On the mismatch between salinity tolerance and preference for an invasive fish:
a case for incorporating behavioral data into niche modeling

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Abstract

Many estuarine species are euryhaline, tolerating a broad range of salinity conditions, such that data on their salinity tolerances can provide little information about a species' distribution and abundance. This is particularly true for nonnative species, known to be tolerant of a broad range of conditions. Instead, data on a species' abiotic or habitat preferences may improve prediction of a nonnative species' potential range, if introduced or if undergoing range expansion. At minimum, information about abiotic preferences may be telling of areas where the probability of nonnative occurrence or density may be higher, and if present, of areas that confer higher fitness. In this study, the salinity preference of the nonnative African jewelfish (*Hemichromis letourneuxi*), a recent and rapidly-expanding invader in the Florida Everglades, was quantified in laboratory trials. Despite the broad salinity tolerance of African jewelfish (up to 50), trials show a strong preference for freshwater conditions. When presented with a salinity gradient, over 50% of observations in timed videotaped trials were collected in the lowest salinity chamber (0.3), suggesting an affinity for low salinity, which was unaffected by the sex or body condition of study fish. Fish clearly avoided mid and full salinity conditions. Findings suggest that their distribution may be considerably more limited, and that the species may have higher invasion success in oligohaline habitats, than predicted based on their salinity tolerance. Results have important implications for nonnative species niche modeling, and argue for better integration of behavior along with physiological responses when examining species distributions in dynamic environments.

Keywords: physiological limits; salinity preference; fish; invasive species; behavior; species distribution

1. Introduction

Salinity is a primary determinant of ecological processes in coastal systems. In fishes, salinity affects physiology and individual performance (Boeuf and Payan, 2001), species distributions (Lorenz and Serafy, 2006), the strength of species interactions (Alcaraz et al., 2008), and thus the structure and functioning of estuarine communities (Barletta et al., 2005). Yet many estuarine species, both resident and transient taxa, are euryhaline, tolerating a broad range of salinity conditions (Nordlie, 2006), such that data on their salinity tolerances can provide little information about a species' actual or potential distribution or abundance. This is particularly true for nonnative fishes, known to have broad tolerances (Kolar and Lodge, 2001), including salinity (Bringolf et al., 2005; Lorenz and O'Connell, 2008; Schofield et al., 2011).

A growing area of research on nonnative species focuses on forecasting their potential range once they invade (e.g., Lowe et al., 2012). This involves ecological niche models (ENMs) where distributional data from a species' native range are used to model and delineate suitable habitats in the invaded range based on climatic factors and the species' physiological requirements (Jeschke and Strayer, 2008; Venette et al., 2010). Yet given the broad tolerances of nonnative species, ENMs based solely on abiotic features and/or climate could result in an overestimation of the predicted invaded range (e.g., Guisan et al. 2014). One venue for improvement is the refinement of information on ecophysiological tolerances by incorporating knowledge of a species' abiotic or habitat preferences. By preference, we refer to an organism's disproportional use of certain resources, habitats or abiotic conditions over others (Johnson, 1980). A species may tolerate certain broad habitat or abiotic conditions such as salinity, but may prefer a subset of these. For instance, goldspotted killifish *Floridichthys carpio*, a resident

estuarine species, can experimentally tolerate salinities as high as 90, and is known to occur at salinities ranging from 0 to >50 (Nordlie, 2006), but when presented with a salinity gradient, prefers intermediate salinities (10-30; McManus et al., 2014). Preferences for certain abiotic conditions constitute then behavioral mechanisms that can keep animals within viable or optimal conditions, and allow them to avoid adverse ones (Curtis and McGaw, 2012).

In this study, the salinity preference of the nonnative African jewelfish, *Hemichromis letourneuxi* was quantified. African jewelfish is currently the most abundant nonnative fish in Everglades National Park (ENP; Kline et al., 2014; Langston et al., 2010; Lopez et al., 2012). The species is native to northern Africa, where it is common in rivers, floodplains and lakes, and known to occur in brackish coastal areas (Bailey, 1994; Lamboj, 2004; Loiselle, 2000). African jewelfish is the most widespread of the genus *Hemichromis*, and thus tolerant of broad abiotic and habitat conditions (Loiselle, 2000; Lowe-McConnell, 1991; Schofield et al., 2009). Laboratory trials show that jewelfish has 100% survival when exposed to progressively increasing salinities as high as 50, and when exposed to acute salinities (i.e., abrupt salinity changes), it has 100% survival at salinities as high as 20 (Langston et al., 2010). In the Everglades, African jewelfish has been spreading from freshwater marshes into the mangrove zone (Lopez et al., 2012), and has been collected at maximum salinities of 4 (Rehage and Lorenz unpub. data), but the extent to which this species will become a dominant invader in coastal habitats remains unknown. Elsewhere in southern Florida, the species has been collected at salinities as high as 28 - 31.5 (Idelberger, 2011; Langston et al., 2010).

The following questions were tackled in this study: (1) When given a gradient of salinity choices, what salinities does African jewelfish prefer? and (2) Is salinity preference influenced by body condition and sex? Our objective was to assess whether Everglades habitats of certain

salinity ranges have a higher potential for invasion. The salinity preference of African jewelfish was tested by tracking the behavior of individual fish exposed to a salinity gradient (0 to 100% saltwater) in an experimental setting. As seen in previous preference studies, we hypothesized that African jewelfish would prefer salinity conditions that were significantly narrower and lower than its broad tolerance range (McManus et al., 2014; Serrano et al., 2010).

2. Material and Methods

2.1 Laboratory trials

To examine the salinity preference of African jewelfish, paired laboratory trials were conducted on individual, wild African jewelfish (standard length = 44.8 ± 0.7 mm, wet weight = 2.98 ± 0.16 g, $n = 60$). Jewelfish were collected from a shallow freshwater, man-made lake at Fairchild Tropical Botanic Garden, Miami, Florida, using unbaited minnow traps on March 16, 2010. The African jewelfish is abundant in freshwater habitats throughout South Florida, but found at low abundances in the invasion front in mangrove habitats (Rehage and Lorenz unpub. data). Because the directionality of the invasion in the Everglades is from freshwater habitats to estuarine mangroves (Lopez et al., 2012), fish from freshwater environments were used in trials. Salinity conditions at the site of collection were fresh, even during the peak of the dry season (Feb-May salinities: 0.63 ± 0.0007 SE, range = 0.58 - 0.70, $n = 1,151$). A deployable YSI[®] recorded salinity conditions every 30 min for 9-day periods monthly between February and May 2010.

Trials were conducted over a 15-day period between March 29 and April 19, 2010. On each trial day, salinity preferences were compared between two treatments: (1) a salinity gradient and (2) a freshwater control, with 2 replicates per day (2 treatments x 2 replicates x 15 days = 60

fish tested). Trials lasted 7.5 hrs and were conducted between 11 am and 8 pm. Jewelfish were not fed during observations. Prior to trials, fish were housed in 795 L freshwater outdoor tanks, and fed a combination of live prey (Eastern mosquitofish, *Gambusia holbrooki*), fish food flakes, and frozen bloodworms *ad libitum*.

Trials were conducted in 4, 207.5-L Staalnd tanks that use 5 U-shaped chambers to create a static salinity gradient (Fig. 1; Staalnd, 1969). The static salinity gradient forms as a result of differential density layering, and is stable for several days (Bos and Thiel, 2006; Curtis and McGaw, 2012; McManus et al., 2014). A salinity gradient was established in two tanks (hereafter gradient treatment), while two tanks were kept at 100% freshwater (hereafter freshwater treatment). In the gradient treatment, we obtained a full salinity gradient across the five chambers. By using a full salinity gradient, we could gain insight into whether the entire saline environment is equally vulnerable to invasion or certain salinity conditions may be at greater risk. Mean salinities ($\pm$ SE) measured at the start of trials were 0.3 ($\pm$ 0.03), 10.6 ($\pm$ 0.15), 18.5 ($\pm$ 0.29), 26.4 ($\pm$ 0.40), and 36.0 ($\pm$ 0.21) for chambers 1-5 respectively. Salinities increased slightly when checked 24 hr later, by an average of 1.2, 0.8, 0.5, and 1.4 in chambers 1 to 4, and decreased by 0.04 in chamber 5. Mean salinity in the freshwater treatment tanks was 0.2 ($\pm$ 0.004 SE).

Each day at the beginning of trials, freshwater tanks were filled with dechlorinated tap water, and gradient tanks were filled by combining fresh and saltwater to obtain the desired chamber salinity. The entire volume of tanks was replaced, and they were cleaned before each trial day. Saltwater was prepared in a large tank by mixing dechlorinated tap water with Instant Ocean[®] salt until reaching a salinity of 35. Removable plastic partitions placed between chambers prevented water from mixing prior to the start of trials. Salinity, dissolved oxygen, and

temperature were measured with a YSI® multimeter in each chamber and tank prior to the start of trial and 24 hours later. Temperature and dissolved oxygen conditions over the 60 trials averaged 23.4° C ($\pm$ 0.09 SE, n = 260), and 2.8 mg/L ($\pm$ 0.05 SE, n = 260) respectively.

At the beginning of trials, a randomly selected fish was placed in chamber 1 of each of the four tanks (Fig. 1), and allowed to acclimate for 15 minutes (Curtis and McGaw, 2012), before partitions were removed and trials were started. Our choice of introducing fish in the lowest salinity chamber is consistent with previous studies that place fish in salinities experienced in the field at the onset of preference trials (McManus et al., 2014; Serrano et al., 2010). This design also matches the directionality of the current range expansion (from freshwater to higher salinity coastal areas), because a major motivation for this study is to gain insight into which habitats and salinity regimes will be most vulnerable to invasion. The location of fish was videotaped with two Sony DCR-SX41 digital video cameras positioned above tanks for a full top view; each camera filming a tank pair (one tank per treatment). Videos were analyzed using point sampling (Martin and Bateson, 2007) to determine the location of fish in each chamber at 5 min into trials, and every 30 min thereafter up to the full 430 minutes of trial time (n = 16 observations per trial, Fig. 2A, B). At the end of trials, fish were euthanized with an overdose of MS-222, measured (standard length), weighed, and dissected for sex determination.

2.2 Statistical analyses

To determine the salinity preference of African jewelfish, we first compared the overall frequency of chamber use (total number of observations per chamber) across the two treatments with a Chi-square test. We then calculated the average chamber use of each fish weighted by the number of observations per chamber (i.e., weighted mean chamber use; Curtis and McGaw,

2012). We compared these weighted means (log-transformed to meet parametric assumptions) between treatments with an ANCOVA (analysis of covariance) that also tested for the effects of four covariates of interest, the sex and body condition of the fish tested, and the temperature and dissolved oxygen conditions measured at the beginning of trials. Body condition provides an overall index of fish health and consists of the ratio of body weight to length cubed (Murphy and Willis, 1996). Body condition has been shown to vary across the invaded range of African jewelfish in the Everglades (Lopez et al., 2012). We calculated the amount of movement during trials by tabulating the number of times fish moved between sequential observations (1 if moved, 0 if no movement and taking the sum them for the 16 observations). We compared these chamber movements between treatments with a Kruskal-Wallis test. To examine variation in chamber use on a chamber by chamber basis, we used Kruskal-Wallis tests to compare the proportion of observations in each chamber across treatments (Bos and Thiel, 2006; McManus et al., 2014). All analyses were performed using SYSTAT[®] 13.

3. Results

Observations conducted every 30 min showed that the African jewelfish was highly mobile in the experimental tanks, thoroughly sampling the five chambers in both treatments (Fig. 2A, B). As predicted, overall chamber use differed between treatments (Chi-square = 141.0, df = 4, $p = 0.0001$). For instance, 22% of all observations were in chamber 1 in the freshwater treatment, while 54% of observations were in chamber 1 in the salinity gradient. In contrast, 14% of observations in the freshwater treatment were in chamber 5, relative to only 1% for the salinity gradient. The movement of jewelfish between chambers did not differ between treatments ($H = 0.543$, $df = 1$, $p = 0.461$). Across treatments and out of the 15 possible chamber switches, fish made an average of 8 chamber movements over total trial duration (Fig. 2C).

Despite similar movements between chambers, African jewelfish varied in their distribution in tanks, exhibiting a significantly lower weighted mean chamber use in the salinity gradient treatment (Table 1). Jewelfish spent more time in the lower chambers in the salinity gradient than in the freshwater treatment (Fig. 3A). Chamber use, however, was unrelated to the body condition and sex of study fish. Similarly, water temperature and dissolved oxygen conditions during trials were unrelated to weighted mean chamber use (Table 1).

On a chamber by chamber basis, Kruskal-Wallis tests indicated a higher use (i.e., preference) of the lowest salinity chamber, and a lower use (i.e., avoidance) of the higher salinity end of the tank relative to the freshwater tank (Fig. 3B). Across trials, 53.5% of observations in the salinity gradient treatment were in the lowest salinity chamber 1 (0.3) relative to 21.8% in the freshwater treatment ($p = 0.0001$). We noted avoidance of the mid and full salinity conditions in chambers 3 and 5 (18.5 and 36.0 respectively, $p < 0.008$). Only 1.3% of observations were in chamber 5 and 13.1% of observations in chamber 3 in the salinity treatment (relative to 13.5% and 28.3% respectively in freshwater tanks). No treatment differences were detected between chambers 2 and 4 ($p > 0.788$).

4. Discussion

Efforts to forecast the potential distribution of nonnative species typically rely on information on physiological tolerances (Langston et al., 2010; Lowe et al., 2012). However, data on a nonnative species' abiotic and/or habitat preferences may provide additional resolution on which habitats have higher suitability and may be at greater risk of invasion. Results from our behavioral trials show that the nonnative African jewelfish prefers a much narrower and lower salinity range than its lethal limit (50; Langston et al., 2010). When exposed to a full salinity

gradient and despite sampling the gradient extensively, African jewelfish showed a consistent preference for the lowest salinity available (0.3), and a clear avoidance of salinities of 18.5 and above. While the species has been detected at salinities above 28 (Idelberger, 2011; Langston et al., 2010), it is not known if the species is established (i.e., reproductive populations) at those higher salinities, nor if individuals collected from higher salinity environments differ in salinity preferences relative to those collected from low salinity environments used in this study. Our results align with the abrupt transfer results of Langston et al. (2010), where mortality was detected when jewelfish were transferred directly from 0 to 20 salinity. Collectively, these findings suggest that (1) the species may experience significant physiological stress above 20, (2) its distribution in the coastal Everglades and other estuarine regions could be more limited than expected based solely on its broad salinity tolerance, and (3) African jewelfish may achieve higher invasion success (i.e., greater abundance and invaded range), and thus have a higher potential for impact on native species and invaded communities at low salinities.

Preference could be an important driver of habitat segregation and niche partitioning among euryhaline species (Bucking et al., 2012). Studies of experimentally-determined salinity preferences are limited, but consistently show that organisms prefer narrower salinity ranges than their known physiological tolerances, in agreement with this study. In our trials, jewelfish avoided chambers 3 and 5 in the salinity gradient treatment corresponding to mid and full salinities. Use of chamber 4 in the salinity gradient treatment was also low, but not significantly different from the control. For fishes, Serrano et al. (2010) showed that gray snapper (*Lutjanus griseus*), a common reef-dependent fish, prefers intermediate salinities (9-23), although they are known to occur in salinities ranging from 0-67. For invertebrates, Curtis and McGaw (2012)

demonstrated that Dungeness crabs (*Cancer magister*) cannot tolerate salinities below 12, and prefer salinities above 32.

Abiotic preferences measured in this and other studies reflect physiological optima related to the energetics of osmoregulation (e.g., Bucking et al., 2012). Salinity can affect energy consumption as fish allocate energy to osmoregulation (or ionoregulation), in order to maintain uniform plasma ion concentrations despite experiencing salinity fluctuations (Boeuf and Payan, 2001; Plaut, 2000). Osmoregulation can be energetically expensive, consuming between 10 to > 50% of the total energy budget of fish (Boeuf and Payan, 2001). Physiologically, the general expectation is that energy consumption (metabolic rate) is minimized at environmental salinities that are isosmotic to blood (9-12; Boeuf and Payan, 2001). We would then expect fish to prefer these isosmotic conditions (e.g., McManus et al., 2014), where metabolic costs are minimized and energy savings can be diverted to optimizing growth and reproduction (Boeuf and Payan, 2001; Plaut, 2000). African jewelfish do not fit this general expectation, and instead prefer lower than isosmotic conditions. Preference for non-isosmotic values has been shown in previous work (Bucking et al., 2012; Serrano et al., 2010), which indicates that preference is affected by other biotic and abiotic factors than solely physiological optimization. Further, independently of affecting osmoregulatory energy expenditure, salinity can directly influence swimming behavior, food consumption, digestion and absorption (Boeuf and Payan, 2001), which could influence preference. Incongruence between physiological optimization and salinity preference could also relate to ontogenetic shifts as organisms switch from optimizing growth and survival to optimizing conditions for reproduction (Schofield et al., 2009; Serrano et al., 2010), and migration (Bos and Thiel, 2006; Poletto et al., 2013).

One of the key questions motivating the present research was, will African jewelfish become a dominant invader of the coastal Everglades? In the southern areas of Everglades, shallow vegetated freshwater wetlands transition to extensive tidal mangrove forests (up to 15 km wide and over 60,000 ha), which dominate the landscape along the southwest Florida coast (Smith et al., 1994). Nonnative fishes account for 5% to 12% of fish in mangrove communities, with Mayan cichlids (*Cichlasoma urophthalmus*) being the dominant invader in this habitat (Kline et al., 2014). Similar to African jewelfish, Mayan cichlids are tolerant of a broad range of salinities (up to 37; Stauffer and Boltz, 1984), but are most often found at oligohaline conditions in the Everglades (Lorenz and Serafy, 2006). Our results indicate that given the preference of African jewelfish for low salinity conditions, and the known occurrence of Mayan cichlids at low salinities, habitats currently invaded by Mayan cichlids may also be highly suitable to African jewelfish. We predict these oligohaline habitats to become more invaded under jewelfish range expansion.

Salinities can fluctuate dramatically in estuaries, including in the coastal Everglades, at multiple spatial and temporal scales. This natural variation can be exacerbated by drainage and impoundment upstream and/or by water management, which can shift long-term salinity regimes, as well as cause sudden, physiologically-stressful salinity changes (Davis et al., 2005; Lorenz and Serafy, 2006; Serafy et al., 1997). Under these conditions, species with broad salinity tolerances may be favored. Since the salinity tolerances of South Florida nonnative fishes are broader than those of many native wetland fishes (Schofield and Nico, 2009), the currently altered hydrological regime of the Everglades could favor nonnative fishes in coastal areas. If true, ongoing efforts to restore the Everglades by increasing inflows into the southern part of the ecosystem and restore the natural seasonality of sheet flow (Sklar et al., 2005) should counteract

this potential advantage of nonnatives. At the same time, restoration in the mangrove zone aims to increase the pooling of freshwater at the ecotone, resulting in a wider and seasonally-extended oligohaline zone (Davis et al., 2005). Given that African jewelfish prefers low salinity, an expansion of oligohaline condition could increase the availability of preferred habitat, and potentially for other nonnatives (e.g., Mayan cichlids). Additional research is needed to assess salinity preferences of other fishes in the system, both nonnative and native (e.g., McManus et al., 2014; Serrano et al., 2010), and to link these preferences to field distributions, and thus better understand how fish communities will respond to hydrological restoration.

Our work has important implications for niche modeling. There is a pressing need to forecast species distributions in response to rapid global change, including invasions (Guisan et al., 2014). Yet, ENMs are often criticized because they provide poor estimates of a species' niche space and its underlying biology (Jeschke and Strayer, 2008; Venette et al., 2010). For instance, ENMs typically ignore biotic interactions and the effects of dispersal limitation (Jeschke and Strayer, 2008), although these are known to improve model fit (e.g., Gonzales-Salazar et al., 2013). We propose that habitat and/or abiotic preference data could contribute to the improvement of ENMs. We hypothesize species to occupy a subset of suitable areas (i.e., realized niche), and preferred habitats or abiotic conditions to occur in a subset of the occupied areas (Fig. 4). Although climatic factors and physiological tolerances may shape the boundaries of a species' distribution (lightest grey shading in Fig. 4), preference data could, at minimum, allow us to identify core areas within these boundaries (black shading in Fig. 4). In these core areas, the probability of occurrence should be highest, and if present, the invading species should achieve the highest individual and population fitness (e.g., abundance), providing a finer scale of

resolution at which to evaluate invasion risk and impact, and pinpointing priority areas to be targeted by management.

4.1 Conclusions

Overall, these findings emphasize the value of considering the behavior of individuals when aiming to better understand species distributional patterns. Along with physiological adjustments, behavioral ones are an integral component of how species respond to dynamic environments. Fish can use fine scale movement to compensate for physiological imbalances, integrating behavior and physiology (Bucking et al., 2012; Poletto et al., 2013). However, this vital link between physiology and behavior is largely ignored in current species distribution modeling, and thus we argue for incorporation of preference data, in addition to information on ecophysiological constraints, into the forecasting of nonnative species distributions. Information on species' abiotic and/or habitat preferences, independent of distributional data, is also of value in altered systems where present environmental regimes may be vastly different from natural ones. Here, resource management aims to better understand how species respond to natural abiotic gradients, which may be absent in the altered system. Preference data could prove useful when setting restoration targets and managing abiotic gradients to more closely resemble natural regimes (McManus et al., 2014; Polleto et al., 2013; Serrano et al., 2010).

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421

Figure Captions

Fig. 1. Schematic of a Staaland tank used to measure the salinity preference of African jewelfish. Numbers correspond to the five U-shaped chambers that in the salinity gradient treatment hold increasing salinities: 0.3, 10.6, 18.5, 26.4, and 36 in chambers 1-5 respectively. Fish are added to chamber 1 at the beginning of trials.

Fig. 2. Locations of each African jewelfish ($n = 60$ fish) across the 450 min of trial time and across the 5 tank chambers in A- the freshwater control, and B- salinity gradient treatments. Lines track the location of each fish across chambers at observations conducted every 30 min. (16 total). Bold lines show one track selected at random from each treatment, and show that fish are active and sample multiple chambers over trial time. C- Mean number of movements across chambers in both treatments over trial time (± 1 SE).

Fig. 3. A-Mean weighted chamber use (± 1 SE) by African jewelfish, and B- Mean proportion of observations (± 1 SE) in each chamber across the freshwater and salinity gradient treatments ($n = 30$ fish per treatment). Asterisks denote statistical differences at $\alpha \leq 0.05$.

Fig. 4. Conceptual diagram of the relationship among preference and tolerance for a particular habitat or abiotic variable and a species' field distribution. Shades of color indicate areas of preferred conditions (black), of species occurrence (dark grey), and where conditions are suitable (tolerance, light grey). A species occurs in a subset of suitable habitat where it can tolerate habitat and/or abiotic conditions. Preferred habitat or abiotic conditions occur in a subset of the area occupied by the species. Species performance is expected to be highest in core, preferred habitat areas.

Figure 1

Figure 3

Figure 4

Table 1. Results of ANCOVA testing the effects of treatment (freshwater versus salinity gradient), body condition, sex, temperature and dissolved oxygen on chamber use (weighted mean) of individual African jewelfish.

Factors	F _{df}	P value
Treatment	7.3 _{1, 54}	0.009
Body condition	0.8 _{1, 54}	0.370
Sex	0.3 _{1, 54}	0.582
Water temperature	0.02 _{1, 54}	0.895
Dissolved oxygen	1.2 _{1, 54}	0.289