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# The effects of temperature on the feeding performance of invasive fishes

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**Abstract:** It has been hypothesized that the effects of the coupling of climate-change and invasive-species phenomena exceed the impact of each separately on ecosystem dynamics and stability. However, very few studies address the interaction between these two most alarming concerns of science and society. Using two Florida invasive fishes, *Pteroisvolitans* and *Cichlasoma urophthalmus*, this study attempts to address this synergy by providing empirical evidence that (1) demonstrates how the performance of invasive species responds to environmental-temperature change, and (2) enhances our understanding of the implications of species invasion in the light of the global-climate-change phenomenon. Kinematic analyses revealed the following results: (1) At a given temperature (20°C, 25°C, and 30°C) prey-capture kinematics differed between species; (2) Each species maintained similar excursion and timing kinematics throughout the range of water temperatures; (3) The temperature-independence of the average kinematic values is reinforced by the consistent kinematic profile throughout the temperature range. We propose that more research is needed to corroborate the plausible avenues where the interplay between climate-change and invasive-species phenomena may be demonstrated, including: (1) the temperature-induced effects on physiological and mechanical processes; (2) the likelihood that these physiological effects extend to whole-organism performance; and (3) the resilience of invasive species and their resistance of whole-organism performance to temperature change.

**Keywords:** Invasive Fishes, Climate Change, Environmental Temperature, Lionfish, Mayan Cichlid, Performance

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## 1. Introduction

Scientists and society have always been concerned about the introduction and proliferation of exotic species in invaded ecosystems for well-known reasons. Among others, invasive species are vectors for diseases [1-3], change existing community structure [4-6], alter food webs [7-9], hybridize [10-12], and drive native species into extinction [9,13-14]. Our growing concern about the consequences of climate change, in general, and how global warming mediates the performance and spread of invasive species, in particular, underscores the need for contemporary research that addresses how the performance of invasive species is affected by environmental temperature [15-17]. Physiological processes such as metabolic rate, as well as contractile properties and mechanics of skeletal muscles are affected by body and environmental temperature [18-24]. For example, poikilotherms such as fishes swim and feed differently when subjected to varying levels of environmental temperature [21,25-31]. The majority, if not

all of existing literature deal with issues of invasive species apart from climate change phenomenon. However, it has been hypothesized that the synergy between these two major ecological and societal concerns, i. e., *climate change and invasive species*, is more important than their individual contributions to global change [32,33]. In this study, we attempt to address this synergy by providing empirical evidence that (1) demonstrates how the performance of invasive species responds to environmental-temperature change, and (2) enhances our understanding of the implications of species invasion in the light of the global-climate-change phenomenon.

Kinematics is a prominent metric of whole-animal performance and has been used extensively in contemporary research that investigates the effects of environmental temperature on animal locomotion and to a much lesser extent, on feeding performance [26-30,34-36]. In the North American native-fish species, bluegill (*Lepomis macrochirus*) [29] and largemouth bass, *Micropterus salmoides* [30] the timing of kinematic events

during prey capture was slower in colder than in warmer water temperatures. In contrast, Sloan and Turingan [35] and Turingan and Sloan [36] concluded that the average magnitude of feeding-kinematic events in two Florida nonnative-fish species was not affected by environmental temperature. This study focuses on the kinematics of prey-capture in lionfish, *Pteroisvolitans* and Mayan cichlid, *Cichlasoma urophthalmus*, two invasive Florida (USA) species with contrasting life-history and ecology. This comparison further elucidates the similarity or disparity of temperature response between marine- and freshwater- fish species [37-39].

The lionfish, *Pteroisvolitans*, is native to the Indo-Pacific Ocean [40,41]. Its introduction and rapid expansion in the Caribbean and along the Atlantic coast of the USA is perhaps one of the most alarming threats to the marine fauna of the region [42,43]. Invasive lionfish have been sighted as far south as Jamaica, as far north as Rhode Island, and as far northeast as Bermuda [40,44-46]. It is hypothesized that the initial source of introduction of lionfish into the Western Atlantic Ocean was through an aquarium-fish release in Biscayne Bay, Florida in 1992 [41,46,47]. Gut-content analyses of invasive lionfish have revealed that this fish feeds on a diverse group of native Atlantic coral reef fish species [42,46]. Also, Layman and Allgeier [48] found that invasive lionfish in the Bahamas, fed almost exclusively on small coral-reef fishes. A more comprehensive study of Bahamian lionfish diet by Morris and Atkins [42] revealed that by volumetric contribution, 78% and 14% of their diet comprised of teleost fishes and crustaceans respectively. More interestingly, the teleost-fish diet included 21 families and 41 species of coral-reef fishes, providing empirical evidence of the ecological impact of this invasive piscivore. Piscivory is perhaps facilitated by a suction-feeding mechanism and characteristic rapid-strikes on more mobile, elusive prey. The lionfish modulates its suction-feeding performance when feeding on fish and crustacean prey [49].

The Mayan cichlid, *Cichlasoma urophthalmus*, is native to fresh- and brackish-waters of Mexico, the Yucatan Peninsula and Isla Mujeres, Belize, Guatemala, Honduras, and Nicaragua [50,51]. It is believed to have been introduced in the Everglades National Park, Florida (USA) in 1983 [52]. Its range of invasive distribution in Florida extends as far north as Merritt Island on the east coast and Tampa area on the west coast [36,53]. The invasive Mayan cichlid has a generalist diet compared to the piscivorous diet of the invasive lionfish; it feeds on detritus, plants, invertebrates and fish [52,54-57]. Just like the generalized species in the family Cichlidae, the Mayan cichlid has an oral-jaw prey-capture mechanism and a well-developed pharyngeal-jaw apparatus for prey-processing that is characteristic of the family [58].

Both invasive lionfish and Mayan cichlid have continued to spread from the warmer waters of south Florida to the colder, northern regions of the state [53,59]. Along the east coast of Florida where the distribution of both invasive

species overlap, the average annual water temperature ranges from 20°C to 30°C [60]. The 10°C-range of environmental temperature experienced by both invasive species provides a basis for the central question in this study, “How does feeding performance of these invasive species respond to environmental change?” The known effects of temperature on the physical properties of water that affect predator-prey interactions, and on the contractile properties of muscles that drive kinematics serve as the premise for testing three hypotheses: (1) At a given temperature, the prey-capture kinematics differ between both invasive fish species. (2) The prey-capture kinematics of each invasive fish species varies across environmental temperatures. (3) The kinematic profiles of each species will vary across temperature regimes.

## 2. Materials and Methods

Four *P. volitans* collected from Sebastian Inlet and four *C. urophthalmus*, collected from Merritt Island, Florida were acclimated and trained for high-speed filming in the fish ecophysiology laboratory at Florida Institute of Technology. Each fish was housed in 38l filming tanks filled with 24ppt water, and then filmed at 20°C, 25°C and 30°C. Temperature was raised from 20°C to the higher filming temperatures at a rate of 1°C daily using a water heater. Each fish was filmed using a Red Lake High-Speed Motionscope 2000S camera with a shutter speed of 1/1000s at 250 frames s<sup>-1</sup> while feeding on live mosquito fish (*Gambusia holbrooki*). Feeding sessions were recorded every other day and fish were not fed in between recording sessions in order to keep their motivation high, enabling them to execute maximum prey-capture performance during filming. At least four feeding bouts were recorded for each fish. Four films were analyzed per fish at each of the three experimental temperatures using MaxTRAQ (Version 2.2.4.1 InnoVision Systems, Inc.).

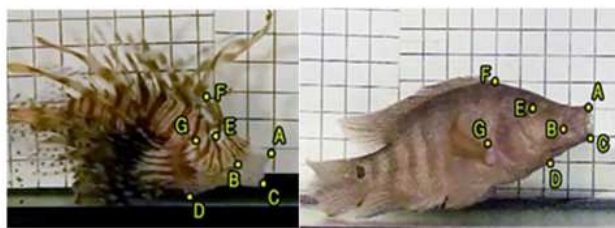
Each film was played back frame-by-frame to measure eight kinematic variables used to compare prey-capture kinematics between the two nonnative species and among three temperature regimes. The four displacement-kinematic variables are defined in Table 1 and Figure 1. Time to reach the maximum displacement-kinematic variables defined in Table 1 namely time (s) to maximum gape, hyoid depression, lower jaw angular displacement and cranial rotation were measured relative to the frame prior to mouth opening.

Table 1 shows definition and measurement of the excursion-kinematic variables used to examine variation in feeding performance between species and across temperatures. The timing variables for each of these maximum excursion variables were also calculated along with duration of feeding bout (s). Duration of feeding bout was defined as the time elapsed between the frame just before the initiation of mouth-opening and the frame at which the mouth fully closed after prey capture. These identified hotspots are illustrated in Figure 1.

**Table 1.** Description of the method of measuring the excursion-kinematic variables; refer to Figure 1 for the hotspots referenced in the descriptions.

Kinematic Variable	Description
Maximum Gape (mm)	Maximum distance measured from the anteriormost tip of the premaxilla to the anteriormost tip of the dentary when the mouth is open. Points (A) to (C).
Maximum Hyoid Depression (mm)	Maximum length measured from the center of the eye to the anteriormost point of the mouth at full depression. Points (E) to (D).
Maximum Lower Jaw Angular Displacement (degree)	Maximum rotation of the lower jaw measured by the line segments AB to BC.
Maximum Cranial Rotation (degree)	Maximum rotation of the neurocranium dorsally and posteriorly, measured by the angle formed from line segments AG to GF.

Figure 1 shows representative frames at maximum kinematic excursion from a film of each fish capturing prey. Each frame identifies the hotspots used to measure the excursion-kinematic variables identified in Table 1 for lionfish (left panel) and Mayan cichlid(right panel).



**Figure 1.** Representative frames for lionfish (left) and Mayan cichlid (right) showing the kinematic hotspots identified in Table 1.

To test the above-stated research hypotheses, the kinematic variables were log<sub>10</sub>-transformed and subjected to a 2-way Repeated Measures Multivariate Analysis of Covariance (MANCOVAR) with species and temperature as the main effects, the nine kinematic measurements as the dependent variables and fish standard length as the covariate. Previous studies on the kinematics of both species indicated that body size was correlated with kinematic variables, thus, an analysis of covariance was necessary to eliminate the confounding effects of body size on the results of the inter specific comparisons [35,36,57]. Kinematic profiles were produced from frame-by-frame analysis of the feeding films and recording the magnitude of the kinematic excursion at 3-millisecond intervals. Mean kinematic excursion at time intervals of the four fish per species was plotted against time, as shown in Figure 2.

### 3. Results

Regardless of temperature, once the prey was introduced into the filming tank, each of the experimental fishes aggressively suction-fed on the prey. Playing back the feeding films at a much slower rate than the 250 frames per second recording rate revealed some interesting behavioral

differences between the two species when they captured prey. Lionfish approached the prey slowly, but, employed an explosive suction-feeding technique to rapidly capture the prey. In some films, cavitation, which was visible as streaks of bubbles in the vicinity of the lionfish mouth upon prey capture, was evident [61]. In contrast, the Mayan cichlid swam toward the prey upon introduction and suction fed on it, as described by Young [57]. These behavioral differences are confirmed in the subsequent MANCOVAR comparing the mean values of the kinematic variables between the two invasive fishes (Table 2).

The MANCOVAR revealed that prey-capture kinematics varied between species ( $F_{8,136} = 5.545$ ;  $P = 0.000$ ), but, remained consistent across temperature ( $F_{15,136} = 1.280$ ;  $P = 0.218$ ) (Table 3). *Post-hoc* univariate hypothesis tests revealed that maximum gape, time to maximum hyoid depression, maximum cranial rotation and time to maximum cranial rotation differed between the two species (Table 4). Prey-capture kinematics is invariant across temperature in both species (Table 5).

Table 2 shows the Mean and Standard Error of the Mean (S.E.M.) of the nine kinematic variables used to examine variation in feeding kinematics between species and across environmental temperature regimes.

Table 3 shows the results of the Two-Way Repeated Measures Multivariate Analysis of Covariance (MANCOVAR) on the nine kinematic variables used to examine variation in feeding kinematics between species and across environmental temperature regimes.

Table 4 shows results of the Post-MANCOVAR Hypothesis Test to determine the relative contribution of species-effect to the variation of prey-capture kinematics between species and across environmental temperature regimes.

Table 5 shows the results of the Post-MANCOVAR Hypothesis Test to determine the relative contribution of temperature-effect to the variation of prey-capture kinematics between species and across environmental temperature regimes.

**Table 2.** Mean and Standard Error of the Mean (S.E.M.) of kinematic variables.

Kinematic Variable	20° C		25° C		30° C	
	M	Mean ± S.E.M.	M	Mean ± S.E.M.	M	Mean ± S.E.M.
Maximum Gape (mm)	M	10.28 ± 1.07	M	10.12 ± 1.07	M	8.83 ± 1.07
	L	13.24 ± 1.07	L	11.35 ± 1.07	L	12.39 ± 1.07
Time to Maximum Gape	M	10.12 ± 1.07	M	0.18 ± 1.17	M	0.17 ± 1.17

Kinematic Variable	20° C		25° C		30° C	
		Mean ± S.E.M.		Mean ± S.E.M.		Mean ± S.E.M.
(ms)	L	0.17 ± 1.17	L	0.14 ± 1.17	L	0.16 ± 1.17
Maximum Hyoid Depression (mm)	M	3.86 ± 1.11	M	3.72 ± 1.11	M	4.28 ± 1.11
Time to Maximum Hyoid Depression (ms)	L	4.70 ± 1.11	L	5.47 ± 1.11	L	5.21 ± 1.11
Maximum Cranial Roatation (degree)	M	0.39 ± 1.26	M	0.31 ± 1.26	M	0.22 ± 1.26
Time to Maximum Cranial Rotation (ms)	L	0.12 ± 1.26	L	0.10 ± 1.26	L	0.10 ± 1.26
Maximum Lower Jaw Angular Displacement (degree)	M	76.03 ± 1.04	M	76.21 ± 1.04	M	75.34 ± 1.04
Time to Lower Jaw Angular Displacement (ms)	L	97.05 ± 1.04	L	103.75 ± 1.04	L	91.62 ± 1.04
Feeding Duration (ms)	M	0.39 ± 1.22	M	0.27 ± 1.22	M	0.23 ± 1.22
Maximum Lower Jaw Angular Displacement (degree)	L	0.17 ± 1.22	L	0.15 ± 1.22	L	0.19 ± 1.22
Time to Lower Jaw Angular Displacement (ms)	M	174.98 ± 1.09	M	173.78 ± 1.09	M	175.79 ± 1.09
Feeding Duration (ms)	L	177.83 ± 1.09	L	140.60 ± 1.09	L	174.5 ± 1.09
Maximum Lower Jaw Angular Displacement (degree)	M	0.20 ± 1.19	M	0.21 ± 1.19	M	0.17 ± 1.19
Time to Lower Jaw Angular Displacement (ms)	L	0.25 ± 1.19	L	0.23 ± 1.19	L	0.18 ± 1.19
Feeding Duration (ms)	M	0.64 ± 1.15	M	0.52 ± 1.15	M	0.48 ± 1.15
Feeding Duration (ms)	L	0.59 ± 1.15	L	0.45 ± 1.15	L	0.48 ± 1.15

Table 3. Results of the Two-Way Repeated Measures Multivariate Analysis of Covariance (MANCOVAR).

Source	SS	df	Mean Squares	F-Ratio	p-Value
Kinematics Temperature	0.185	16	0.012	1.280	0.218
Kinematics Species	0.108	16	0.007	0.751	0.737
Kinematics Standard Length	0.363	8	0.045	5.034	0.000
Error	1.225	136	0.009		

Table 4. Results of the Post-MANCOVAR Hypothesis Test.

Post-hoc for Species effect					
Source	SS	df	Mean Squares	F-Ratio	p-Value
Maximum Gape (mm)	0.016	1	0.016	6.720	0.019
Error	0.040	17	0.002		
Time to Maximum Gape (ms)	0.009	1	0.009	0.747	0.399
Error	0.206	17	0.012		
Maximum Hyoid Depression (mm)	0.019	1	0.019	3.653	0.073
Error	0.091	17	0.005		
Time to Maximum Hyoid Depression (ms)	0.285	1	0.285	10.582	0.005
Error	0.458	17	0.027		
Maximum Cranial Rotation (degree)	0.018	1	0.018	23.31	0.000
Error	0.013	17	0.001		
Time to Maximum Cranial Rotation (ms)	0.073	1	0.073	3.736	0.070
Error	0.332	17	0.020		
Maximum Lower Jaw Angular Displacement (degree)	0.001	1	0.001	0.371	0.550
Error	0.057	17	0.003		
Time to Maximum Lower Jaw Angular Displacement (ms)	0.005	1	0.005	0.346	0.564
Error	0.259	17	0.015		
Duration of Feeding	0.002	1	0.002	0.182	0.675
Error	0.162	17	0.010		

Table 5. Results of the Post-MANCOVAR Hypothesis Test.

Post-hoc for Temperature effect					
Source	SS	df	Mean Squares	F-Ratio	p-Value
Maximum Gape (mm)	0.010	2	0.005	2.155	0.147
Error	0.040	17	0.002		
Time to Maximum Gape (ms)	0.037	2	0.018	1.1516	0.248
Error	0.206	17	0.012		
Maximum Hyoid Depression (mm)	0.008	2	0.004	0.78	0.474
Error	0.091	17	0.005		
Time to Maximum Hyoid Depression (ms)	0.097	2	0.049	1.808	0.194
Error	0.458	17	0.027		
Maximum Cranial Rotation (degree)	0.004	2	0.002	2.327	0.128
Error	0.013	17	0.001		
Time to Maximum Cranial Rotation (ms)	0.032	2	0.016	0.818	0.458
Error	0.332	17	0.020		

Post-hoc for Temperature effect						
Source	SS	df	Mean Squares	F-Ratio	p-Value	
Maximum Lower Jaw Angular Displacement (degree)	0.014	2	0.007	2.075	0.156	
Error	0.057	17	0.003			
Time to Maximum Lower Jaw Angular Displacement (ms)	0.067	2	0.033	2.185	0.143	
Error	0.259	17	0.015			
Duration of Feeding	0.060	2	0.030	3.15	0.069	
Error	0.162	17	0.010			

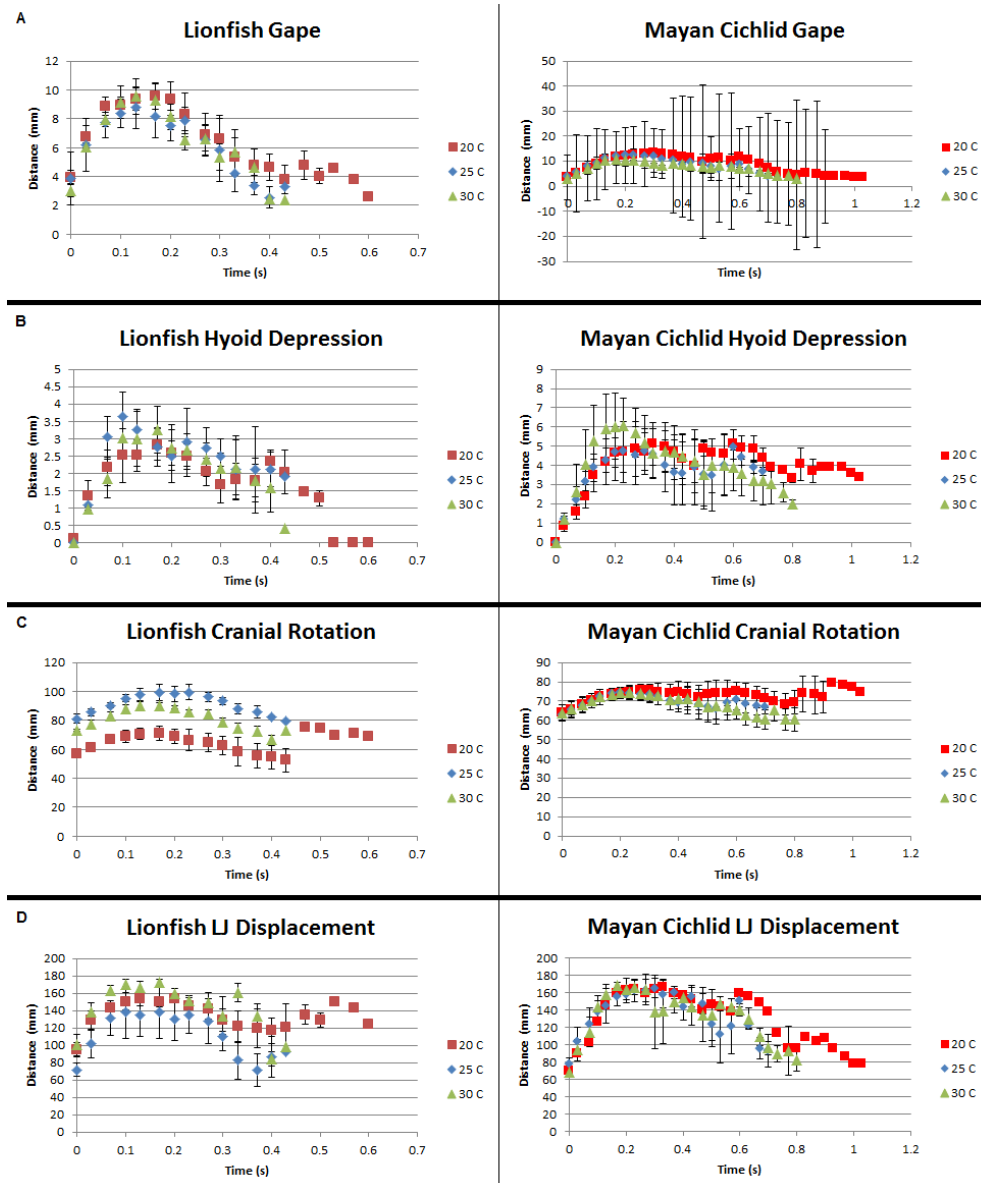


Figure 2. Kinematic profile comparing the time-course of each of the four kinematic-excursion variables in each species across environmental-temperature regimes.

Figure 2 shows that the time course of each kinematic-excursion variable (i.e., kinematic profile) remains consistent for all water-temperature settings in both lionfish and Mayan cichlid.

#### 4. Discussion

The urgent need to understand the consequences of the

interaction between climate change and invasive species phenomena for population dynamics and community structure of native flora and fauna benefits from empirical data that demonstrate how organismal performance is affected by environmental change. One of the predicted impacts of climate change on the biology and ecology of exotic species is the northerly (or southerly) spread of tropical-invasive species, facilitated by the warming of the

atmosphere and aquatic ecosystems in subtropical and temperate latitudes [62]. As poikilotherms, variations in the feeding performance and ecology of invasive fishes are expected to be consistent with predictions based on the known effects of temperature on the physiology and ecology of heterothermic, aquatic animals [63]. For example, the velocity of fin propulsion during swimming and mouth-opening during feeding, behaviors fueled by skeletal-muscle contraction and relaxation, are expected to double when ambient temperature is increased by 10°C. This is because at the physiological level of analysis, there is a twofold increase in the rate of muscular contraction and relaxation for every 10°C increase in temperature [18-23]. At the ecological level of analysis, the food habit of some temperate fishes, such as largemouth bass, *Micropterus salmoides*, and pumpkinseed sunfish, *Lepomis gibbosus*, change seasonally, consistent with the seasonal cooling and warming of lakes or rivers in temperate ecosystems [64-66].

The highlight of this study is the persistent lack of temperature effects on the magnitude of kinematic excursion (e.g., peak gape), speed of cranial movement (e.g., time to peak gape) and the time course of jaw movements (e.g., gape profile) in the two contrasting models of invasive species reported here. A similar pattern of invariant feeding kinematics across temperature regimes was seen in another Florida invasive species, the pike killifish, *Belonesox belizanus* [35]. In all of these invasive species, the interspecific variation in feeding kinematics was consistent with species-specific differences in prey-capture techniques employed to capture their primary food item. The pike killifish is a piscivorous specialist, with relatively long upper and lower jaws that are characteristic of ram-suction feeders [67,68]. The lionfish is an ambush predator, feeding primarily on fish prey [49]. The Mayan cichlid is a generalist predator, feeding on elusive fish and crustaceans, as well as non-elusive, relatively hard molluscs [57]. Notwithstanding this interspecific variation in feeding behavior, each species consistently utilized its optimal prey-capture kinematics in all environmental-temperature regimes. More interestingly, the temperature-independent feeding kinematics of these three Florida-invasive species is inconsistent with the findings of the only two other papers that reported the effects of temperature on feeding kinematics in fishes. The prey-capture kinematics in both Florida-native centrarchid fishes, bluegill *Lepomis microchirus* and largemouth bass *Micropterus salmoides* were affected by environmental-temperature change [29,30]. Among other feeding-kinematic variables that were affected by temperature, it took longer for fishes to reach peak gape in colder than in warmer temperatures [29,30]. Although not as high as predicted, the rate of gape change during prey-capture in these native fishes increased as water temperature dropped 10°C from ambient. This interesting contrast in the effects of temperature on feeding kinematics between invasive and native fishes in Florida inspires one to question, "Do

sympatric nonnative and native species respond differently to environmental-temperature change?"

Species that adapt to a wide range of environmental biotic and abiotic factors that are introduced into ecosystems beyond their native distributions establish invasive populations at a faster rate than those species with narrow environmental tolerance [69-72]. Two tropical species, the lionfish *P. volitans* and the Mayan cichlid *C. urophthalmus*, are among the most dominant nonnative fish-species in the state of Florida [53,59]. Both species tolerate a wide range of environmental temperature and salinity conditions [54,73-76]. In addition, within the range of prey that each species could capture using the species-specific prey-capture mechanism and technique described previously, both fishes have plastic food habits and are capable of consuming novel prey available in the invasive habitats [68]. Thus, these nonnative fishes are well adapted to locally available prey resources; they are voracious, highly competitive predators in their invaded ecosystem [42,46,51,52]. The ability of lionfish and Mayan cichlid to respond positively to the biological and physical conditions in their invaded ecosystems allows them to continually expand their nonnative range of distribution, especially in Florida, USA.

Global-climate change in general and global-temperature change in particular has important consequences for the performance of invasive species because of (1) the temperature-induced effects on physiological and mechanical processes [63,77]; (2) the likelihood that these physiological effects extend to whole-organism performance [e.g., 29,30]; and (3) the resilience of invasive species and their resistance of whole-organism performance to temperature change [35,36, this study]. These plausible avenues where the interplay between climate-change and invasive-species phenomena may be demonstrated, need further investigation and confirmation.

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