Invariant Feeding Kinematics of Two Trophically Distinct Nonnative Florida Fishes, *Belonesox belizanus* and *Cichlasoma urophthalmus* across Environmental Temperature Regimes

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Abstract

Nonnative fishes have the ability to adapt to environmental conditions in the invaded ecosystem and utilize resources that may have been absent in their native ecosystem. *Belonesox belizanus* and *Cichlasoma urophthalmus* are both nonnative fishes in Florida. Ecomorphological studies conclude that *C. urophthalmus* is a trophic generalist while *B. belizanus* is a trophic specialist. The current Florida distribution of these species indicates that *C. urophthalmus* spreads northerly into the colder regions of Florida at a faster rate than *B. belizanus*. Is it conceivable that this variation in rate of spread is due to differences in temperature response between these ecomorphologically distinct nonnative fishes? This study was designed to test the hypothesis that the prey-capture kinematics and behavior differ between *C. urophthalmus* and *B. belizanus* at a given temperature and across temperatures. Two-Way Repeated Measures Multivariate Analysis of Covariance (MANCOVAR) revealed that (1) at a given temperature, excursion and timing variables differed between species and (2) the kinematics of prey-capture did not vary across temperatures in both species. This interspecific comparison suggests that both species have the same temperature tolerance and that any difference in their rate of spread across Florida may be driven by factors other than species-specific physiological tolerance to temperature.

Keywords: *Cichlasoma urophthalmus*, *Belonesox belizanus*, invasive species, specialist, generalist

1. Introduction

The ecological impacts of nonnative fishes in invaded ecosystems are well documented: they spread diseases and carry pathogens (Weinstein et al., 1997; Britton, Davies, Brazier, & Pinder, 2006; Gozlan, St-Hilaire, Feist, Martin, & Kent, 2005), alter native-fish community structure (Crowder, 1984; Douglas, Marsh, & Minckley, 1994; Singh, Pathak, & Lakra, 2010), wrought changes in trophic dynamics (Mooney & Cleland, 2001; Perry, Lodge, & Feder, 2002; Sato et al., 2010), establish more tolerant hybrid populations (Miley, 1978; Ogutu-Ohwayo, 1990; Bacheler, Neal, & Noble, 2004), and reduce biodiversity, ultimately driving biological homogenization (McKinney & Lockwood, 1999; Rahel, 2007; Sato et al., 2010). In addition to the biological and ecological impacts of nonnative species, local and national economies have been negatively impacted by the proliferation of invasive species. For example, in the United States of America, the cost of nonnative species, largely from loss of revenue is estimated at over 120 billion US dollars annually (Pimentel, Zuniga, & Morrison, 2005). Knowledge of the potential ecological and economic consequences of species invasions continue to stimulate research on the underlying mechanisms that drive the spread of nonnative species in their invaded ecosystem.

One interesting facet of invasive-species research is the elucidation of the response of nonnative species to environmental temperature. This is particularly underscored by our continuing search for information that furthers our understanding of the adaptive response of populations to climate change (Davis & Shaw, 2001; Baker, McClanahan, & Glynn, 2004; Charmantier et al., 2008). The response of organisms to environmental temperature is rooted from its influence on physiological processes that alter functional performance. For example, it is well known that metabolic rate is directly proportional to environmental temperature (Cossins & Bowler, 1987; Clarke & Johnston, 1999; Gillooly, Brown, West, & Savage, 2001) and the contractile property of

skeletal muscle is altered by temperature (Rome & Sosnicki, 1990; Josephson, 1993; Watabe, 2002; Malek, Saiadi, Abraham, Grundy, & Gerhard, 2004). In fishes and other ectotherms, environmental temperature has profound effects on swimming (Rome, Swank, & Coughlin, 2000; Herbing, 2002; Lee et al., 2003; Green & Fisher, 2004) and feeding (Wintzer & Motta, 2004; DeVries & Wainwright, 2006) performance. As poikilotherms, individual fishes have a range of temperature that is optimal for their physiological performance, thus, environmental temperature is one of the most important abiotic factors that limit the distribution of fish populations (Shafland & Pestrak, 1982; Rome & Sosnicki, 1990; Wintzer & Motta, 2004; DeVries & Wainwright, 2006).

Most of what is known about the effects of temperature on the feeding kinematics of fishes is based on experiments that determined immediate responses to acute temperature change in their native range (Wintzer & Motta, 2004; DeVries & Wainwright, 2006). Wintzer and Motta, (2004) concluded that in bluegill (*Lepomis macrochirus*) subjected to a 6°C change in temperature within 48 hours, several timing variables including time to maximum gape and time to maximum lower jaw depression increased as water temperature decreased. Likewise, DeVries and Wainwright (2006) found that a 6-9°C change in temperature within an hour to ten hours caused the time to reach maximum gape in *Micropterus salmoides* increase with decreasing temperature. In this study, we determined for the first time, the effect of temperature on the prey-capture kinematics of nonnative fishes. In addition, the response of two nonnative fishes with contrasting food habits to temperature was investigated.

Pike killifish, *Belonesox belizanus* (Poeciliidae), a Mexican and Central American native species was introduced in south Florida in the late 1950s and has been identified as one of the most abundant nonnative fishes in Florida (Hubbs, 1936; Rosen & Bailey, 1963; Belshe, 1961; Miley, 1978; Anderson, 1980; Kerfoot, Lorenz, & Turingan, 2011). It is characterized as a specialist predator, with an oral-jaw apparatus well designed for piscivory. Pike killifish achieves a large gape formed by the elongated premaxilla and the mandible, lined with large unicuspid teeth (Greven & Brenner, 2008; Ferry-Graham, Hernandez, Gibb, & Pace, 2010). The ability of pike killifish to independently rotate its premaxilla posterodorsally, facilitated by the premaxillomandibular ligament and a twisting maxilla, further enhances gape (Ferry-Graham et al., 2010) (Figure 1).

Mayan cichlid, *Cichlasoma urophthalmus*, native to waters ranging from eastern Mexico to Nicaragua (Miller, 1966) manifests the traits of a typical invasive species, including tolerance to extreme variations in salinity (Martinez-Palacios, Ross, & Rosado-Vallado, 1990; Stauffer & Boltz, 1994; Schofield, Loftus, & Fontaine, 2009) and temperature (Marinez-Palacios & Ross, 1992; Stauffer & Boltz, 1994). In addition, gut content analysis revealed that *C. urophthalmus* has a generalist diet, feeding on detritus, plants, invertebrates and fish (Martinez-Palacios & Ross, 1988; Chávez-López, Peterson, Brown-Peterson, Morales-Gomez, & Franco-Lopez, 2005; Bergmann & Motta, 2005; Hellig, Kerschbaumer, Sefc, & Koblmüller, 2010). Like other species of the family Cichlidae, the Mayan cichlid has a generalized fish oral jaw mechanism for prey capture and well developed pharyngeal jaws for prey-processing (Hulsey, 2006).

Both pike killifish and Mayan cichlid have continued to spread northerly from their point of introduction in south Florida toward the colder regions of Florida (Belshe, 1961; Miley, 1978; Anderson, 1980; Kerfoot et al., 2011).The average annual temperature within the current distribution of both nonnative fishes ranges between 20°C and 30°C (http://www.nodc.noaa.gov/dsdt/cwtg/all.html). Preliminary experiments in the laboratory indicated that fishes exposed to temperature lower than 20°C did not eat. The inherent effects of temperature on the contractile properties of muscles that drive prey-capture kinematics and on the physical properties of water that affect predator and prey behaviors serve as the premise for testing two hypotheses: at a given temperature (20°C, 25°C & 30°C) the prey-capture kinematics differ between both nonnative fish species, and the prey-capture kinematics of each nonnative fish species vary across temperatures.

2. Materials and Methods

Four *B. belizanus*, collected from the Florida Everglades National Park 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 (for *C. urophthalmus*) and 0ppt (*B. belizanus*) 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 RedLake High-Speed Motionscope 2000S camera with a shutter speed of 1/1000s at 250 frames s[-1] while feeding on live mosquito fish (*Gambusia holbrooki)*, a natural prey for both species. Feeding sessions were recorded every other day and fish were not fed in between recording sessions. 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 (ms) to maximum gape, hyoid depression, and cranial rotation were measured relative to the frame prior to mouth opening.

Table 1. Kinematic variable 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.

Table 1 shows definition and measurement of the excursion-kinematic variables used to examine variation in feeding performance between species and across temperatures. Identified hotspots are illustrated in Figure 1.
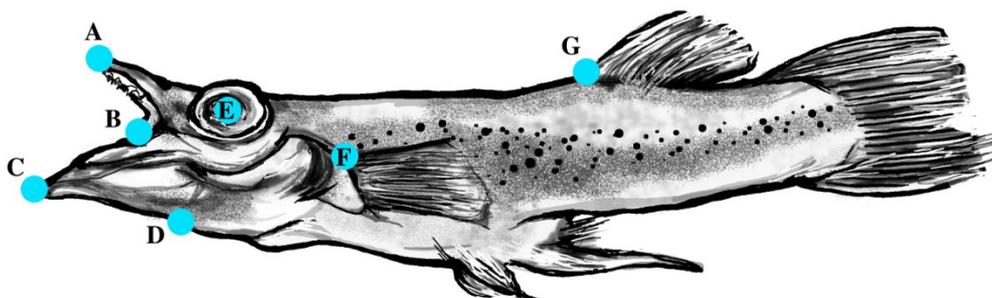

Figure 1. Diagram of a pike killifish, *B. belizanus*, showing the hotspots used in defining and measuring the excursion-kinematic variables identified in Table 1. Corresponding homologous hotspots were used in the Mayan cichlid, *C. urophthalmus*

To test the above-stated research hypotheses, the kinematic variables were $\log_{10}$-transformed and subjected to a 2-way Repeated Measures Multivariate Analysis of Covariance (MANCOVAR) with species and temperature as the main effects, the eight kinematic measurements as the dependent variables and fish standard length as the covariate.

3. Results

Both species of nonnative fishes fed aggressively at 20°C, 25°C, and 30°C. In general, *B. belizanus* approached the prey slowly and as soon as the prey was within 30 mm of the predator, *B. belizanus* lunged toward the prey, opened its mouth widely and snapped at the prey. In contrast, *C. urophthalmus* behaved more aggressively; as soon as the prey was introduced into the filming tank, *C. urophthalmus* rapidly swam toward the prey and suction-fed on the prey instantaneously. Initial examination of the kinematic variables indicates that *B. belizanus* achieves a greater maximum gape than that of *C. urophthalmus* (Table 2). In contrast, the lower jaw of *C. urophthalmus* rotated to a much higher angular displacement compared to that of *B. belizanus*. Time to reach these maximum kinematic values appear consistently across the three temperature treatments. The MANCOVAR revealed that prey-capture kinematics varied between species ($F_{1,64} = 7.32$; P = 0.009), but, remained consistent

across temperature ($F_{2,64}$ = 0.070; P = 0.933) (Table 3). Fish standard length had no confounding effect on kinematic performance ($F_{1,64}$ = 0.061; P = 0.328) (Table 3). Post-hoc univariate hypothesis test revealed that all of the kinematic variables differed between the two species (Table 4). Prey-capture kinematics in both species is invariant across temperature (Table 5).

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

Kinematic Variable		20° C Mean ± S.E.M.		25°C Mean ± S.E.M.		30°C Mean ± S.E.M.
Maximum Gape (mm)	P	17.16 ± 1.67	P	18.30 ± 2.32	P	17.20± 1.65
	M	14.84 ± 0.44	M	13.91 ± 0.29	M	11.83 ± 2.01
Time to Maximum Gape (ms)	P	14.33 ± 1.92	P	12.67 ± 0.39	P	27.00 ± 8.65
	M	33.56 ± 5.29	M	30.67 ± 1.84	M	26.22 ± 4.62
Maximum Hyoid Depression (mm)	P	5.035 ± 0.32	P	6.55 ± 0.96	P	5.28 ± 0.66
	M	4.10 ± 0.26	M	4.05 ± 0.18	M	3.68 ± 0.60
Time to Maximum Hyoid Depression (ms)	P	18.00 ± 2.28	P	17.89 ± 0.46	P	32.33 ± 8.95
	M	29.89 ± 4.24	M	43.22 ± 2.65	M	25.78 ± 3.48
Maximum Cranial Rotation (degree)	P	20.064 ± 4.08	P	16.94 ± 1.86	P	20.58 ± 1.70
	M	37.38 ± 2.01	M	42.05 ± 1.28	M	38.89 ± 0.46
Time to Maximum Cranial Rotation (ms)	P	16.67 ± 2.07	P	13.78 ± 1.59	P	32.83 ± 9.25
	M	5.33 ± 0.54	M	4.78 ± 0.64	M	4.83 ± 0.83
Maximum Lower Jaw Angular Displacement (degree)	P	83.91 ± 8.03	P	84.16 ± 2.92	P	84.92 ± 1.18
	M	171.52 ± 5.32	M	170. 68 ± 3.39	M	164.23 ± 7.12
Time to Lower Jaw Angular Displacement (ms)	P	14.33 ± 1.92	P	13.44 ± 0.56	P	26.83 ± 8.67
	M	29.78 ± 5.93	M	34.67 ± 0.48	M	25.39 ± 6.27

P = Pike killifish, *Belonesox belizanus*; M = Mayan cichlid, *Cichlasoma urophthalmus*.

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

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

Source of Variation	SS	df	Mean Squares	F-Ratio	p-Value
Species	0.46	1	0.46	7.32	0.009
Temperature	0.004	2	0.004	0.07	0.933
Standard Length (SL)	0.06	1	0.061	0.098	0.328
Error	0.062	64	0.062	-	-

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

Table 4. Results of the Post-MANCOVAR Hypothesis Test

Source	SS	df	Mean Squares	F-Ratio	p-Value
Maximum Gape (mm)	0.20	1	0.20	22.82	0.000
Error	0.57	64	0.009	-	-
Time to Maximum Gape (ms)	1.006	1	1.006	34.54	0.000
Error	1.86	64	0.029	-	-
Maximum Hyoid Depression (mm)	0.36	1	0.36	18.94	0.000
Error	1.20	64	0.019	-	-
Time to Maximum Hyoid Depression (ms)	0.42	1	0.42	17.64	0.000
Error	1.50	64	0.024	-	-
Maximum Cranial Rotation (degree)	1.64	1	1.64	155.98	0.000
Error	0.67	64	0.01	-	-
Time to Maximum Cranial Rotation (ms)	3.92	1	3.92	84.34	0.000
Error	2.98	64	0.046	-	-
Maximum Lower Jaw Angular Displacement (degree)	1.25	1	1.23	465.75	0.000
Error	0.17	64	0.003	-	-
Time to Maximum Lower Jaw Angular Displacement (ms)	0.80	1	0.80	24.089	0.000
Error	2.123	64	0.033	-	-

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 *B. belizanus* and *C. urophthalmus*.

Table 5. Results of the Post-MANCOVAR Hypothesis Test

Source	SS	df	Mean Squares	F-Ratio	p-Value
Maximum Gape (mm)	0.058	2	0.029	3.25	0.045
Error	0.57	64	0.009	-	-
Time to Maximum Gape (ms)	0.028	2	0.014	0.48	0.622
Error	1.86	64	0.029	-	-
Maximum Hyoid Depression (mm)	0.06	2	0.032	1.72	0.187
Error	1.20	64	0.019	-	-
Time to Maximum Hyoid Depression (ms)	0.10	2	0.050	2.12	0.129
Error	1.52	64	0.024	-	-
Maximum Cranial Rotation (degree)	0.036	2	0.018	1.72	0.187
Error	0.67	64	0.010	-	-
Time to Maximum Cranial Rotation (ms)	0.30	2	0.15	3.28	0.044
Error	2.98	64	0.046	-	-
Maximum Lower Jaw Angular Displacement (degree)	0.00	2	0.00	0.074	0.929
Error	0.17	64	0.003	-	-
Time to Maximum Lower Jaw Angular Displacement (ms)	0.019	2	0.01	0.29	0.750
Error	2.12	64	0.033	-	-

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 *B. belizanus* and *C. urophthalmus* across environmental temperature regimes.

4. Discussion

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 (Arthington & Mitchell, 1986; di Castri, 1990; Sakai et al., 2001; Lee, 2002). Two tropical species, the pike killifish, *B. belizanus,* and the Mayan cichlid, *C. urophthalmus*, introduced into south Florida, USA in the 1950s and 1980s, respectively, are among the most dominant nonnative fish-species in the state (Belshe, 1961; Miley, 1978; Anderson, 1980; Kerfoot et al., 2011). Both species tolerate a wide range of environmental temperature (9-30°C for pike killifish and 15-39°C for Mayan cichlid) and salinity (0-35ppt for pike killifish and 0->37ppt for Mayan cichlid) (Martinez-Palacios & Ross, 1992; Stauffer & Boltz, 1994; Chávez-López et al., 2005; Paperno, Ruiz-Carus, Krebs, & McIvor, 2008; Schofield et al., 2009; Kerfoot et al., 2011; Kerfoot, 2012). Despite their contrasting feeding functional morphology and prey-capture behavior, there is an overlap in the species and size composition of the prey they consume (Harms, 2011; Young, 2011). Prey selectivity is dependent on the relative proportion of prey organisms in their environment (Harms & Turingan, 2012). Thus, these nonnative fishes are well adapted to locally available prey resources; they are voracious, highly competitive predators in their invaded ecosystem (Turner & Snelson Jr., 1984; Chávez-López et al., 2005; Bergmann & Motta, 2005; Greven & Brenner, 2008; Kerfoot et al., 2011; Kerfoot, 2012; Harms & Turingan, 2012). The ability of pike killifish 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.

What is striking about the *B. belizanus* and *C. urophthalmus* is their equally successful invasion of Florida waters, yet each represent a different trophic niche as defined by their feeding functional morphology and behavior: *B. belizanus* has a specialist, piscivorous feeding mechanism whereas *C. urophthalmus* has the generalist-teleost feeding mechanism (Bergmann & Motta, 2005; Hellig et al., 2010; Ferry-Graham et al., 2010). *B. belizanus* has evolved a unique feeding mechanism that is equipped with long oral jaws that can be opened widely to achieve a relatively large gape during prey-capture. It is also hypothesized that achieving a large gape is further facilitated by the presence of a premaxillomandibular ligament and a unique joint that allows postero-dorsal rotation of the premaxilla (Ferry-Graham et al., 2002; Porter & Motta, 2004; Greven & Brenner, 2008; Grubich, Rice, & Westneat, 2008; Ferry-Graham et al., 2010). However, recent laboratory experiments concluded that *B. belizanus* was capable of feeding on non-fish prey, such as live ghost shrimp using its piscivorous-feeding mechanism and a stereotypical feeding repertoire (Harms & Turingan, 2012). The relatively wide diet breadth of *C. urophthalmus* is consistent with having a generalized teleost feeding mechanism (Bergmann & Motta, 2005; Young, 2011). It is conceivable that the interspecific variation in prey-capture kinematics between these two nonnative fishes is driven by the difference in the design of the feeding mechanism and behavior between species.

Having two model nonnative fish species with contrasting feeding mechanisms provides an opportunity to explore the generality of conclusions drawn from studies that investigate the effects of temperature on the performance of whole organisms, particularly aquatic poikilotherms such as fishes. Do temperature-induced effects on performance manifest themselves equally between generalist- and specialist-feeding nonnative fishes? Comparing consequences of temperature on performance between specialist- and generalist-nonnative species is important because it helps elucidate our understanding of how functional specialists keep up with generalists in performing challenging tasks such as capturing novel prey in invaded ecosystems. In addition, knowledge of how specialists and generalists respond to environmental temperature gives conservation biologists and ecologists the ability to understand important ecological and biological processes including range and rate of expansion of nonnative species in their invaded ecosystem.

Environmental temperature has consequent implications for aquatic-organismal performance because of temperature-induced effects on physiological and mechanical processes (Vogel, 1994; Hachachka & Somero, 2002). For prey-capture in fishes the physiological effects of temperature are exhibited in the observed variation in the values of performance metrics (e. g., maximum gape, time to reach maximum gape and other kinematic variables) across different temperature treatments. Kinematics is largely driven by muscles, and it is well known that contractile properties of muscles are influenced by ambient temperature (Josephson, 1993; Kingsolver & Huey, 1998; Johnston & Temple, 2002). The mechanical effect of ambient temperature on organismal performance is rooted from the inherent effects of temperature on the dynamic viscosity of water (Vogel, 1994). In general, water viscosity increases with decreasing temperature; consequent drag on the feeding mechanism during prey-capture is also altered (Emlet & Strathmann, 1985).

To date, there are two studies that addressed the effects of temperature on the feeding kinematics of teleost fishes

(Wintzer & Motta, 2004; DeVries & Wainwright, 2006). In both studies, centrachid fishes *Lepomis microchirus* and *Micropterus salmoides* responded similarly to acute changes in environmental temperature. For example, time to reach maximum gape increased as the environmental temperature decreased (Wintzer & Motta, 2004; DeVries & Wainwright, 2006). In this study, regardless of the contrasting feeding mechanism of *B. belizanus* and *C. urophthalmus*, the kinematics of prey-capture in both nonnative fishes was largely unaffected by environmental temperature. We postulate that the disparate responses of the prey-capture kinematics to environmental temperature between the Wintzer and Motta (2004) as well as the DeVries and Wainwright (2006) studies and this study is a consequence of the temporal course of the temperature change. In the former studies, environmental temperature was altered acutely, by up to 6-9°C within an hour to ten hours, whereas in this study, temperature was raised from 20°C to 30°C at a rate of 1°C daily. In rapid or acute changes in temperature, such as those demonstrated by the former studies, fish may have not been given enough time to fully acclimate its physiological functions, thus the whole-organism-performance consequence of the environmental-temperature-induced physiological response may have been more severe. Whole-organism performance is unaltered by subtle changes in temperature (i.e., 1°C within 24 hours) even if the difference between the extreme ranges of temperature (e.g., 10°C difference between low and high temperature regimes) is considered high among physiologists (i.e., Q_{10} values). Therefore, it is imperative to consider the rate of change in temperature when quantifying the effects of environmental temperature on organismal performance. We propose that based on the invariant pattern of feeding kinematics across environmental temperature regimes observed in this study, nonnative fishes could better adapt to chronic changes in temperature.

Acknowledgments

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