett. 15: 1475–1493.*

Lockwood J.L., Cassey P. & Blackburn T. 2005: The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol. 20: 223–228.*

Marchetti M.P., Moyle P.B. & Levine R. 2004a: Alien fishes in California watersheds: characteristics of successful invaders. *Ecol. Appl. 14: 587–596.*

Marchetti M.P., Moyle P.B. & Levine R. 2004b: Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. *Freshw. Biol. 49: 646–661.*

Moyle P.B. & Light T. 1996: Biological invasions of fresh water: empirical rules and assembly theory. *Biol. Conserv. 78: 149–161.*

Olden J.D. & Jackson D.A. 2002: A comparison of statistical approaches for modelling fish species distributions. *Freshwater Biol. 47: 1976–1995.*

Olden J.D., Poff N.L. & Bestgen K.R. 2006: Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. *Ecol. Monogr. 76: 25–40.*

Ortega H., Guerra H. & Ramirez R. 2007: The introduction of nonnative fishes into freshwater systems of Peru. In: Bert T.M. (ed.), Ecological and genetic implications of aquaculture activities. *Springer, Dordrecht, Netherlands: 247–278.*

R Core Team 2020: R: a language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria.*

Ribeiro F., Elvira B., Collares-Pereira M.J. & Moyle P.B. 2008: Life-history traits of non-native fishes in Iberian watersheds across several invasion stages: a first approach. *Biol. Invasions 10: 89–102.*

Richardson D.M., Pysek P., Rejmanek M. et al. 2000: Naturalization and invasion of alien plants: concepts and definitions. *Divers. Distrib. 6: 93–107.*

RStudio Team 2020: RStudio: integrated development for R. *RStudio, Inc., Boston, USA.*

Ruesink J. 2005: Global analysis of factors affecting the outcome of freshwater fish introductions. *Conserv. Biol. 19: 1883–1893.*

Sargent R.C., Taylor P.D. & Gross M.R. 1987: Parental care and the evolution of egg size in fishes. *Am. Nat. 129: 32–46.*

Schofield P.J. & Loftus W.F. 2015: Non-native fishes in Florida waters: a literature review and synthesis. *Rev. Fish Biol. Fish. 25: 117–145.*

Schofield P.J. & Schulte J.M. 2016: Small but tough: what can ecophysiology of croaking gourami *Trichopsis vittata* (Cuvier, 1831) tell us about invasiveness of non-native fishes in Florida? *NeoBiota 28: 51–65.*

Shafland P.L., Gestring K.B. & Stanford M.S. 2008: Florida's exotic freshwater fishes. *Fla. Sci. 7: 220–245.*

Simberloff D. 2009: The role of propagule pressure in biological invasions. *Annu. Rev. Ecol. Evol. Syst. 40: 81–102.*

Taylor J.N., Snyder D.B. & Courtenay W.R., Jr. 1986: Hybridization between two introduced, substrate-spawning tilapias (Pisces: Cichlidae) in Florida. *Copeia 1986: 903–909.*

Teresa F.B. & Goncalves-de-Freitas E. 2011: Reproductive behavior and parental roles of the cichlid fish *Laetacara araguaiae*. *Neotrop. Ichthyol. 9: 355–362.*

Thompson K.A., Hill J.E. & Nico L.G. 2012: Eastern mosquitofish resists invasion by nonindigenous poeciliids through agonistic behaviors. *Biol. Invasions 14: 1515–1529.*

Trewavas E. 1983: Tilapiine fishes of the genera *Sarotherodon*, *Oreochromis*, and *Danakilia*. *British Museum of Natural History, London, UK.*

Tuckett Q.M., Deacon A.E., Fraser D. et al. 2021: Unstable intraguild predation causes establishment failure of a globally invasive species. *Ecology 102: e03411.*

Tuckett Q.M., Ritch J.L., Lawson K.M. & Hill J.E. 2016: Implementation and enforcement of best management practices for Florida ornamental aquaculture with an emphasis on nonnative species. *N. Am. J. Aquacult. 78: 113–124.*

Turner G.F. 2007: Adaptive radiation of cichlid fish. *Curr. Biol. 17: R827–R831.*

United States Geological Survey 2021: Nonindigenous aquatic species database. Downloaded on May 2021. *http://nas.er.usgs.gov/*

Vila-Gispert A., Alcaraz C. & Garcia-Berthou E. 2005: Life-history traits of invasive fish in small Mediterranean streams. *Biol. Invasions 7: 107–116.*

Vilizzi L., Copp G.H., Adamovich B. et al. 2019: A global review and meta-analysis of applications of the freshwater fish invasiveness screening kit. *Rev. Fish Biol. Fish. 29: 529–568.*

Vilizzi L., Copp G.H., Hill J.E. et al. 2021: A global-scale screening of non-native aquatic organisms to identify potentially invasive species under current and future climate conditions. *Sci. Total Environ. 788: 147868.*

Winemiller K.O. 1989: Patterns of variation in life-history among South American fishes in periodic environments. *Oecologia 81: 225–241.*

Winemiller K.O. 1995: Fish ecology. In: Nierenberg W.A. (ed.), Encyclopedia of environmental biology, vol. 2. *Academic Press, San Diego, USA: 49–66.*

Winemiller K.O. & Rose K.A. 1992: Patterns of life-history diversification in North American Fishes: implications for population regulation. *Can. J. Fish. Aquat. Sci. 49: 2196–2218.*