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Research Article

Dietary flexibility despite behavioral stereotypy contributes to successful invasion of the pike killifish, *Belonesox belizanus*, in Florida, USA

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Abstract

It is well known that the establishment of invasive-fish populations depends on the ability of introduced individuals to adapt to environmental conditions in the invaded ecosystem, including the ability to feed on diverse, locally available prey resources. Furthermore, the current invasive-biology paradigm postulates that having a generalist-food habit is key to the successful invasion of a novel community by exotic species. This study investigated how the invasive pike killifish, *Belonesox belizanus*, has succeeded in establishing exotic populations in Florida, USA despite having a feeding apparatus that is characteristic of a specialized piscivore (i.e., fish-eating fish). Pike killifish collected from their point of introduction in south Florida were (1) filmed using high speed video while feeding on live fish- and shrimp-prey to determine whether prey type affects prey-capture kinematics and then (2) subjected to a prey-selectivity experiment to determine which prey type (live fish or shrimp) the invasive pike killifish eats when both prey are available in the environment. Results indicated that (1) prey-capture kinematics were not affected by prey type, indicating that consumption of fish and shrimp prey was accomplished using a stereotypical feeding repertoire, and (2) pike killifish consumed fish and shrimp when both prey were available in the feeding environment. It is concluded that the invasive pike killifish has the ability to feed on alternative, locally available prey using its piscivorous feeding functional morphology and prey-capture kinematics. This study contributes a new perspective to our understanding of the mechanisms that underlie success of exotic fishes in invaded communities. That is, the ability of a functional-morphological specialist to utilize stereotypical prey-capture kinematics (= *behavior*) in consuming alternative, locally available prey types (= *dietary flexibility*) contributes to the establishment of invasive populations. It is evident that these functional specialists are not constrained in their diet, thus, enabling them dietary flexibility and enhancing their invasive potential.

Key words: Poeciliidae; invasion; feeding specialist; prey selectivity; functional morphology; prey capture kinematics; non-native freshwater fishes

Introduction

Understanding how invasive species respond to environmental conditions in the recipient ecosystem promotes understanding of the processes that contribute to adaptive evolution in invasive species. The invasive-species response to local conditions in the invaded environment largely depends on the possession of key traits, including physiological and behavioral tolerance to environmental temperature, salinity and water quality, and a generalist food habit (Rahel and Olden 2008; Rahel et al. 2008). Results of previous experiments have elucidated our understanding of the physiological tolerances of invasive species (Arthington and Mitchell 1986; di Castri 1990; Moyle and Light 1996). However, information about the functional and behavioral basis of the generalist-food habits of invasive species is scarce. In this study, we assessed the feeding performance of a successful invasive fish, the pike killifish (*Belonesox belizanus* Kner, 1860), which has a feeding mechanism that is uncharacteristic of an invasive-generalist species.

Pike killifish are native to Mexico and Central America (Hubbs 1936; Rosen and Bailey 1963). After the introduction of 50 pike killifish into a ditch in Miami-Dade County, Florida, USA in 1957, this exotic population has continued to extend its distribution northward, becoming one of the most successful invasive-fish species in Florida (Belshe 1961; Miley 1978; Anderson 1980; Kerfoot et al. 2011; FWC 2012). Pike killifish is commonly found within submerged vegetation in slow-flowing rivers, lakes, ditches, and brackish waters (Meek 1904; Hubbs 1936; Loftus et al. 2004). These habitats facilitate the ambush prey-capture technique that they use to feed primarily on fish prey (Belshe 1961; Anderson 1980; Turner and Snelson Jr. 1984; Greven and Brenner 2008). Functional morphologists and evolutionary ecologists have concluded that the pike killifish is a specialist piscivore, feeding exclusively on fish-prey (Greven and Brenner 2008; Ferry-Graham et al. 2002). It has evolved a unique feeding apparatus, equipped with elongated oral jaws and an independently mobile premaxilla (upper jaw), allowing it to achieve an unusually large gape to capture fish-prey (Ferry-Graham et al. 2002, 2010). This specialist-feeding functional morphological design and an apparent piscivorous food habit present a plausible dilemma for invasive-species biologists. How does a specialist predator become a successful invasive species?

The main goal of this study is to address the above paradox for the first time. We hypothesize that a functional specialist does not have to be a feeding specialist. Understanding how a specialist-invasive species consumes different prey types is imperative, especially in elucidating the ability of functional specialists to accomplish contrasting tasks such as feeding on different, locally available prey organisms (i.e. *Gambusia affinis, G. holbrooki* and *Palaemonetes* sp). This study investigated the ability of pike killifish to feed on two contrasting prey types that are locally available in their invasive range: live fish and live shrimp. The live fish are generally surface-dwelling prey with variable coloration and patterns. They also exhibit a more subtle and streamlined escape response (i.e. forward-directed movement by caudal fin propulsion) relative to a live shrimp (Domenici 2002; Gibb et al. 2006). The live shrimp are generally translucent, bottom-dwelling prey, which exhibit a more cryptic behavior and a more rapid, instantaneous escape response (i.e. backward-directed movement by tail-flip propulsion) (Arnott et al. 1998, 1999). The specific objectives of this study were (a) to contrast the pattern of kinematics when pike killifish feed on fish and when they feed on shrimp and (b) to determine pike killifish prey selectivity when both prey types are available in their environment. The specific hypotheses were (1) pike killifish utilize distinctly different kinematic profiles when feeding on shrimp than when feeding on fish, (2) pike killifish consume fish prey rather than shrimp prey when given the same density of these two prey types, and (3) pike killifish eat shrimp prey when it is the only available prey in its environment.

Methods

Pike killifish were collected in August 2010 from Florida's Everglades National Park (Permit # EVER-2010-SCI-0010). Drop nets were used to collect pike killifish during the night, near drainage areas and in ditches off of State Road 9336, with the maximum distance of 8 km from the park entrance. Fish were transported to and maintained in the fish laboratories at Florida Institute of Technology following the Institutional Animal Care and Use Committee protocol (#101202).

Prey Capture Kinematics

Eight individual pike killifish were placed in eight separate 37.8 liter glass-filming tanks. The bottom of each filming tank had approximately 2.5 cm thick sand and gravel, and artificial vegetation similar to the natural habitat of the Florida invasive pike killifish. Water in the filming tanks was maintained at 0 psu and 20°C. A 2 cm × 2 cm grid was placed at the back of the tank as reference for measurement of the kinematic variables. Each fish was acclimated to feeding in filming conditions (in the presence of two 250 watt flood lamps and camera set-up) for two to three weeks prior to recording. Filming commenced when each pike killifish willingly fed on fish or shrimp prey in front of the high-speed camera. High-speed videos [(250 frames per second (fps) using RedLake MotionScope 2000S)] were recorded of pike killifish capturing fish or shrimp prey.

During filming, each pike killifish was presented, in random order, with either a ghost shrimp (*Palaemonetes* sp.) or a mosquitofish (*Gambusia holbrooki*) individually. These were chosen as representative prey because they are commonly found in their invaded habitat. They have also been found in the guts of wild-caught pike killifish (Miley 1978), and exhibit very contrasting escape responses and overall body shapes, as described in the introduction.

Each film was reviewed and a frame-by-frame examination of each event was conducted to measure 11 kinematic variables that represent the feeding repertoire of pike killifish. In addition to the linear and angular displacement variables

Table 1. Description and measurement of the linear- and angular-displacement kinematic variables using the points of reference ("landmarks") depicted in Figure 1. Time zero is indicated as "T0".

Kinematic Variable	Description and Measurement
Maximum Hyoid Depression (mm)	Maximum length measured from the center of the eye to point (D) at full depression, irrespective of cranial elevation.
Maximum Gape (mm)	Maximum distance measured from the anterior-most tip of the premaxilla (A) to the anterior-most tip of the dentary (B), when mouth is open.
Maximum Angular Displacement of the Lower Jaw (degree)	Maximum rotation of the lower jaw measured by the line segments EF to FB.
Maximum Cranial Rotation (degree)	Maximum rotation of the neurocranium dorsally and posteriorly, measured by the angle formed from line segments CE and EG from T0 to maximum gape. Cranial rotation assists in achieving maximum gape whilst elevating the premaxilla.
Cranial Rotation at Maximum Gape (degree)	Cranial rotation measured as the difference at T0 to maximum gape, using the angle formed by line segments CE to EG.
Premaxilla Displacement (degree)	Maximum displacement of the premaxilla relative to the lower jaw, measured from maximum gape to mouth closed as the premaxilla snaps after prey capture; using the angle formed by line segments AC to CB.

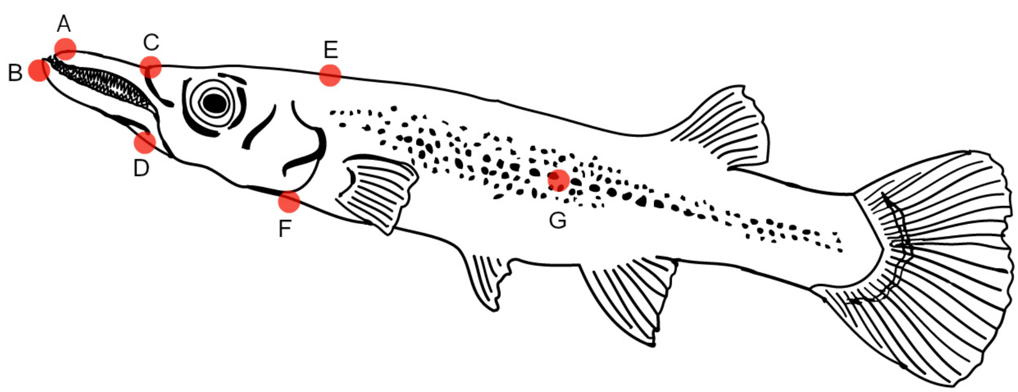

Figure 1. Diagram of a representative Florida invasive pike killifish showing the "landmarks" used to measure the kinematic variables described in Table 1. The landmarks are the points on the body used for drawing line segments. Points A, B, C, D are associated with the upper and lower jaws, while E and F are prominent in cranial rotation. Point G is the midpoint of the body.

defined in Table 1 and Figure 1, time (ms) to maximum hyoid depression, maximum gape, and maximum cranial rotation relative to the frame prior to mouth-opening, as well as duration of feeding bout (ms) and attack velocity (mm s^{-1}) were measured. Six videos of each of the eight pike killifish were analyzed, totaling 48 feeding events for kinematic profile analysis.

Prey Selectivity

Four pike killifish were randomly assigned to four 18.9 liter tanks (one fish per tank). Each experimental tank simulated the pike killifish natural environment as described in the previous description of the filming tanks. Each pike killifish was fed live ghost shrimp (*Palaemonetes* sp.) and mosquitofish (*Gambusia holbrooki*) at varying prey densities (= treatments): (1) 4-fish:0-shrimp (i.e., fish-prey); (2) 2-fish:2-shrimp (i.e., 50:50 fish- and shrimp-prey); and (3) 0-fish:4-shrimp (i.e., shrimp-prey). At the end of a 2-hour feeding period, the number of prey eaten was recorded. The treatments were replicated four times per fish. Prey was randomly selected from a stock of prey sized at 40-60% of the maximum gape of the individual pike killifish (Richard and Wainwright 1995). Prey

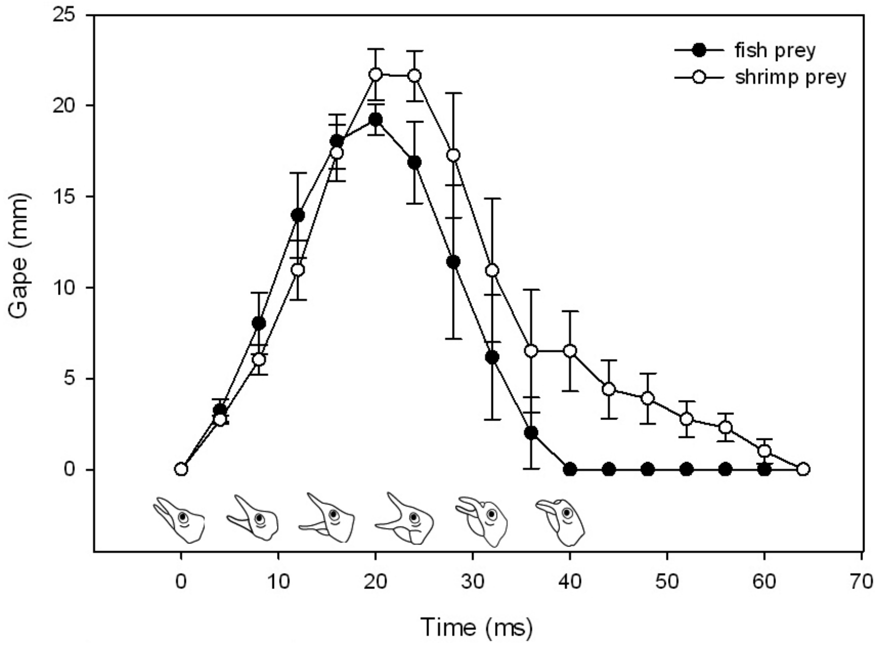

Figure 2. Change in gape (mm) over time (ms) in the Florida invasive pike killifish when feeding on shrimp and fish prey. Data points represent the Mean of 48 feeding trials and the error bars represent the Standard Error of the Mean.

density was maintained at four items throughout the duration of the study, as pike killifish became satiated after three to four items (Harms, personal observation). This density promoted "selection" of prey rather than "preference", which resembles an actual situation the pike killifish would encounter in its invaded range. The fish initially consumes optimal prey items (i.e. fish prey) but then must select for those less favorable, as optimal items diminish in abundance (i.e. a switch from "preference" to "selection"). Equal prey density allowed the pike killifish to encounter each prey with equal opportunity, despite the contrasting escape responses and location of prey within the tank (i.e. bottom-dwelling shrimp versus surface-dwelling fish).

Analyses

To test the hypothesis that pike killifish prey-capture kinematics differed between prey types, the kinematic variables were subjected to a Repeated Measures Multivariate Analysis of Covariance (MANCOVAR) using SYSTAT 12, with prey as main effects, fish-standard length as covariate and individual fish as the repeated measure. An average of three values of each kinematic variable for each prey type per fish was utilized for the MANCOVAR, demonstrating a truly replicated design (n=8) consistent with other published methods (Ferry-Graham et al. 2010). Sigma Plot 11 was used to generate kinematic profiles.

Wilcoxon Signed Rank Test (SPSS 18) compared the significant difference between the number of prey consumed and the hypothesized median consumption of zero in treatments where only one of the prey types (fish or shrimp) was present in the environment. A Chi Square Test was used to test the hypothesis that the proportion of prey eaten is not statistically different from the expected 50:50 chance consumption when both fish- and shrimp-prey (i.e., 2-fish:2-shrimp treatment) were present in the environment.

Results

Prey Capture Kinematics

MANCOVAR revealed no significant difference in prey-capture kinematics among pike killifish ($p= 0.824$), prey type ($p= 0.480$) and fish standard length ($p= 0.237$) (SL) (Table 3). The consistency of the pike killifish prey-capture behavior between fish- and shrimp-prey is

Table 2. Descriptive statistics of prey-capture kinematics for pike killifish feeding on fish and shrimp prey items.

Variable	Fish Prey Mean	±S.E.M.	Shrimp Prey Mean	±S.E.M.
Maximum Hyoid Depression (mm)	6.071	0.673	5.534	0.384
Maximum Gape (mm)	17.760	1.028	17.737	1.180
Feeding Bout (ms)	38.333	2.319	57.166	9.027
Time to Maximum Gape (ms)	21.417	2.191	36.833	8.822
Time to Maximum Hyoid Depression (ms)	26.333	2.043	42.833	8.963
Time to Maximum Cranial Rotation (ms)	42.333	5.993	58.500	8.501
Attack Velocity (mm s-1)	1143.075	97.227	741.352	71.709
Maximum Angular Displacement of Lower Jaw (degree)	93.008	0.385	96.050	1.368
Premaxilla Displacement (degree)	69.202	5.032	57.087	3.820
Cranial Rotation at Time Zero (T0) (degree)	17.208	1.985	13.670	2.898
Cranial Rotation at Maximum Gape (degree)	9.500	1.369	7.670	1.109

Table 3. Results of Repeated Measures Multivariate Analysis of Covariance testing the effects of prey type, individual fish and standard length (covariate) on the prey-capture kinematics of pike killifish.

Effect	Wilk's Lambda	d.f.1	d.f.2	F	Significance
Kinematic*Fish	0.377	10	7	0.496	0.824
Kinematic*PreyType	0.194	10	1	1.244	0.480
Kinematic*SL	0.105	10	7	2.567	0.237

further illustrated in the descriptive statistics (Table 2) and the kinematic profiles, for example the gape profile presented in Figure 2. It is evident that the pike killifish utilizes the same prey-capture behavior to feed on fish- and shrimp-prey. Slight variations in particular kinematic variables and timing are present, but the overall feeding pattern remains the same.

Prey Selectivity

One-Sample Wilcoxon Signed Rank Test revealed that pike killifish fed on either fish- or shrimp-prey when either food resource was available in the environment (4-fish:0-shrimp treatment: W= 120, n=4, p<0.001; 0-fish:4-shrimp treatment: W= 105, n=4, p<0.001). An average of each treatment indicated that pike killifish consumed equal amounts of both prey types. However, the median number of shrimp consumed in the 0-fish:4-shrimp treatment was two items. The Chi Square Test revealed that when both fish- and shrimp-prey were equally available in the environment (i.e., 2-Fish:2-Shrimp treatment), pike killifish fed equitably on both prey types and showed no preference for a particular prey type (χ^2 = 0.067; d.f.= 1, p= 0.796).

Discussion

In general, species with a wide environmental tolerance are more likely to succeed in establishing invasive populations (Arthington and Mitchell 1986; di Castri 1990). The ability of the pike killifish to adapt to the physical conditions in its invaded ecosystem is consistent with that of other invasive fishes in Florida, USA. For example, south Florida pike killifish raised in 9-30°C water survived, suggesting that they have the physiological potential to expand their invasive population into the colder regions of north Florida (Shafland and Pestrak 1982; Kerfoot 2012). Other studies demonstrated that pike killifish tolerate 0-35psu waters, suggesting their ability to migrate into saline habitats, especially in bays and estuaries of the southeastern USA (Meek 1904; Hubbs 1936; Anderson 1980; Moyle and Light 1996). What is striking about the pike killifish is its success in establishing invasive populations despite their specialized feeding morphology and behavior. The feeding apparatus of pike killifish has unique features characteristic of a specialist predator, having evolved a feeding mechanism that is optimized for piscivory (i.e., feeding exclusively on bony fishes) (Ferry-Graham et al. 2002; Greven and Brenner 2008; Ferry-Graham et al. 2010) but has now been demonstrated as a useful trait for capturing a variety of elusive prey. Pike killifish have elongated oral jaws, premaxillomandibular ligaments and a unique ability to independently rotate their premaxilla postero-dorsally, allowing them to achieve a much larger gape during the capture of fish prey (Greven and Brenner 2008; Grubich et al. 2008). Many invasive species are euryphagous; however, the feeding functional morphology of the pike killifish does not immediately indicate a variable diet. This observation promotes the assumption of dominant piscivory, which would be disadvantageous to success as an invasive predator. However, gut-content analysis revealed that shrimp and other non-fish prey had been consumed, albeit minimally, by the invasive pike killifish in Florida (Miley 1978; Harms personal observation).

The Florida invasive pike killifish utilizes a stereotypical pattern of prey-capture kinematics when feeding on fish- and shrimp-prey (Ferry-Graham et al. 2002; Wainwright et al. 2008). Stereotypy is defined as a behavior that does not vary significantly during the capture of different prey types (Wainwright et al. 2008). The lack of modulation (i.e., prey-type specific prey-capture kinematics) in the feeding behavior of fishes has been demonstrated in other fish species including two clariid species (van Wassenbergh et al. 2006). In these stereotypical fish, including the Florida invasive pike killifish, some individuals may demonstrate variability in certain prey-capture kinematic variables among prey types. However, this prey-induced variability is not significant enough to change the overall pattern of prey-capture kinematics among prey types. These examples are in contrast to the cheeklined wrasse (*Oxycheilinus digrammus)* and other fish species that could distinctly vary their prey-capture behaviors among different prey types (Ferry-Graham et al. 2001) as evidence of modulatory multiplicity (Liem 1978, 1979). The ability to modulate prey-capture behavior and kinematics is species-specific and is often associated with a generalist-food habit of fishes.

It appears that prey-induced variation in prey-capture behavior is a common trait among invasive species, especially because it is often associated with variation in food habits and the ability to capture locally available prey in the invaded ecosystem (Rahel and Olden 2008; Rahel et al. 2008). The idea of a feeding specialist, such as the pike killifish, succeeding in a non-native environment appears contradictory to the established and accepted notion that invasive species are generalist predators. It is conceivable that the ability of the Florida invasive pike killifish to utilize a stereotypical prey-capture behavior and kinematics to capture fish- and non-fish prey enables it to invade aquatic ecosystems in Florida. Utilizing a piscivorous-feeding functional morphology and prey-capture behavior and kinematics appears not to constrain pike killifish in establishing invasive populations throughout Florida (Belshe 1961; Miley 1978; Anderson 1980; Turner and Snelson Jr. 1984; Kerfoot 2012).

Results of the prey-selectivity experiment confirm the dietary flexibility of the Florida invasive pike killifish. When both fish- and shrimp-prey are available in the environment, the Florida invasive pike killifish shows no preference for fish prey and can switch to eat either fish- or shrimp-prey. Furthermore, pike killifish consume shrimp-prey when it is the only available prey in the invaded environment. Previous research has demonstrated prey-switching in a piscivore (*Esox lucius)* when the preferred fish-prey was unavailable in the predator's environment, similar to the dietary flexibility of pike killifish (Chapman et al. 1989). Apparently, piscivorous fishes alter their dietary preferences according to the locally available prey resources (Chapman et al. 1989). The ability of Florida invasive pike killifish to select and consume shrimp-prey when available in the environment provides evidence of its capability to switch to different prey organisms periodically. Therefore, this invasive species with a specialized feeding strategy can survive in ecosystems that contain its natural prey base (i.e., small fishes), as well as those that contain alternative prey base (i.e., mobile invertebrates, such as shrimp). This prey-switching ability despite its stereotypical, specialized feeding mechanism may contribute to the success of the Florida invasive pike killifish in its non-native environment.

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