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Modeling the Relationship between Environmental Temperature and Feeding Performance in Florida (USA) Nonnative Fishes, with Implications for Invasive-Species Response to Climate Change

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Authors' contributions

Both authors read and approved the final manuscript.

Research Article

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ABSTRACT

Aims: To determine the effect of environmental temperature on the feeding kinematics of two Florida (USA) invasive-fish species, pike killifish *Belonesox belizanus* and Mayan cichlid *Cichlasoma urophthalmus*, in an attempt to explore the adaptive response of whole organism performance to climate change. **Study Design:** Model I (Fixed-Effects Model) Linear Regression Analysis, y-Dependent Variable = Kinematics; x-Independent Variable = Environmental Temperature. **Place and Duration of Study:** Fish Ecophysiology Laboratory, Department of Biological Sciences, Florida Institute of Technology in May-December, 2011. **Methodology:** Four each of *B*. *belizanus* and *C*. *urophthalmus*, collected from invasive populations in Florida were acclimated in 38 liter experimental aquarium, trained, and filmed using high-speed video while eating fish-prey at 20°C, 25°C and 30°C. Four films per invasive-fish species at each temperature were analyzed using MaxTRAQ digitizing software. In each film, three kinematic-excursion (peak gape, peak hyoid depression and cranial elevation at peak gape) and three kinematic-timing (time to peak gape, hyoid depression, and cranial elevation) variables were measured. Each kinematic variable was regressed against temperature to model the relationship between feeding performance and

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environmental temperature.

Results: All experimental fishes behaved normally and fed aggressively in each of the three experimental temperature regimes. It is evident in the feeding kinematics-temperature plots that fish-feeding at each temperature was variable and unpredictable. Out of the 12 regression equations generated to model the relationship between feeding kinematics and environmental temperature, only one (peak gape in *C*. *urophthalmus*) showed a significant slope (Peak Gape = $1.42 + 0.01$ Temperature; $R^2 = 0.22$; $P < 0.01$).

Conclusion: The models defining the relationship between feeding kinematics and environmental temperature are weak, as indicated by the extremely low values of the coefficient of determination (R²). Empirical evidence indicates that the feeding performance of invasive *B*. *belizanus* and *C*. *urophthalmus* is not affected by temperature.

Keywords: Invasive fishes; performance; environmental temperature; climate change.

1. INTRODUCTION

The interaction between two major drivers of change in global environment and society, *climate change and invasive species*, are largely ignored in contemporary research despite expectations that such interaction exceeds the sum of each individual's consequence for global change [1,2]. This study was designed to investigate how environmental temperature affects the feeding performance of two Florida (USA) invasive-fish species in an attempt to contribute to our understanding of species invasion in the light of climate change. Empirical evidence demonstrating the proximate and ultimate response of invasive species to environmental temperature advances our understanding of the ecologic and socio-economic impact of climate change.

It has been purported that ecosystem dynamics are altered by invasive species because they carry and spread novel diseases [3,4,5], alter the community structure of native residents [6,7,8], reorganize native-species food webs [9,10,11], hybridize with native populations [12,13,14], outcompete and eventually drive native populations into extinction, thereby promoting biological homogenization within invaded ecosystems [15,16,11]. Although the mechanisms that underlie the spread of invasive species are complex and largely misunderstood, there is universal agreement that the consequences of species invasion on native ecosystems and societies are enhanced by climate change [1,2]. In the light of our continuing search for information that advance our understanding of climate change and invasive species, this study addresses a key question that is of interest to scientists and societies, but has been largely ignored in scientific research: "How do invasive species respond to environmental change in the invaded ecosystem?" This question will be addressed by modeling feeding kinematics (i.e., feeding kinematics has been used as a metric of performance in animals) and environmental temperature in the Florida-invasive species pike killifish *Belonesox belizanus* and Mayan cichlid *Cichlasoma urophthalmus*. Both species are native to freshwaters of Mexico and Central America [17], feed on detritus, plants, invertebrates and fish [18,19,20,21], and have high tolerance to extreme variations in salinity [22,23] as well as temperature [18,22]. Temperature in the pike killifish and Mayan cichlid native ecosystems are 25-37°C and 20-39°C, respectively [24]. After their introduction to south Florida in the 1950s (pike killifish) and 1980s (Mayan cichlid), their populations have spread northward, becoming two of the most successful invasive-fish species in Florida [25,12,26,27,28]. The average annual temperature within the current distribution of the Florida-invasive pike killifish and Mayan cichlid ranges between 20°C and 30°C [29] (Fig. 1).

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Fig. 1. Map of Florida, USA showing the current distribution of invasive *Belonesox belizanus* **(Red) and** *Cichlasoma urophthalmus***(Blue). Zone of overlap between the of Florida, (Blue). two species is indicated by the purple-colored area. Temperature on the right side of the map indicates the average annual water temperature across the state. This map was modified from [30] from [30]**

With the known shifts in performance and ecology of fishes through space and time [e.g., 31;20;32], it is imperative to elucidate how environmental temperature affects the physiological (e.g., speed of muscle-driven behaviors) and ecological (e.g., role in the food web) performance of invasive species. Furthermore, information generated in this study may advance our understanding of how tropical-invasive species are predicted to move towards the poles as global temperature is expected to rise. the known shifts in performance and ecology of fishes through space and (32), it is imperative to elucidate how environmental temperature at ological (e.g., speed of muscle-driven behaviors) and ecological (e.g., role in p

2. MATERIAL AND METHODS

Four each of two Florida-invasive fishes, pike killifish *B*. *belizanus* and Mayan cichlid *C*. *urophthalmus* were collected from their invaded habitats in the Everglades National Park and Merritt Island, respectively. Each fish was acclimated and trained in 38 liter filming aquarium. *B*. *belizanus* was kept in 0ppt water and *C*. *urophthalmus* was maintained in 24ppt water, *B*.*belizanus*was

resembling the average annual salinity of their Florida habitats. After two weeks of acclimation, each fish was filmed at 20°C, 25°C and 30°C, consistent with the temperature in its Florida habitats. Attempts to film fish at 15°C failed because fish ceased feeding at this temperature; fishes were not filmed above 30°C. A portable water heater was used to raise water temperature at a rate of 1°C per day to the filming temperature. When each invasive fish aggressively fed on fish-prey (*Gambusia holbrooki)* at each environmental temperature, feeding bouts were filmed using high-speed video (i.e., Red Lake High-Speed Motionscope 2000S camera with a shutter speed of 1/1000s at 250 frames s⁻¹). Four films were analyzed per fish at each of the three experimental temperatures using MaxTRAQ (Version 2.2.4.1 Innovision Systems, Inc.).

Three kinematic-excursion (i.e., distance (mm) and angular (°): peak gape, peak hyoid depression, and cranial elevation at peak gape) and three kinematic-timing (i.e., time (msec) to peak gape, time to peak hyoid depression, and time to cranial elevation at peak gape) variables were measured as each recording of the feeding bout was played back frame-byframe (see Fig. 2 for the diagrammatic illustration and description of these variables). The timing variables were measured using the frame before the initiation of mouth opening as the reference point. These kinematic variables have been commonly used to quantify the feeding performance of fishes [e.g., 33,34,35].

Fig. 2. Diagram of the invasive Mayan cichlid, *Cichlasoma urophthalmus* **showing the hotspots used in defining and measuring the excursion-kinematic variables: Gape (or Peak Gape) = Maximum distance measured from the anteriormost tip of the premaxilla**

(A) to the anteriormost tip of the dentary (C) when the mouth is open; Hyoid Depression (or Peak Hyoid Depression) = Maximum length measured from the center of the eye (E) to the anteriormost point of the hyoid (D) at full depression; Cranial Rotation (or Cranial Rotation at Peak Gape) = Maximum rotation of the neurocranium dorsally and posteriorly, measured by the angle formed from line segments AG to GF at peak gape. Corresponding homologous hotspots were used in the pike killifish *Belonesox belizanus***.**

To test the hypothesis that feeding kinematics increase as environmental temperature became warmer, each feeding kinematic variable was log_{10} -transformed and subjected to a linear regression analysis with $y =$ kinematic variable and $x =$ environmental temperature using Systat 13 $^\circ$. $^{\circ}$.

3. RESULTS AND DISCUSSION

During each feeding trial, *B*. *belizanus* and *C*. *urophthalmus* remained very active and fed aggressively as soon as the fish prey was introduced into the filming aquarium. There was no visible difference in the general behavior of both invasive fishes as each fed at 20°C, 25°C, and 30°C.

An initial examination of the pattern of distribution of the kinematic variables across environmental temperature reveals that (1) peak gape, peak hyoid depression, and cranial elevation at peak gape as well as the time to reach these maximum kinematic-excursion measurements were variable in both invasive species; and (2) this variability remained consistent across environmental temperature (Figs. 3 & 4). Subsequent linear regression analyses revealed that only one (i.e., peak gape in *C*. *urophthalmus*) out of the 12 models was significant (Peak Gape = $1.42 + 0.01$ Temperature; $R^2 = 0.22$; $P < 0.01$). All 12 regression models were weak, as indicated by the extremely low values of the coefficient of determination (i.e., the maximum value was $R^2 = 0.22$ for peak gape in *C. urophthalmus*). These weak regression models indicate that the variation in feeding kinematics could not be explained by variation in environmental temperature.

It is well known that environmental temperature has profound effects on the behavior and physiology of animals [36]. Substantial evidence indicates that the metabolic rate of animals is directly proportional to environmental temperature [37,38,39]. Furthermore, as a consequence of the direct effects of ambient temperature on the contractile properties of skeletal muscle, it is expected that the rate of muscle-fiber contraction and relaxation correlates with temperature [40,41,42,43]. This well-known change in the rate of physico chemical reactions with ambient temperature has led researchers to expect the rate of behavioral performance in aquatic poikilotherms, such as feeding and swimming, to change with environmental temperature as well. Fish, being known to exhibit a wide tolerance of temperature have become a popular model to investigate the responses of poikilotherms to ambient-environmental temperature. For example, some species of tuna (Scombridae) and swordfish (Xiphiidae) exhibit heterothermy (i.e., those that allow their entire body temperature to fluctuate with the environmental temperature) or regional heterothermy (i.e., those that allow inner body temperature to be different from the rest of the fish body) [44]. As poikilotherms, the physiological performance of fishes are expected to reach optimum levels at a narrow temperature range, thus, environmental temperature is predicted to limit the distribution of fish populations [45,40,33,34,35].

Fig. 3. Bivariate plots showing the relationship between kinematic-excursion variables and environmental temperature. The line in each graph represents the line of best fit and the inset equation defines each regression line. y = Kinematic-Excursion Variable; x = Environmental Temperature; R² = Coefficient of Determination; P = Probability of Rejecting the Null Hypothesis β = 0. Sample size, n (i.e., number of x-y pairs) = 16 (i.e., four feeding bouts in each of four fish in either invasive species). Scale on the y-axis is Log10. Symbols: Fish 1 = Triangle; Fish 2 = Square; Fish 3 = Diamond; Fish 4 = Circle.

Fig. 4. Bivariate plots showing the relationship between kinematic-timing variables and environmental temperature. The line in each graph represents the line of best fit Fig. 4. Bivariate plots showing the relationship between kinematic-timing variables
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(i.e., four feeding bouts in each of four fish in Rejecting the Null Hypothesis β = 0. Sample size, n (i.e., number of x-y pairs) = 16 (i.e., four feeding bouts in each of four fish in either invasive species). Scale on the y axis is Log10. Symbols: Fish 1 = Triangle; Fish 2 = Square; Fish 3 = Diamond; 1 Fish Fish 4 = Circle.**

The limited research investigating the effects of temperature on the feeding kinematics of The limited research investigating the effects of temperature on the feeding kinematics of
fishes revealed mixed results [33,34,35]. Wintzer& Motta [33] and DeVries& Wainwright [34]

showed significant differences in feeding performance across a 10-degree range in temperature in native centrarchid fishes. In contrast, Sloan & Turingan [35] showed no significant difference in feeding performance among different temperature regimes in two Florida-invasive fish species. It is conceivable that these contrasting results suggest that (1) feeding performance response to environmental temperature differs between native and invasive fishes; and (2) this difference in whole-organismal response is reflective of the wider tolerance to temperature fluctuation in invasive- relative to native-fish species. Resolution of these conflicts may be advanced by future comparative analyses involving more species of invasive and native fishes, especially those that have known direct or indirect interactions in invaded ecosystems.

The importance of invasive-species research involving whole-organismal (e.g., feeding performance) response to environmental change (e.g., temperature) is particularly underscored by our lack of understanding of how populations respond to climate change [46,47,48]. Organismal response to climate change may be mitigated by its ability to compensate for changes in environmental temperature through acclimation (in captive, artificial environments), acclimatization (in natural environments), and adaptation (evolution) [49]. Exploring the extent to which each of these mechanisms contributes to organism climate change relationships undoubtedly inspires future invasive-species research. The lack of a good fit between feeding kinematics and environmental temperature in pike killifish and Mayan cichlid suggests that these invasive species possess physiological and behavioral mechanisms to compensate for the predicted effects of temperature on organismal performance. Another compensatory mechanism that may underlie the ability of pike killifish to extend its Florida population northerly toward the colder region of the state is the ability of the species to vary its temperature tolerance throughout its life-history [27]. Kerfoot [27] concluded that juvenile pike killifish has a much lower lethal temperature tolerance compared to its neonate and adult conspecifics. It is postulated that the juvenile stage fish serve to buffer the population from the adverse effects of environmental temperature change, thus facilitating their spread northerly in Florida [27]. These compensatory mechanisms may facilitate the spread of invasive species and further increase the negative impacts they cause to native species and ecosystems. With the predicted increase in global temperature, and especially with the warming of environments in higher latitudes, the expansion of the range of distribution of invasive, tropical species becomes alarming.

4. CONCLUSION

Feeding kinematics in the two Florida (USA) invasive species *B*.*belizanus* and *C*. *urophthalmus* is variable within, but, consistent among environmental temperature regimes. The models defining the relationship between feeding kinematics and environmental temperature are weak, as indicated by the extremely low values of the coefficient of determination. Empirical evidence indicates that the feeding performance of invasive *B*. *belizanus* and *C*. *urophthalmus* is not affected by temperature.

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ETHICAL APPROVAL

All authors hereby declare that all guidelines and procedures of the Institutional Animal Care and Use Committee (IACUC) of the Florida Institute of Technology (IACUC Approval # 101202) were followed, as well as specific national laws where applicable. All experiments have been examined and approved by the appropriate ethics committee.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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