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Trait Variation in an Everglades Invasive Species: Life histories, Boldness, and Dispersal in the African Jewelfish

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TRAIT VARIATION IN AN EVERGLADES INVASIVE SPECIES: LIFE HISTORIES,

BOLDNESS, AND DISPERSAL IN THE AFRICAN JEWELFISH

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Diana Paola Lopez

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To: Dean Kenneth Furton
        College of Arts and Sciences

This thesis, written by Diana Paola Lopez, and entitled Trait Variation in an Everglades Invasive Species: Life histories, Boldness, and Dispersal in the African Jewelfish, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this thesis and recommend that it be approved.

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Date of Defense: June 9, 2011

The thesis of Diana Paola Lopez is approved

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Florida International University, 2011

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DEDICATION

Finishing my thesis is the result of my dedication and hard work, but all this work would not have been possible without the support and love of those who have believed in my capabilities. I want to thank my parents, my husband, and my sisters for believing in me. Also, I want to dedicate my thesis to my cousin Steven Lopez.

Finally, I offer this achievement to the one who has been next to me my entire life, God.

El hacer publica esta tesis, resultado de estudio y dedicación, ha sido posible gracias a las personas que han creído desde siempre en mis capacidades y en mi tenacidad de alcanzar los objetivos propuestos. Estas personas son mis padres, mi esposo, y mis hermanas. También quiero dedicar especialmente todo mi trabajo en estos dos años a mi primo Steven López.

Finalmente y mas importante dedico este logro a quien me ha puesto en donde estoy y ha estado conmigo durante toda mi vida, Dios.

ABTRACT OF THE THESIS

TRAIT VARIATION IN AN EVERGLADES INVASIVE SPECIES: LIFE HISTORIES,

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by

Diana Paola Lopez

Florida International University, 2011

Miami, Florida

Professor Jennifer S. Rehage, Major Professor

Invasive range expansion is correlated to life- history variation, boldness and dispersal behavior. The invasion of the African Jewelfish in Everglades National Park provides an opportunity to test life-history trait variation, boldness and dispersal behavior in the invasion success of this species.

My study examined variation in somatic traits, boldness, and dispersal of jewelfish across their invaded range. Life histories were examined on wild individuals. Boldness and dispersal were tested in outdoor experimental tanks. Tested populations from the invasion front have higher somatic traits, but they were not bolder than longer established populations.

Understanding the underlying mechanisms of invasions are key for the development of strategies looking to contain invaders and prevent their spread.

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INTRODUCTION

Worldwide, anthropogenic stressors are causing species distributions to change. Climate change, land-use change, habitat fragmentation/loss, and species translocations are resulting in dramatic range shifts, contractions, and expansions among native and non-native taxa (Case and Taper 2000; Parmesan and Yohe 2003; Phillips et al., 2010a; Sato et al., 2010). These distributional changes are often accompanied by new selection pressures, as organisms often encounter different habitats, environmental conditions, and biotic interactions (Suarez and Tsutsui 2008). Organisms may encounter evolutionarily-novel conditions resulting from human-induced rapid environmental change (HIREC; Sih et al., 2011). For example, organisms moving into urban environments may experience relaxed predation and high resource levels relative to natural habitats (Gilroy and Sutherland 2007). Both rapid, adaptive evolutionary responses and phenotypic plasticity will aid species in coping with these novel conditions (Hendry et al., 2008; Sexton et al., 2009).

In the context of invasions, several recent studies show both evidence of rapid genetic evolution and plasticity, primarily along the leading edge of an invasion (Phillips et al., 2010b; Table 1). Individuals from populations on the leading edge of an invasion are expected to experience stronger selection than individuals from the core or longer-established populations (Burton et al., 2010; Phillips et al., 2010a). Selective forces acting on the invasion front can be investigated by comparing traits of long-established versus frontier populations, but these adaptive responses can only be compared if the invasion history of the target species is well-understood (Phillips et al., 2010a). Further, examining adaptive responses of non-native populations along an invaded range can

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provide valuable insights on the dynamics helping invaders to colonize novel territories (Sakai et al., 2001), as well as provide an opportunity to study rapid evolutionary change (Thomas et al., 2001).

Although an extensive body of theoretical work addresses the potential mechanisms that drive range expansions, as well as what limits species distributions (Holt et al., 2005; Hughes et al., 2007; Phillips et al., 2008; Barton et al., 2009; Burton et al., 2010; Kubisch et al., 2010), additional empirical work is needed to understand the complexity of range dynamics in nature (Holt et al., 2005). As invaders colonize new territories, they are known to invest more energy into reproduction in response to lower conspecific density and competition at the expanding edge of the range (Travis and Dytham 2002; Phillips et al., 2008; Phillips 2009; Burton et al., 2010; Phillips et al., 2010a), and evolve life-history strategies such as higher growth rates to offset the high costs of novelty (Phillips 2009).

Knowledge of the invasion history of a non-native organism is often difficult to acquire because the origin of many invasions is unknown, and many invasive populations are the product of multiple introductions (i.e., Collins et al., 2002, Kolbe et al., 2004). Further, the record of spread is equally difficult to observe and track (Lodge et al., 2006), especially in highly-mobile animals that disperse long distances (Nathan et al., 2003). For instance, only fourteen studies of three vertebrate invasive species have tracked their spread (Table 1). The invasion of cane toads, *Rhinella marinus,* in Australia provides one of the few examples where the invasion sequence is well-known (Phillips et al., 2007), and considerable research effort has been devoted to identify the attributes that enable

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range expansion (Table 1). For example, invasion-front cane toads demonstrate an accelerated range advance (Urban et al., 2008), and higher dispersal rates compared to populations behind the expanding range (Phillips et al., 2010a). Behavioral, morphological, and life-history adaptations have increased the spread rate, and fitness of cane toad populations along their expanding edge (Phillips et al., 2006; Alford et al., 2006; Phillips 2009; Llewelyn et al., 2010). In terms of their life-histories, cane toads from their invasion front have higher growth rates when compared to older established populations (Phillips 2009). Similarly, the recolonization of western bluebirds (*Sialia mexicana*) over the northwestern United States has been facilitated by the coupling of high levels of aggression and dispersal in populations at the expanding margin (Duckworth and Badyaev 2007). These case studies show that beyond life histories, behavioral attributes are also under strong selection at the expanding edge of invading populations (Sih et al., 2011).

Among behavioral traits, boldness, a behavioral trait defined as the propensity of individuals to explore unfamiliar space and take risks (Wilson et al., 1993; Wilson et al., 2010), has been shown to be a key trait aiding invasion success (Rehage and Sih 2004; Cote et al., 2010). Yet, whether boldness is also an advantageous trait at the leading edge of an invasive range expansion is not known. Boldness may play a role in the dispersal of organisms because bold individuals willing to move through space and take risks are consequently better dispersers than shy individuals (Fraser et al., 2001). The coupling of boldness and dispersal tendency could be a highly-selected trait combination at the invasion-front leading to rapid spread. In this study, I examined variation in boldness,

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dispersal tendency, and life histories across populations of a recent fish invader in the Florida Everglades. The objective of this study was to better understand if these traits play a role in range expansion, and how the traits are responding to changes in selective regimes along the range.

Seventeen non-native fish species are currently established in Everglades National Park (ENP) (Shafland et al., 2008). Among those, a recent invader is the African Jewelfish *Hemichromis letourneuxi,* a small predatory cichlid (Rehage et al., 2009; Dunlop-Hayden and Rehage 2011), introduced to urban canals of South Florida in the 1960´s (Rivas 1965). This recent invader was first detected in ENP in 2000 (Kline 2008), and since then has rapidly spread at a rate of approximately 4 km/yr from the northeastern boundary of the park through freshwater marshes, and to western and southwestern areas at the marsh-mangrove ecotone (Rehage et al., unpubl. data; Figure 1). African Jewelfish are the most abundant recent fish invader found throughout ENP freshwater marshes (Kline 2008). The jewelfish invasion provides a unique opportunity to track the range expansion and spread across multiple habitat types. By comparing three invasion-front and three longer-established populations, I examined behavioral and life history traits that may be under strong selection favoring the rapid colonization of novel habitats. Using dissected wild-caught fishes from the six populations, I compared fish condition, gut-fullness, and reproductive allocation. In videotaped behavioral assays, I compared boldness, and dispersal tendency of wild caught fish from the same six populations. Dispersal tendency refers to the propensity of individuals to move across

relatively long distances, and is expected to be correlated to true measures of field dispersal (Fraser et al., 2001; Kobler et al., 2009; Rehage and Sih 2004).

Following Burton et al., (2010), I hypothesized that invasion-front populations of African Jewelfish in ENP would allocate more resources to reproduction and be better dispersers than older, well-established populations. Other studies have classified populations at the leading invasion front as "r-selected" on the basis of classic ecological theory (Phillips 2009, Burton et al., 2010). Because dispersal and boldness have been shown to be correlated (Fraser et al., 2001; Rehage and Sih 2004; Duckworth and Badyaev 2007), I also expected frontier populations to be bolder than well-established populations along the invaded range. Bold individuals are highly exploratory and active (Wilson and Godin 2009). Thus, behaving boldly may be an advantage at the expanding front where individuals encounter novel conditions. As the invasion proceeds, advancing range populations experience low intraspecific competition (Travis and Dytham 2002; Phillips et al., 2010a), coupled with naïve prey (Rehage et al., 2009; Sih et al., 2010; Dunlop-Hayden and Rehage 2011). Thus, jewelfish at the frontier may experience high abundance of resources (Bohn et al., 2004), and better feeding opportunities, and therefore, be better fit than well-established populations. I expected fish from the invasion-front to be in better condition, and have greater allocation to reproduction relative to populations behind the leading front.

Boldness is considered to be an important component of animal personality (Conrad et al., 2011). Personality is defined as the consistent behavioral differences between individuals over time and across situations (Sih et al., 2004; Reale et al., 2007;

Reale et al., 2010). According to Stamps and Grothius (2010), in order to study personality and behavioral consistency, we need to record the behavior of the same individuals in different sets of external stimuli. A secondary objective of the behavioral component of this study was to assess personality by examining correlations between boldness measures and dispersal tendency. I expected pairs to be consistently bold or shy on both experiments, such that fish pairs behaving boldly were expected to emerge early in both tests and remain active. I also hypothesized a positive relationship between boldness measures and dispersal (Figure 2a).

METHODS

Study System

Over the past 11 years, jewelfish spread from L31W canal and adjacent marshes along the eastern boundary of the Park in a westerly direction, but are now entering mangrove oligohaline habitats (Figure 1; Kline 2008, Rehage et al., unpubl. data). The marsh area that was first invaded and inhabited the longest by jewelfish is a karst graminoid wetland with relatively short-hydroperiod (5-6 months of flooding over the year) (Kobza et al., 2004). Because of the short duration of flooding, these habitats are predator-limited (Chick et al., 2004), and community structure is dominated by small poeciliids, centrarchids, and other nonnative cichlids (particularly juvenile Mayan cichlid, *Cichlasoma urophthalmus,* and Black Acara, *Cichlasoma bimaculatum;* Kobza et al. 2004). The marsh surface is also dotted by a mosaic of depressions in exposed limestone outcroppings (from a few cm to > 60 cm deep) (Loftus 2006). Solution holes serve as important dry season refugia for many aquatic organisms (Kobza et al., 2004; Ruetz et

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al., 2005). Seasonal movement by fishes in and out of these dry-down refugia (and others, e.g., alligator holes, mangrove creeks; Palmer and Mazzotti 2004, Rehage & Loftus 2007) is critical to individual survival and population persistence (Chick et al., 2004; Obaza et al., 2011).We expect dispersal to be an adaptive trait for Everglades native fishes, as well as for recently arrived non-native taxa.

I collected African Jewelfish from six sites within ENP in the summer and early fall of 2009 (Table 2). Three of the populations used for the study correspond to the invasion-front, and three are longer-established populations (Figure 1). All fish were collected using unbaited minnow traps randomly deployed in marshes, near road culverts, and next to canals. Water depth ranged between 30 - 100 cm. I collected a total of 256 jewelfish to assess life histories, and 192 for behavioral trials that compared boldness and dispersal tendency (Table 2).

Life History Traits

Fish captured for life history assessments were euthanized immediately at capture with an overdose of the anesthetic MS-222 (Nickum et al., 2004), fixed in 10% formalin, and preserved in 70% ethanol. In the laboratory, all fish were measured in mm standard length (SL), weighed to the nearest 0.01 g, and dissected to determine sex, allocation to reproduction, and gut content extraction. I then calculated fish condition (K), as the ratio of the fish's body weight (W) and SL (Williams 2000):

$(K) = 100000 \ W \ (g) \ / \ SL^3 \ (mm)$

During dissections, all stomach contents were extracted (including detritus) and weighed individually to estimate a gut fullness index (GFI) (Yanagisawa and Sato 1990). Small fishes and shrimp were easily identified in the majority of stomach contents (Jungman et al., unpubl. data).

(GFI) = wet weight of gut contents (g) /wet body weight (g) * 1OO

Finally, I used the gonadosomatic index (GSI) to quantify the reproductive investment of females using the following formula (Kreiner et al., 2001; Bohn et al., 2004):

(GSI) = wet weight of gonad (g) / (Wet body weight (g) – Gonad wet weight (g)) * 100

Separate generalized linear mixed models (GLMM; Proc Mixed in SAS 9.2) were fitted to the life histories using K, GFI, or GSI as dependent variables, and population type (invasion front vs. interior) as the main fixed effect. Population nested within population type was fitted as the random effect (Bolker et al., 2009). For the K and GFI models, sex was added as an additional fixed effect. Significance for the random effect was determined by using a log-likelihood ratio test, which follows a chi-square distribution (i.e., Newman-Pearson criterion; Kurvers et al., 2009). Because the GFI and GSI residuals were not normal, they were log-transformed prior to analyses (Bland and Altman 1996).

Behavioral Assays

Fish used in behavioral assays were captured from the same invasion-front and from areas with longer-established populations (Table 2), brought back to the laboratory,

and housed in outdoor 795 l tanks by population until trial dates (2-4 months). Some populations required considerable effort to collect, possibly because collections were made in the wet season, when fish were dispersed over the landscape. Also, it may be possible that the densities of some of the populations were low leading to increased effort of capture. The holding period falls within the range of other published behavioral studies, including ones assessing boldness and dispersal behavior (1-6 months; Ioannou et al., 2008, Cote et al., 2010, Harcourt et al., 2010, Schurch and Heg 2010). Stock populations were fed a combination of live prey (dominated by native mosquitofish, *Gambusia holbrooki*), frozen bloodworms, and fish food flakes *ad libitium*.

I quantified boldness and dispersal tendency of the six study populations in outdoor experimental tanks (Figure 3). Trials were conducted between November 12 and December 7, 2009. Because jewelfish are highly social (D.P. Lopez *pers. obs*, Loiselle 2000, Schofield et al., 2007; Rehage et al., 2009), I used pairs of individuals for all behavioral trials. Previous experimental assays of dispersal have used groups instead of solitary individuals (Gilliam and Fraser 2001; Rehage and Sih 2004; Meylan et al., 2009; Cote and Clobert 2010). Dispersing fishes may rely on social information to navigate their environments (Frost et al., 2007), and to facilitate decision making (Seppanen et al., 2007). A total of 16 pairs per population were videotaped over 4 time blocks (6 populations per day x 4 days per block x 4 blocks = 96 fish pairs), with a replicate of each population tested daily, in two consecutive behavioral assays. For all pairs, a boldness assay (hereafter Boldness1) was conducted between 09:00 and 12:00, followed by a combined boldness and dispersal tendency assay conducted between 13:00-17:00 (hereafter Boldness2-Dispersal). For all pairs, I allowed at least four hours between the

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two assays. The order of fish pairs tested in the morning trials was the same as the afternoon tests. Since temperature may be a strong influence on behavioral parameters (Biro et al., 2010), water temperature was recorded at the beginning of each trial. At the end of the experiments, fish were euthanized with an overdose of MS-222, measured, weighed, fixed in 10% formalin for 2-5 days, and stored in 70% ethanol for later sex identification via dissection.

Boldness1 Assay

I characterized boldness using a standard emergence test; shown to be an effective method to measure boldness and exploratory behavior (Bell 2005; Brown et al., 2005; Wilson and Godin 2009). In an emergence test, fish are added to a novel arena, placed in a refuge, and the time to emerge from the refuge is quantified, with the notion that bolder individuals will emerge sooner. My experimental tank included a refuge box (21 x 30 x 30cm) placed in the center of a 795 l outdoor tank (Figure 3a). The box was equipped with a removable door that allowed fish to emerge. Artificial plants were placed inside and outside the refuge box to provide structure, and gravel was used as substrate. The tank depth was kept at 15 cm to prevent subjects from swimming above the refuge and the artificial plant, thus information about the environment could only be gained by moving around these objects. We recorded fish behavior using a Sony DCR-SX41 digital video camera mounted directly above the boldness setup to give a full top view of the experimental tank.

For each trial, I selected a random pair of fish from a stock tank, placed them into the refuge box (Figure 3a), and gave them a 10-min acclimation period. At the end of this

period, the trapdoor was remotely and gently lifted (using a 150 cm line, pulled from behind a blind), and the fish pair was free to emerge and explore the tank arena for 20 min. The following timed parameters (in seconds) were recorded: (1) latency to emerge, (2) proportion of trial time spent back in the refuge (added for all returns to the refuge post the first emergence), (3) proportion of time spent in the artificial plant outside of the refuge, and (4) proportion of time spent swimming in open water. Fish that did not emerge from the refuge were assigned a maximum latency to emerge score of 1200 sec, and no further behavioral measures were conducted on these individuals. At the end of each Boldness1 trial, the pair was removed from the tank, placed in a separate holding tank (35 x 20 x 13 cm) until the Boldness2-dispersal test was conducted in the afternoon.

Boldness2-Dispersal Assay

For the second behavioral assay, the setup was similar to the Boldness1 setup with an identical emergence tank (center refuge box, gravel, and artificial vegetation inside and outside the refuge in the same locations), a 3 m long channel (35 cm wide), which connected the emergence tank to a second tank, where the fish could disperse and explore a new area (Figure 3b). In this setup, both tanks and the channel were covered with gravel as a substrate, and in the second tank, habitat complexity was similar to that of the emergence tank (one artificial plant placed near the center). In this assay, I characterized the repeatability of boldness, as well as the dispersal tendency of the subjects by giving them the opportunity to explore and move into a new area of the experimental setup (Figure 3b). Movement from the emergence tank to the second tank through the

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connecting channel (Figure 3b) mimics the movement of Everglades fishes in and out of dry-down refugia as water level fluctuate seasonally (Kobza et al., 2004).

Similarly to Boldness1, fish pairs were removed from the holding tank, placed in the refuge box (Figure 3b), and given a 10-min acclimation period. Following acclimation, the trapdoor was opened, and behaviors were recorded for 20 min. For this experiment, a second video camera recorded the full view of the channel, which was marked every 30 cm with bright colored tape to allow the observer to note the distance covered by dispersing fish. From the two recordings, I extracted measures of the same four behaviors recorded in Boldness1, with the exception that time spent swimming here included time spent swimming in the new area (i.e., channel and second pool). In addition, I measured another four behaviors: (5) latency to disperse (the time fish first entered the channel), (6) the number of dispersal attempts (the number of times fish entered the channel), (7) maximum dispersal distance across all dispersal attempts (in m, if fish reached the second tank, the maximum distance of 3 m was given), and (8) the proportion of trial time spent in the new environment [(time spent in channel + second pool) / 20 min trial time]. As in Boldness1, fish that did not exit the refuge were assigned a maximum latency to emerge score of 1200 sec. Similarly, those fish that emerged but did not disperse were assigned a maximum latency to disperse score of 1200 sec. All behavioral variables were quantified by a single observer (D.P.L.) using JWatcher ® (v1.0) (http://www.jwatcher.ucla.edu/).

From the videotapes, I quantified behavioral data separately for each focal fish, and averaged the scores to obtain a pair mean to be used in all statistical analyses. The

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four variables recorded in Boldness1 were incorporated into a principal component analysis (PCA). The first principal component score (hereafter B1) from the Boldness1 assay explained 75.4% of the variance (Table 3). Similarly, the eight behavioral variables measured in the Boldness2–Dispersal test were added into a second PCA (Bell and Stamps 2004). The first two principal component scores from the second behavioral assay explained 87.7% of the variance. The second principal component score loaded in the same direction as in B1 (Table 3) and was designated as a second boldness index (B2). Dispersal dimensions were explained by the first principal component score designated D1 (Table 3). Boldness and dispersal dimensions were defined with PCA factor loadings greater than 0.32 (Tabachnik and Fidell 1996). B1, B2, and D1 PCA scores were used in further analyses (Table 4). Since low PCA scores corresponded to bold pairs, I inverted the scale by reversing the sign of all boldness scores (i.e., B1 and B2) in further analysis. Inverting the scale of PCA scores can aid in interpretation of results (Bell 2005; Dingemanse et al., 2007).

I fitted a generalized linear mixed model (GLMM; Proc Mixed in SAS 9.2) to B1 and B2 scores together (Table 4). Main fixed effects included population type (invasion-front vs. long-established), trial (B1 vs. B2), water temperature, condition factor (averaged for the pair), and sex designation of the pair (female, male, or mixed, as determined by dissection, after trials). Population nested within population type was fitted as a random effect to account for possible variation among populations (Bolker et al., 2009). A separate GLMM using the same fixed and random effects (except for trial) was fitted to D1 scores obtained from the PCA analysis of the Boldness2-Dispersal assessment to examine variation among population types and populations. Significance

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for the random effect was determined as previously mentioned in the life history trait analyses. I used a graphical representation of behavioral reaction norms to visualize the relationship among behaviors for each pair of jewelfish over a contextual gradient consisting of Boldness1, Boldness2, and Dispersal (Dingemanse et al., 2010). The relationship between Boldness1 and Dispersal was tested using a simple linear regression (Brown et al., 2005)

RESULTS

Life History Trait Variation

I found consistent differences in life history traits between invasion-front and well-established populations of non-native African Jewelfish from ENP. Condition factor and gut fullness index from frontier populations were significantly higher than those of the longer-established populations (Figure 4a, b; Table 5). As expected, females across population types were in better condition than males. Likewise, reproductive traits displayed significant spatial variation. Females from the invasion front showed higher reproductive investment than females from the older established populations (Figure 4c; Table 5). Reproductive investment (GSI) averaged 3.5 for the invasion front, relative to 2.2 for the interior populations. I also found population level differences on all life histories (Figure 4; Table 5).

Behavioral Traits

Boldness1

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Movement and exploratory behaviors (i.e., proportion of time swimming and proportion of time using habitat structure) loaded negatively and opposite to shy behaviors (i.e., proportion of time back in the refuge and latency to emerge, Table 3). From the PCA results, I considered pairs with a B1 above 1 to be bold, pairs with scores between 0 and 1 intermediate, and those with scores less than 0 as shy (Figure 2b). Bold subjects had low emergence times, spent more time exploring the tank, and spent less time going back to the refuge than shy individuals. In this first assessment of boldness, roughly 40% of the pairs from the invasion front, and 50% from longer-established populations emerged from the refuge. For the fish that emerged, emergence, on average, occurred at 9.5 min into the 20 min trial. Boldness1 did not differ between invasion-front and long-established populations, and there were no significant differences among individual populations (Figure 5).

Boldness2 and Dispersal

Influential factor loadings on component score one (D1) corresponded to dispersal variables (Table 3), including proportion of time swimming, suggesting that this particular behavior considerably affects the dispersal tendency of individuals. Since latency to disperse loaded negatively and opposite to all other dispersal variables, high D1 scores correspond to high dispersal tendency. From observations, most dispersing individuals explored the whole experimental set up accompanied by their partner, and reached the second tank after several exploratory attempts. In this trial, average emergence time for all pairs was 6 min, while for those that dispersed, dispersal took an average of 10 min and after 2 attempts. Overall, 70% of jewelfish from the invasion-

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front populations, and 70% from longer-established populations emerged from the refuge, and for those that emerged, about 17% from the invasion-front, and 32% from the long-established populations dispersed into the new areas of the experimental setup (Figure 3b). Invasion-front populations were not bolder than well-established populations, and there were no significant differences among the six individual population in boldness scores (Figure 5; Table 4). Although, I found no significant differences in dispersal tendency between invasion front and longer-established populations, there was one population that showed significantly higher dispersal tendency than all other populations (Figure 6; Table 4). Surprisingly, this high dispersal population was a longer-established population, located at the eastern boundary of ENP (the L31W marsh population, Figure 2). All other fixed effects tested in the models (water temperature, sex, condition factor) did not affect the behavior of fish in experimental pairings (Table 4). And, I did not find strong correlations between the boldness and dispersal scores of the populations (Invasion-front: $r^2 = 0.08$, $P = 0.05$; longer-established: $r^2 = 0.05$, $P = 0.13$) (Figure 2b).

DISCUSSION

Understanding the ecological and evolutionary processes that allow populations to adapt to novel conditions remains an important question in the study of species distributions (Gaston 2009). Biological invasions provide an opportunity to examine the underlying mechanisms allowing rapid distributional shifts, and the limits to range expansions (Sexton et al., 2009). However, since tracking invasive spread is often difficult, few studies have examined animal trait variation (e.g., morphological, behavioral, and life-history) of a non-native range expansion (Table 1). As a species

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colonizes new ranges, population dynamics, fitness, and behaviors may shift or be selected in response to novel conditions (Figure 7). A recent model by Fogarty et al., (2011) showed that certain life-history strategies coupled with a mix of behavioral types lead to higher speed of invasion. Asocial individuals spread more quickly than their social congeners, and developed higher individual growth rates at low intraspecific density; yet, a faster rate of spread was seen when a mix of behavioral types (i.e., asocial and social) was present. In this study, I examined life history and behavioral mechanisms that may help non-native jewelfish to spread in their South Florida invaded range. Jewelfish from frontier populations had higher indices of reproductive investment, condition, and gut fullness (GSI, K, and GFI respectively) than their conspecifics from longer-established populations. On the other hand, the coupling of boldness and dispersal tendency did not appear to be important traits facilitating spread, since fish from frontier and interior populations were equally bold and showed similar dispersal behaviors in the two lab assays.

Life History Trait Variation

Variation in life history strategies results in response to environmental heterogeneity. In an invasion, novel selection pressures in both the establishment and spread phase can result in significant variation in these traits (Sakai et al., 2001; Allendorf and Lundquist 2003; Suarez and Tsutsui 2008). Comparisons of life history traits between a species native and non-native range (Gurevitch et al. 2011), as well as between populations along the invaded range have provided evidence that phenotypic plasticity and rapid evolution both are key mechanisms underlying successful invasions

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(Olden et al. 2006; Fox et al. 2007; Phillips 2009; Joanna et al. 2011). For example, the invasion of two goby species (*Neogobius kessleri* and *Neogobius melanostomus*) in the Danube river may be partially attributed to enhanced somatic condition and growth rates, resulting from improved food availability and selective predation of highly-abundant amphipods in the non-native range (Polacik et al. 2009). In invasive cane toads, rapid evolution of higher individual growth rates in the frontier populations has contributed to their accelerated range expansion in Australia (Phillips 2009).

Ecological theory suggests that populations undergoing range expansion should differentially invest in dispersal and evolve life history traits that allow for rapid colonization (Travis and Dytham 2002; Hughes et al., 2007; Phillips et al., 2008; Burton et al., 2010; Kubisch et al., 2010; Phillips et al., 2010a). Thus, pioneer populations are expected to invest more energy in reproduction compared to long-established populations (Burton et al., 2010; Phillips et al., 2010). My life history results matched these theoretical predictions. Non-native African Jewelfish from frontier populations were in better condition, invested more resources into reproduction, and had higher gut fullness than those from longer-established populations. Possibly, higher gut fullness and body condition are a consequence of lower conspecific density, leading to higher availability of food resources or more feeding opportunities. Copeland et al., (2010) noted that changes in body condition occur as a result of factors that influence consumption. A study of round gobies (*Neogobius melanostomus*) along their invasive range in the Trent River, Ontario showed higher GFI and K in invasion-front populations, partly as a result of variation in diet composition and resource availability between core and expanding

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populations (Raby et al., 2010). Higher prey abundance and more feeding opportunities may also be the result of prey naiveté at the expanding margin (Rehage et al., 2009, Sih et al., 2010, Dunlop-Hayden and Rehage 2011). Whether the differences in body condition and gut fullness of my focal populations are a consequence of more feeding opportunities or differences in resource availability remains unclear. Additionally, sampling is needed to determine if prey availability or quality is, in fact, higher at the front of this invasion.

A reduced population density on the expanding edge of a population often drives selection for an increase in reproductive investment (Bohn et al., 2004; Phillips et al., 2008; Burton et al., 2010; Phillips et al., 2010a; Phillips et al. 2010b). The rapid spread of African Jewelfish within ENP could be partially attributed to their adaptive capacity to alter life history strategies, such as reproductive investment, in response to population dynamics (i.e., conspecific density), and/or novel environmental conditions. Bohn et al., (2004) attributed the rapid spread of the invasive fish *Coregonus albula* along the Pasvik River to the ability of the species to be phenotypically plastic. Pioneer populations of *C. albula* traded off growth to higher reproductive investment at low densities compared to older populations at upstream sites. Further work is needed to relate the effect of population density on reproductive allocation at the invasion front of jewelfish as a key selective force. It is also plausible that the difference in reproductive investment is the result of the proximity of older established populations to canal habitats where overall habitat quality may be low. Predator and non-native fish abundance is higher in marshes near canals (Rehage and Trexler 2007), thus foraging success and habitat quality may be

lower as a result of higher predation risk and/or interspecific competition (Nilsson et al., 2010)

Behavioral Trait Variation

Beyond life histories, behavioral mechanisms, although less-studied, are thought to be an essential underlying component of invasion success (Holway and Suarez 1999; Brooks and Jordan 2010; Sih et al., 2011; Tuomainen and Candollin, *in press*). Among behavioral traits, dispersal may be the most common trait favored in populations along an invasion front, and the mechanisms leading to better dispersal are the focus of several invasive trait studies (Table 1). For example, Child et al., (2008) documented that the presence of potential cannibalistic conspecifics induces higher dispersal behavior in invasive cane toads in Australia. In western bluebirds, populations along the range margin show higher dispersal, which is positively related to aggressive behavior (Duckworth and Badyaev 2007). In invasive mosquitofish (*Gambusia affinis*) and native Trinidad killifish (*Rivulus hartii*), boldness has been linked to higher dispersal (Fraser et al., 2001; Rehage and Sih 2004; Cote et al., 2010). My results did not agree with these previous studies. I did not find a strong boldness-dispersal behavioral correlation along the invasion that may account for the rapid expansion of jewelfish in ENP. Cote et al., (2010) found that dispersal tendency was not tightly associated to a boldness-exploration-activity behavioral axis, but dispersal was more closely related to the sociability of the individuals. In their study, asocial mosquitofish (*Gambusia affinis)* tended to disperse larger distances if they originated from high-density pools.

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Thus, it is possible that other sets of behaviors (i.e., aggression, voracity, or social interactions) might be more important in aiding a species to spread than dispersal tendency and boldness. Perhaps, high intraspecific density encourages moving out of a social group, since elevated conspecific aggression leads to mortality in large groups of jewelfish (D.P. L. *pers. obs.,* Schofield et al., 2007). Alternatively, it is possible that the link between a bold personality and dispersal tendency may be restricted to a specific age class or sex group, which was not explored in this study. Three-spined sticklebacks (*Gasterosteus aculeatus*) from a low predation site are bold and aggressive as juveniles, but these behavioral traits, and the correlation between them disappears at sub-adulthood and adulthood. But, strong behavioral correlations remain constant throughout ontogeny in stickleback populations where predation pressure is high (Bell and Stamps 2004). Similarly, dispersal of the cichlid *Neolamprologus pulcher* in its native range is restricted to a single age class or sex (Stiver et al., 2007; Schurch and Heg 2010). In my study, fish tested were not restricted to a particular size, developmental stage, or sex; but I did not find a relationship between size or condition and the behaviors measured.

On the other hand, it may not be advantageous to behave boldly when reproductive investment is high. A model by Wolf et al., (2007) showed that personality traits such as boldness arise depending on the probability of future reproduction. If an individual invests highly on reproduction to obtain high fitness returns in the future, then it should be risk-averse. Contrary, risk-prone individuals invest fewer resources into reproduction. Thus, in the context of colonization, it may not be adaptive to be risk-prone (bold). Among non-native eastern mosquitofish (*Gambusia holbrooki*) introduced to

Australia, female fecundity was negatively correlated to boldness. Females that put more resources into reproduction minimized predation risk, were more cautious, and took longer time to emerge from refuge (Wilson et al., 2010). In this study, female jewelfish from frontier populations had higher reproductive investment, but were not bolder than those from longer-established populations.

Study Implications

Rapid adaptation to novel conditions (e.g., range expansion) is often driven by changes in behavioral responses (Sih et al., 2011), as well as life history variation (Bohn et al., 2004; Ribeiro and Collares-Pereira 2010; Joanna et al., 2011). By investigating the behavioral and life-history mechanisms used by non-native populations to cope with novelty in their invaded range, we can better understand the role of species traits in invasions (Gurevitch et al., 2011). In addition, a framework on the key invasion processes and mechanisms for the many non-native fish currently established in ENP can provide insight for incorporating non-native fish invasion management into Everglades restoration efforts; currently a missing piece. Efforts to restore hydrological connectivity and sheetflow and to revise water delivery into the system (Rutchey et al., 2008) may provide opportunities for the containment of current invasions, and the prevention of future ones. Aside from prevention, active management strategies can be developed, such as, management by directed evolution (MDE). MDE involves manipulating traits in order to create coexistence of native and non-native species (Davis 2009). For instance, invasiveness may be manipulated by understanding which traits allow an invader to colonize novel territories rapidly. I expect that behavioral traits coupled with other traits

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will be important mediators of how invasive organisms deal and respond to environmental heterogeneity and novelty in an invasion, and deserve greater attention.

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Table 1. Previous animal studies comparing traits between invasion front and long-established populations.

Species	Trait favored at invasion front	Mechanism	Reference	Evolution/Plasticity
Rhinella marinus	Dispersal	Heritability	Phillips et al. 2010a	Evolution
Rhinella marinus	Dispersal ability	Endurance	Llewelyn et al. 2009	Evolution
Rhinella marinus	Growth rate	Early reproduction	Phillips et al. 2009	Evolution
Rhinella marinus	Dispersal	Path straightness, movement lenght	Alford et al. 2009	Evolution
Rhinella marinus	Rate of invasion	Long-distance jump dispersal, abiotic conditions	Urban et al. 2008	Evolution / plasticity
Rhinella marinus	Dispersal behavior	Cannibalistic conspecifics	Child et al. 2008	Unknown
Rhinella marinus	Dispersal rate	Movement distance and duration	Phillips et al. 2008	Evolution
Rhinella marinus	Movement rate	Abiotic conditions	Phillips et al. 2007	Evolution / plasticity
Rhinella marinus	Long-distance movement	Road corridors	Brown et al. 2006	Unknown
Rhinella marinus	Dispersal speed	Leg lenght	Phillips et al. 2006	Evolution
Sialia mexicana	Dispersal, reproduction	Aggression	Duckworth 2008	Evolution
Sialia mexicana	Dispersal	Aggression	Duckwoth and Badyaev 2007	Evolution
Sturnus vulgaris and carpodacus mexicanus	Propagule dispersal	Habitat quality	Gammon and Maurer 2002	Unknown
Neogobius melanostomus	Gut fullness index and condition factor	Prey composition	Raby et al. 2010	Unknown

Table 2. Location and number of fish collected (n) for the project components: behavioral assays (B) and life history assessment (LH).

Sampling Site	Location	Test	Collection Dates	N_{LH}	N_B	N_{Total}
Invasion Front						
	$25^0$26'N;					
	$80^0$47'W					
Pahayokee (PH)		B	8 July - 16 July 2009	46	32	78
		LH	21 Aug - 25 Sept 2009			
	$25^0$20'N;					
	$80^0$50'W					
Mahogany Hammock (MH)		B	8 July - 9 July 2009	34	32	66
		LH	19 Aug - 20 Aug 2009			
	$25^0$17'N;					
	$80^0$48'W					
East of Paurotis Pond (PP)		B	16 July - 23 July 2009	33	32	65
		LH	19 Aug - 21 Aug 2009			
Long-established						
	$25^0$37'N;					
	$80^0$35'W					
Chekika (CK)		B	16 Aug - 17 Aug 2009	37	32	69
		LH	3 Oct 2009			

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$25^0 28'N;$

$80^0 35W$

L31W Marsh (LW)	B	8 July - 14 Aug	2009	40	32	72
	LH	8 Oct 2009				

$25^0 24'N;$

$80^0 36'W$

Taylor Slough (TS)	B	23 July - 13 Aug	2009	66	32	98
	LH	28 Aug - 25 Sept	2009			
			Total	256	192	448

Table 3. Results of principal component analysis on behavioral measures. Loadings, eigenvalues and explained variance are given for the emerging axes.

Boldness 1	Behavior	Loadings B1		%Variation explained	Eigenvalue
	Latency to emerge	**0.5299**		75.4	3.0162
	Proportion of time back in refuge	**0.5608**			
	Proportion of time in outside plant	**-0.4345**			
	Proportion of time swimming	**-0.4647**			
Boldness 2-Dispersal		**Loadings B2**	**Loadings D1**	%Variation explained	Eigenvalue
	Latency to disperse	-0.1736	**-0.4022**	64.81	5.1847
	Maximum dispersal distance	0.1935	**0.4070**		
	Number of attempts to disperse	0.1961	**0.3913**		
	Proportion of time in new area	0.2306	**0.3745**		
	Proportion of time swimming	-0.0114	**0.4084**		
	Latency to emerge	**0.3792**	-0.3327	87.66	1.828
	Proportion of time back in refuge	**0.4806**	-0.3161		
	Proportion of time in outside plant	**-0.6825**	0.0245		

Table 4. Source of variation in boldness and dispersal. Results are from GLMMs with population nested within population type entered as random effects. Sample sizes are in Table 2.

Source	Boldness 1 and Boldness 2			Dispersal		
	df	*F*	*P*	*df*	*F*	*P*
Fixed effects						
Population type	1, 6	0.24	0.64	1, 6	1.16	0.32
Trial	1, 185	0.01	0.91	–	–	–
Condition factor	1, 165	1.07	0.30	1, 96	1.85	0.18
Water Temperature	1, 187	0.47	0.49	1, 90	0.6	0.44
Sex	2, 190	0.58	0.56	2, 93	0.00	1.00
Random effect						
Population (Pop Type)	–	–	>0.05	–	–	<0.01

Table 5. Results from GLMM to examine the effects of location (invasion front vs. long-established), population (CK, LW, TS, PH, MH, and PP), and sex on the life history traits of jewelfish. Significant results are shown in bold.

Source	Condition Factor (K)			Gut Fullness Index (GFI)			Gonadsomatic Index (GSI)		
	df	F	P	df	F	P	df	F	P
Fixed effects									
Population type	1	7.98	**0.05**	1	24.16	**<0.0001**	1	3.63	**0.05**
Sex	1	15.66	**<0.0001**	1	0.22	0.64	–	–	–
Pop type * Sex	1	0.5	0.48	1	0.69	0.41	–	–	–
Random effect									
Population (Pop Type)	–	–	**<0.01**	–	–	**<0.01**	–	–	**<0.01**

Figure 1. Map of Everglades National Park showing the location of study sites where populations were sampled, the range advance, and the time and locations of spread records of jewelfish within ENP.
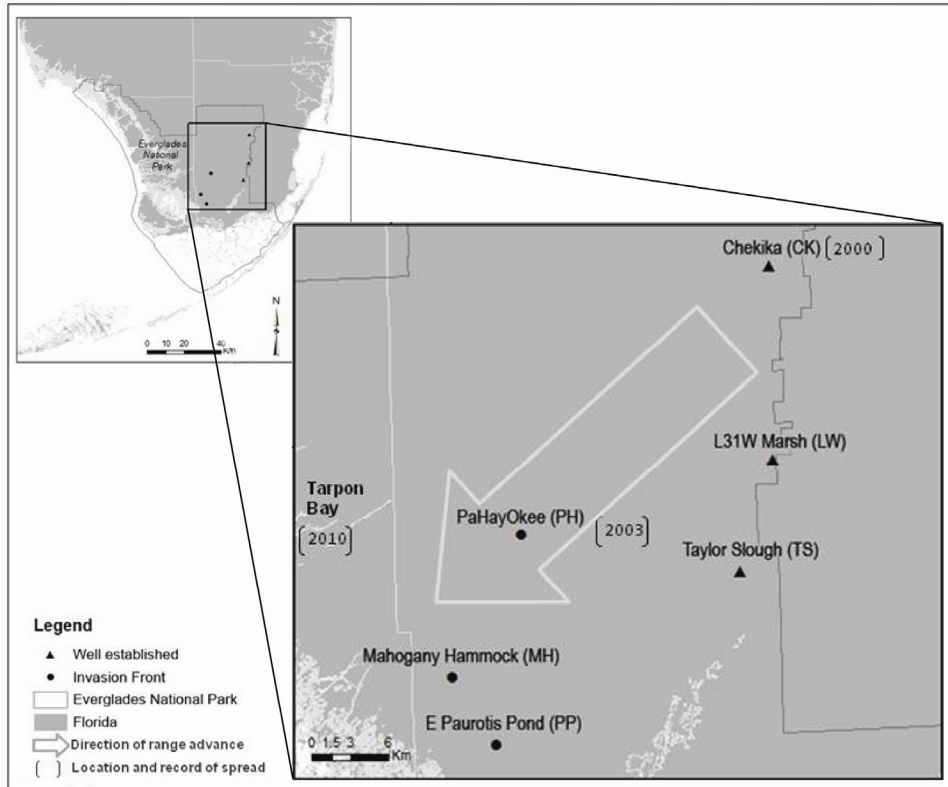
Figure 2. PCA scores from each individual tested. **a**) Expected results and **b**) results obtained from the boldness 1 and 2 behavioral observations as well as from the dispersal tendency assay.
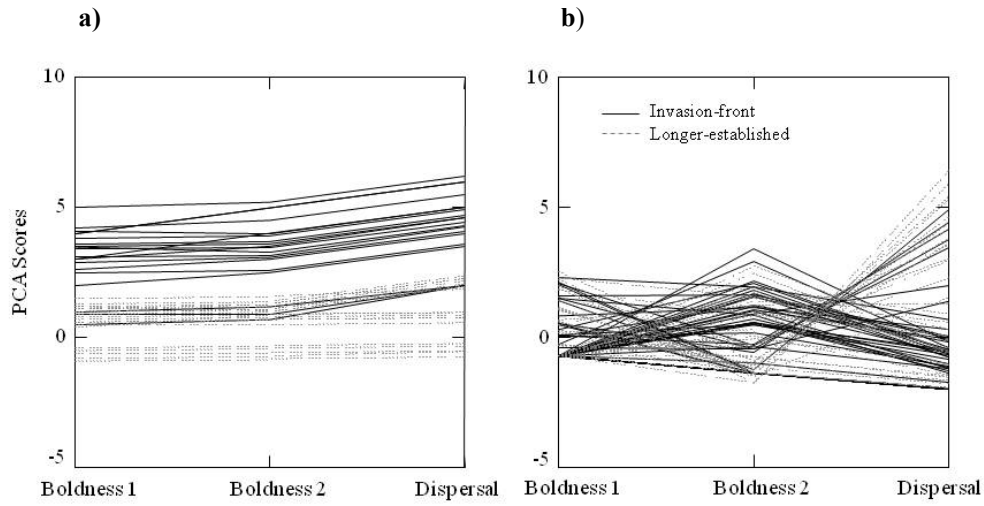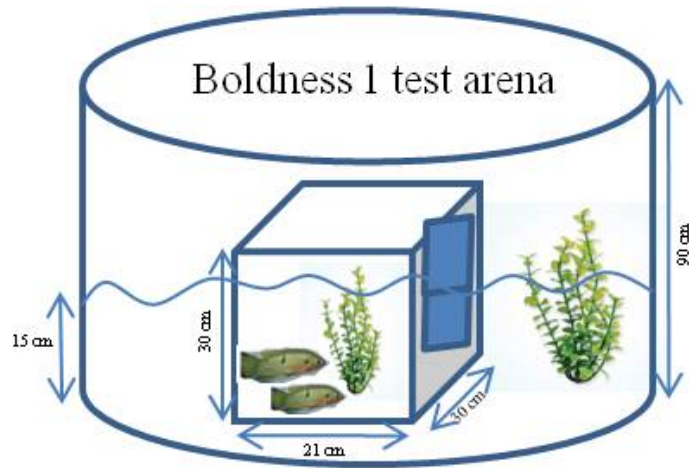
Figure 3. Diagram of experimental set ups **a**. Boldness1 assessment. **b**. Boldness2-dispersal assessment.

a.

b.
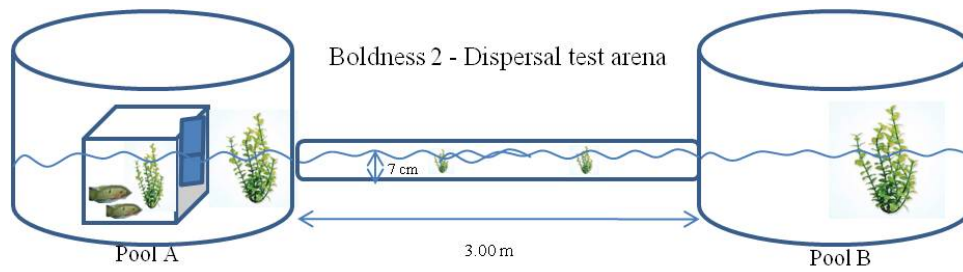
Figure 4. Life history trait variation between invasion-front and longer-established populations. **a**). mean body condition, **b**) mean gut fullness index (GFI), and **c**) mean gonadosomatic index (GSI) of African jewelfish populations.

a)
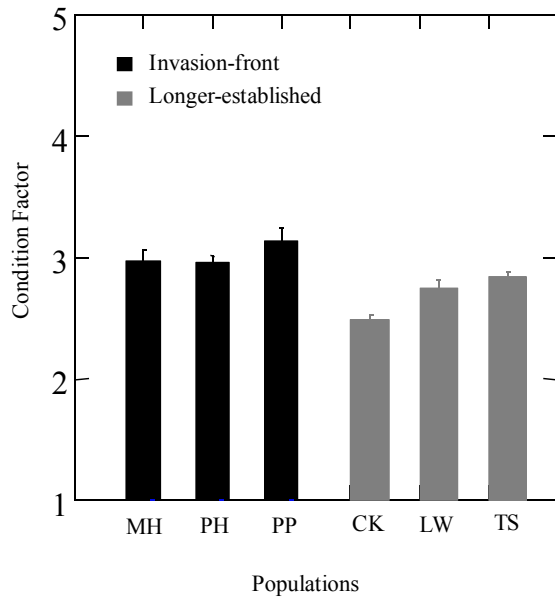
b)
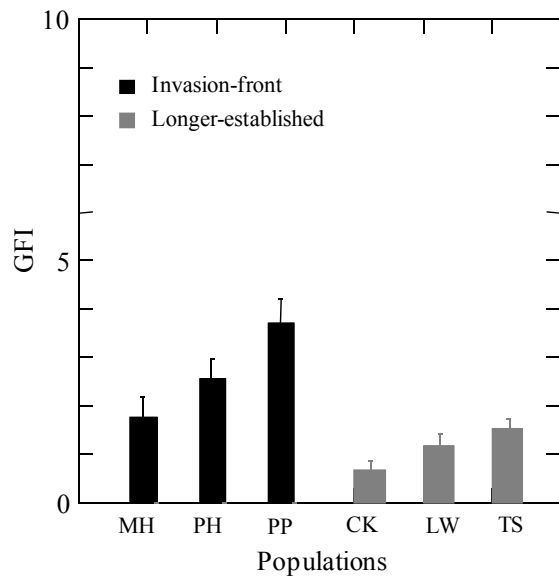
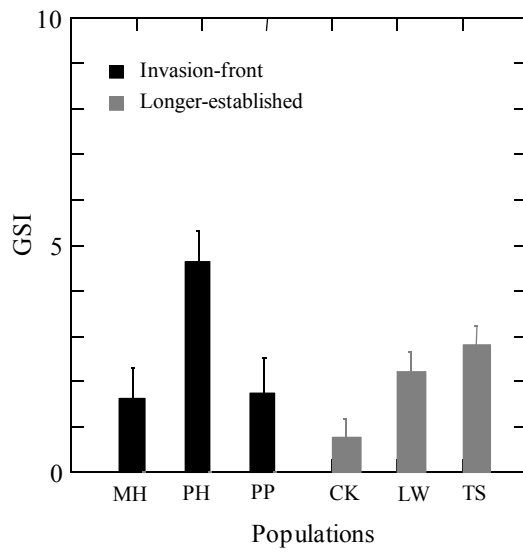
c)

Figure 5. Mean PCA scores for boldness from the first and second trial (B1 and B2) for Invasion Front (F) and Longer-established (L) populations of African jewelfish.
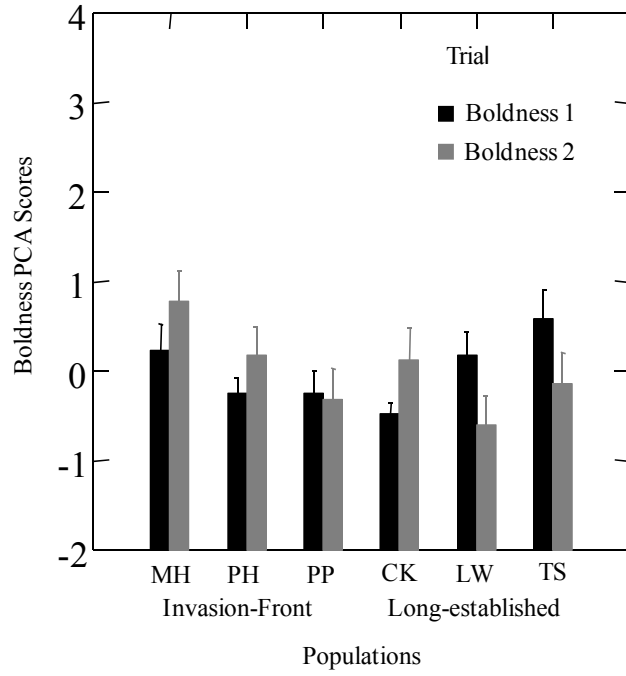
Figure 6. Mean dispersal component scores for Invasion-front and Longer-established
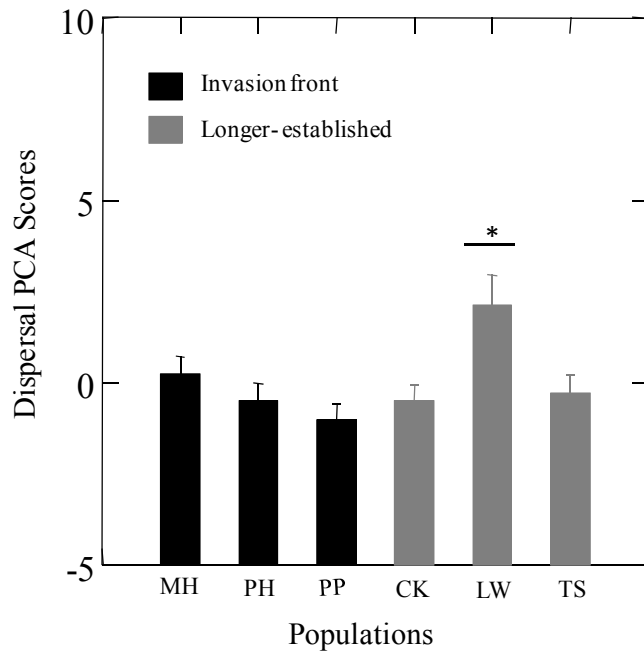populations of African jewelfish.

Figure 7. Range expansion trait variation between invasion-front and long-established population. (**+)** more, (**-**) less.