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Jewels for Dollars: Native and Nonnative Freshwater Fish Interactions in a Stressful Dry Down Environment

Vanessa Trujillo
Florida International University, nessa.trujillo@gmail.com

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

JEWELS FOR DOLLARS: NATIVE AND NONNATIVE FRESHWATER FISH INTERACTIONS IN A STRESSFUL DRY DOWN ENVIRONMENT

A dissertation submitted in partial fulfillment of

the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

BIOLOGY

by

Vanessa Trujillo

2017

To: Dean Michael R. Heithaus
College of Arts, Sciences and Education

This dissertation, written by Vanessa Trujillo, and entitled Jewels for Dollars: Native and Nonnative Freshwater Fish Interactions in a Stressful Dry Down Environment, having been approved in respect to style and intellectual content, is referred to you for judgment.

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

M. Danielle McDonald

John C. Withey

Robert Lickliter

Jennifer S. Rehage,Co-Major Professor

Philip K. Stoddard,Co-Major Professor

Date of Defense: March 27, 2017

The dissertation of Vanessa Trujillo is approved.

Dean Michael R. Heithaus
College of Arts, Sciences and Education

Andrés G. Gil
Vice President for Research and Economic Development
and Dean of the University Graduate School

Florida International University, 2017

DEDICATION

I dedicate this dissertation to my family and friends. Without their patience, understanding and loving support, the completion of this work would not have been possible.

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I would like to express my appreciation to members of my committee for their guidance, support and patience during the term of my candidature. Their valuable assistance in providing me with my research direction has been most appreciated. I would also like to thank past and present members of the Stoddard and Rehage Lab plus my numerous volunteers that made data collection possible. A special thanks to Jeff Kline and Zach Fratto for assisting me with their knowledge about the ecosystem and teaching me all of the freshwater fish in Everglades National Park.

I have found my coursework throughout the Curriculum and Instruction program to be challenging and exciting, providing me with the tools with which to explore both field and experimental research in multiple settings.

ABSTRACT OF THE DISSERTATION

JEWELS FOR DOLLARS: NATIVE AND NONNATIVE FRESHWATER FISH INTERACTIONS IN AN ALREADY STRESSFUL DRY DOWN ENVIRONMENT

by

Vanessa Trujillo

Florida International University, 2017

Miami, Florida

Professor Jennifer S. Rehage, Co-Major Professor

Professor Philip K. Stoddard, Co-Major Professor

Vertebrate populations are subjected to novel anthropogenic stressors that are expected to multiply exponentially in the future. Introductions of nonnative species and human-altered hydrology are among these stressors to native species communities. The Rocky Glades, located in Everglades National Park, may serve as a population sink for native species that typically do not survive the altered hydrology of the dry season, and as a source of nonnative species that may be better adapted to chronically stressful conditions. In the seasonally-flooded Everglades, the nonnative African Jewelfish invaded in the 1960s and has since shown rapid range expansion. African Jewelfish are aggressive and territorial, thus they are predicted to be more successful at acquiring space and resources, and may displace native Sunfishes. I monitored assemblages of fish across time in experimental mesocosms and solution holes and quantified survivorship and body condition of both natives and nonnatives. Overall, native Sunfish did poorly while nonnatives had higher survivorship over the course of the dry season. Unexpectedly, no evidence indicated that Jewelfish reduced survival of native Sunfish. I compared aggressive interactions between native Dollar Sunfish and nonnative African Jewelfish in Sunfish populations either sympatric or allopatric with Jewelfish. Sympatric Dollar Sunfish were twice as likely to approach African Jewelfish as allopatric ones. My study suggests native species can survive invasion through behavioral adaptation to nonnative competitors. Characterizing interactions between native and nonnative species and identifying their niche use can assist in understanding the challenges of native species conservation in the face of species invasions.

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ABBREVIATIONS AND ACRONYMS

D	Dollar Sunfish
ENP	Everglades National Park
J	African Jewelfish
LILA	Loxahatchee Impoundment Landscape Assessment

CHAPTER I

GENERAL INTRODUCTION

The introduction of a nonnative species can have multiple effects that modify traits and behaviors of native species, alter how ecosystems function, and impose socioeconomic costs (Smith, Hewitt and Klenk 2012; Loope 2004; Coutenay 1986). Damaging effects produced by nonnatives include, but are not limited to, displacement of natives from preferable habitat (Houser, Ginsberg and Jakob 2014; Brooks and Jordan 2010), changes in native behavior, reduction or loss of native populations (Dorcas et al. 2012; Kaufman 1992) along with changes to native communities and key ecosystem processes (Capps and Flecker 2013; Koehn 2004; Starling et al. 2002).

The goal of my dissertation is to understand interactions between native and nonnative taxa and compare their role in aquatic communities and thus measure their influence on native competitors. To explore interactions on native species caused by nonnative invaders, I focused on Everglades National Park (ENP) where 17 nonnatives fishes have been documented over the past 50 years (Kline et al. 2013; Shafland, Gestring and Stanford 2008; Loftus 2000). Although nonnative fish have increased species richness of ENP by 50%, relatively few studies have recognized any significant ecological effects from these fish introductions, which have led to conflicting perspectives on the overall effects of nonnative aquatic taxa in the ecosystem (Schofield et al. 2013; Trexler et al. 2000; Shafland 1996). Managers need to understand the behavioral dynamics, particularly in those habitats where nonnative species are abundant (e.g., Rocky Glades and canals), along with how they affect survivorship and body condition of native taxa. Understanding behavioral dynamics requires empirical approaches that manipulate the presence of nonnatives and closely examines how natives and nonnatives interact and thus quantify the mechanisms for interaction (e.g., Porter-Whitaker et al. 2012; Brooks and Jordan 2010; Rehage et al. 2009).

In my dissertation, I investigated how native and nonnative freshwater fish interactions differed by observing survivorship, body condition, and behavior during interactions between the nonnative African Jewelfish and native Dollar Sunfish. Because of similarities in size and niche occupancy, African Jewelfish have been predicted to compete heavily with native sunfishes, including the Dollar Sunfish (Rehage, Dunlop and Loftus 2009). The African Jewelfish is a piscivorous cichlid that has spread quickly through South and Central Florida (Schofield et al. 2013; Dunlop-Hayden and Rehage 2011; Rehage, Dunlop and Loftus 2009). Dollar Sunfish were once the most abundant sunfish species in the Rocky Glades and made up 16% of total fish caught in solution holes (Rehage et al. 2013). They are now the third most abundant sunfish while Jewelfish are the second most abundant of all fishes caught in solution holes (Trujillo et al. unpublished data). Dollar Sunfish are gape limited in their diet and subsist mainly on aquatic invertebrates such as shrimp and copepods (Warren 2009; Etnier and Starnes 1993). Dollar Sunfish are aggressive towards intraspecific competitors (Etnier and Starnes 1993). The underlying interactions of naïve prey with predators has been well studied (Sih et al. 2010), while naiveté of competitors has not been addressed by previous work.

In Chapter 2, I investigated how replacing a native species with a nonnative at varying ratios in outdoor mesocosms affected the native Dollar Sunfish. I quantified effects of body condition and survivorship across simulated solution holes in the dry season. I also compared how native and nonnative species differed in their responses across treatments and time.

In Chapter 3, I surveyed deep refuge (≥ 70cm) solution holes across the dry season in the Rocky Glades. I quantified and compared the effects of survivorship and body condition from beginning to end of the dry season for numerous native and nonnative fish taxa. I also examined the individual and community effects that native and nonnative, predator and/or prey, may have on solution hole community structure.

In Chapter 4, I conducted behavioral assays to examine differences in natives from allopatric versus sympatric populations to a nonnative competitor. I quantified approach along with multiple aggressive responses invoked by African Jewelfish upon Dollar Sunfish from populations with and without a prior history of co-residency. I also compared differences in food response between native and nonnative populations.

I conclude with Chapter 5, where I discuss the broader implications of my research and explore the resilience of native adaptive behavior. I also discuss the uncertainty of climate change, nonnative species expansion, and how it may reverse restoration efforts that might have ultimately assisted in native species persistence.

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CHAPTER II

NONNATIVE AFRICAN JEWELFISH DO NOT COMPETE BUT COPE BETTER WITH ENVIRONEMTNALLY STRESSFUL CONDITIONS THAN NATIVE FISH

Introduction

Native populations are increasingly subjected to novel anthropogenic stressors, particularly species invasions (Wong and Candolin 2015; Vitousek et al. 1997). While severe effects from invasions often result from predation (McCleery et al. 2015; Richmond et al. 2015; Kaufman 1992), competition with nonnative species may also harm native taxa (Bellard, Cassey and Blackburn 2016). Interspecific competition will occur among species that share the same requirements (i.e., occupying similar niches), and those with superior competitive abilities will outcompete others (Dayan and Simberloff 2005; Weiner 1990; Connell 1983; Schoener 1983). Nonnative competitors have been shown to negatively affect native species through displacement from preferred habitats (Houser, Ginsberg and Jakob 2014; Brooks and Jordan 2010) and preferred food resources (Bonnington, Gaston and Evans 2014). However, the effects of competition can be difficult to quantify (Tylianakis 2008; White et al. 2006). For example, a study of nonnative Harlequin Ladybirds and native Flowerbugs found these two insects to be competitors, but their shared food resource was only determined through DNA gut contents analysis (Howe et al. 2016). A better understanding of competitive interactions requires empirical approaches that manipulate both the presence (frequency-dependent effects) and abundance (density-dependent effects) of nonnatives, more clearly elucidating the exact nature of competitive interactions (Tran et al. 2015; Porter-Whitaker et al. 2012; Brooks and Jordan 2010; Rehage, Dunlop and Loftus 2009).

Competition is expected to occur among functionally-similar species (San Sebastian et al. 2015; Bando 2006), which may cause decreased individual growth rates (Jackson et al 2016), shifts in diet (Jackson et al. 2016; Chang et al. 2016), fecundity

(Fraser and Lamphere 2013) and/or spatial sorting of species (Tran et al 2015; Davenport and Lowe 2016). Competition occurs when two or more individuals try to use the same limiting resources and is often context-dependent depending on the habitat (Petren and Case 1998; Petren, Bolger and Case 1993) and can favor nonnative establishment in harsh environments where survival is difficult (Manea, Sloane and Leishman 2016; Bradley et al. 2012). For instance, droughts cause widespread mortality of native vegetation allowing for opportunistic nonnative grasses to outcompete native grasses for resources such as light and space (Manea, Sloane and Leishman 2016). Further, native and nonnatives species often respond differently to environmental conditions (Gido et al. 2013; Brown, Sherry and Harris 2011), and variation can tip the balance of competition, frequently in the favor of nonnative species. For example, the construction of roads and resulting traffic has led to differential effects on movement between native and nonnative squirrels, restricting the use of space by the native species, while nonnatives acquire more resources (Chen and Koprowski 2016). In aquatic systems, alterations to natural hydrological regimes may cause atypical hydrological variation that can favor nonnative taxa, to the detriment of native species (Cervantes-Yoshida, Leidy and Carlson 2015).

Florida Everglades exhibits prominent natural and anthropogenic hydrological variation, which can result in harsh conditions for aquatic organisms, including fishes (McVoy et al. 2011; Kobza et al. 2004; Loftus, Johnson and Anderson 1992). During the dry season, lower water levels force fishes to move from interconnected freshwater marshes into isolated refuge habitats where both abiotic stressors (i.e., poor water quality, low resources), and biotic stressors (i.e., high intraspecific densities, competition and predation) may be strong, particularly as the dry season progresses (Fig.1, Rehage et al.

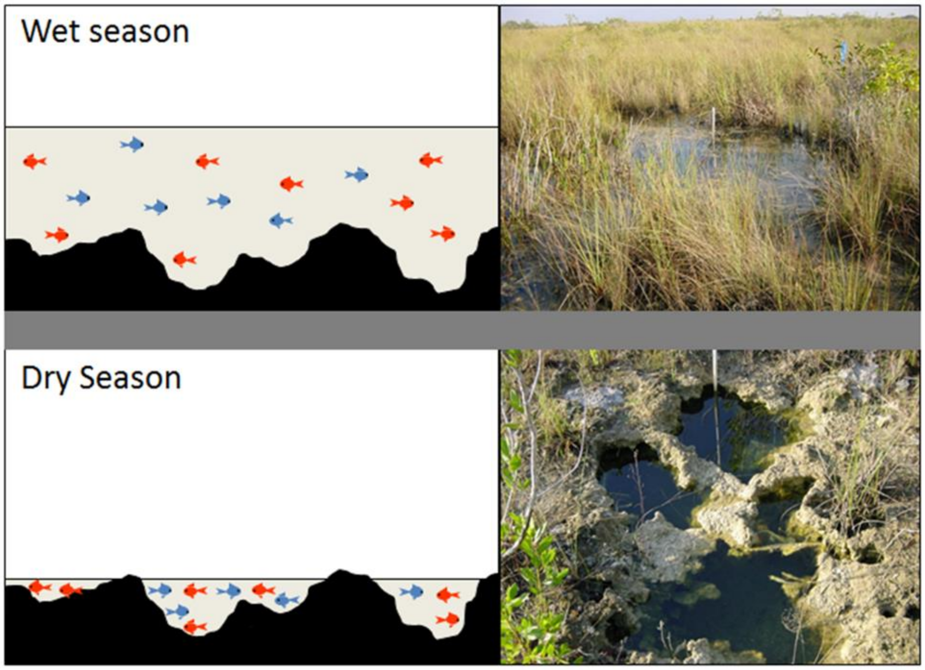

Figure 1: Pictorial and photo of ephemeral landscape depicting marsh and solution holes during the wet and dry season

2014; Parkos, Ruetz and Trexler 2011; Alho 2008; Kobza et al. 2004). Stressful conditions in these refuge habitats have been exacerbated by drainage and impoundment over the past 100 years, which have resulted in more dry downs during the dry season throughout the Southern Everglades, including Everglades National Park (ENP, McVoy et al. 2011). The Rocky Glades is a short hydroperiod wetland habitat located in eastern ENP that has been severely affected by regional drainage (McVoy et al. 2011). The region is dotted by solution holes or karst cavities that retain water when surrounding marshes dry. Solution holes are used by fishes and other aquatic fauna during the dry season (Kline et al. 2013; Rehage et al. 2014). Everglades National Park (ENP) has been invaded by 17 nonnative fish species in the last 50 years, making the Rocky Glades one of the most invaded habitats of the Everglades (Kline et al. 2013; Shafland et al. 2008).

In my study, I asked (1) whether harsh environmental conditions have a differential effect on a native versus nonnative species, and (2) whether the presence of a nonnative harms a native species in the same guild under these harsh conditions. To address these questions, I simulated dry season conditions in experimental refuge habitats (outdoor mesocosms), and varied the presence and relative abundance of the nonnative African Jewelfish, *Hemichromis letourneuxi,* in mesocosms containing native Dollar Sunfish, *Lepomis marginatus*. I quantified survival and body condition of both species over several weeks to simulate stressful dry season conditions where fish are isolated in small pools with decreasing resources. I hypothesized that nonnative African Jewelfish would tolerate these harsh environmental conditions better than the native Dollar Sunfish since successful invaders are known to have broad physiological tolerances (Verbrugge et al. 2012; Hou et al. 2014; Schofield, Loftus and Brown 2007). Also, because the African

Jewelfish is aggressive and territorial (Schofield, Loftus and Brown 2007), an increase in the ratio and density of Jewelfish relative to the native Dollar Sunfish should lower survival and body condition of the native Dollar Sunfish. At elevated densities, nonnative birds, spiders, and weevils have been also shown to harm native species (Anderson 2006; Gruner 2005; Louda et al 1997).

Methods

Study system

During the Everglades dry season (November to May, McVoy et al. 2011), marshes in the Rocky Glades go dry, and fishes are forced to seek out solution holes (local refugia) or return to deeper sloughs (Rehage et al. 2014; Goss, Loftus and Trexler 2013). As surface water recedes, solution holes become occupied by a number of native species (belonging to the families Poeciliidae, Funduilidae, Ictaluridae and Centrarchidae), particularly Eastern Mosquitofish, Sailfin Mollies, Marsh Killifish, Yellow Bullhead, and several sunfishes (*Lepomis* spp.), as well as nonnative species (Cichlidae and Clariidae). Among these nonnative taxa, the nonnative African Jewelfish have become a dominant component of solution holes, outnumbering native species (Kline 2006; Rehage et al. 2014). African Jewelfish invaded ENP in 2000 and since then has expanded rapidly in the region (Lopez, Jungman and Rehage 2012), greatly increasing in abundance (Kline et al. 2013). African Jewelfish's aggression toward other species (Schofield, Loftus and Brown 2007), and bi-parental care (Noble and Curtis 1939) which improves offspring survival in the presence of other piscivorous species likely helped them invade the Rocky Glades. Once solution holes are isolated from the marsh, resources (e.g., water, food, and refuge) and habitat quality (e.g., decreased dissolved oxygen and increased ammonia) continually degrade as the dry season progresses, eventually leading to desiccation and mortality for solution hole inhabitants until the onset of the wet season (Kobza et al. 2004; Rehage et al. 2014).

Experimental design

In a mesocosm setup designed to mimic dry season conditions in solution holes, I varied the presence and ratio of nonnative African Jewelfish to native Dollar Sunfish and compared the effects of varying relative abundances on the survivorship and body condition (a measure of overall health taking into account length and weight) of both species. I simulated dry season conditions for a period of 5 weeks (29 Jul – 1 Sep 2012). I used 30 concrete outdoor mesocosms (each with the capacity to hold 1200 liters and a surface area of $1.06 m^2$) filled with 30 cm of well water (average solution-hole depth, Kobza et al. 2004) at the Daniel Beard Center, in ENP (Fig.2). Stove pipes maintained water depths at 30 cm for the entire duration of the experiment. Using a randomized block design, I assigned the following five treatments (in replicates of six) to mesocosms: a control with eight Dollar Sunfish only (0J:100D), two Jewelfish + six Dollar Sunfish (25J:75D), four African Jewelfish + four Dollar Sunfish (50J:50D), six African Jewelfish+ two Dollar Sunfish (75J:25D), and twelve African Jewelfish + four Dollar Sunfish (75J:25D x2) (Table 1). Four of the five treatments follow a replacement experimental design, where total fish density remained constant, allowing me to examine inter- and intraspecific interactions between the two species (Sih, Englund and Woosler 1998; Schmitz 2007). The fifth treatment maintains a ratio of 75J:25D, but at double the

Figure 2: Photo of experimental tank set-up. 5 treatments (in replicates of 6): a control with 8 Dollar Sunfish only (0J:100D), 2 jewelfish + 6 Dollar Sunfish (25J:75D), 4 African Jewelfish + 4 Dollar Sunfish (50J:50D), 6 African Jewelfish+ 2 Dollar Sunfish (75J:25D), and 12 African Jewelfish + 4 Dollar Sunfish (75J:25D x2)

Treatment	African Jewelfish	Dollar Sunfish	Total fish per treatment
0J:100D	0	8	8
25J:75D	2	6	8
50J:50D	4	4	8
75J:25D	6	2	8
75J:25D X 2	12	4	16
Total # of fish used	144	144	
Mean length (cm) at stocking	5.22 ± 0.04	5.06± 0.06	
Mean weight (g) at stocking	3.98 ± 0.09	3.44 ± 0.12	

Table 1: Total number of fish stocked for each species was 144, breakdown of the 5 treatments (each replicated 6 times) used in the study. Mean lengths of Dollar Sunfish and African Jewelfish were 5.22 and 5.06cm; mean weight of Dollar Sunfish and African Jewelfish were 3.98 and 3.44g at the start of the study.

density of the other treatments to replicate the fact that African Jewelfish are often found in high concentrations in the confined solution hole habitats (Kline et al. 2011).

At the beginning of the experiment, Dollar Sunfish and African Jewelfish were added to standardized, representative solution hole communities. These solution hole communities were composed of the most abundant species typically found in solutions holes (in representative densities): Grass Shrimp (*Palaemonetes paludosus*), Eastern Mosquitofish (*Gambusia holbrooki*), Crayfish (*Procambarus* spp.), Florida Flagfish (*Jordanella floridae*), and Sailfin Mollies (*Poecilia latipinna*) (Gunderson and Loftus 1993; Dorn, Trexler and Gaiser 2006). African Jewelfish consume a varied diet of invertebrates, algae, and fishes in their native range but a picivorous diet characterized fish in their invaded range (Hickley and Bailey 1987; Rehage et al. 2014). Dollar Sunfish are known to consume small invertebrate prey, particularly shrimp and copepods (Warren 2009; Etnier and Starnes 1993). Tanks were also stocked with 2250 mL of periphyton and associated infauna (Turner, Fetterolf and Bernot 1999; Lamberti 1996), collected from the Taylor Slough area. Everglades periphyton is composed up of a complex web of organisms that included live and dead algae, bacteria and detritus, and contain infauna that are prey for Dollar Sunfish and African Jewelfish (Rehage et al. 2014; Bransky and Dorn 2013; Warren 2009; Dorn, Trexler and Gaiser 2006; Turner, Fetterolf and Bernot 1999; Etnier and Starnes 1993; Hickley and Bailey 1987). Tanks were also left uncovered to allow for colonization of aquatic insects. Although dietary overlap between Dollar Sunfish and African Jewelfish may be low, since Jewelfish consume larger prey and more fish, interference competition, aggression and some resource competition for the smaller prey resource was expected. Representative prey species and periphyton were added 24-

48 hours prior to the Sunfish and Jewelfish. Tanks were also provided with 2 concrete blocks to provide structure, and covered with 30% shade-cloth on one end of the tank to simulate shaded conditions found in the field. Using baited minnow traps, dip nets, and boat electrofishing, the two focal species and the smaller taxa from the Rocky Glades region 0 to 4 weeks were collected and kept them in mesocosms prior to the start of the study.

To track changes in body condition over time, African Jewelfish and Dollar Sunfish were tagged on their caudal peduncle with visual implant elastomer tags (Figure 3, Northwest Marine Technology, Inc.) using a two-line color combination. Marked individuals were imaged, weighed, and measured at the beginning and immediately at the end of the study. Fulton's Condition Factor was used as an indicator of body condition (Schmidt-Nielsen 1984):

$$\text{Fulton's condition factor } (K) = \frac{weight}{standard\ length^{3}}$$

Statistical analyses

To examine variation in survivorship and body condition, generalized linear models (GLMs) that tested for the effect of treatment, species and the interaction were used. For survivorship, the proportion of fishes that survived to the end of the study was compared. Proportions were arcsin(x) transformed and checked with Shapiro-Wilks' test for normality.

Percent change in condition was calculated by initial body condition minus final body condition for each individual that survived. Values for change in condition were $\log_{10}(x)$ transformed and checked for normality using the Shapiro-Wilks test. The GLMs

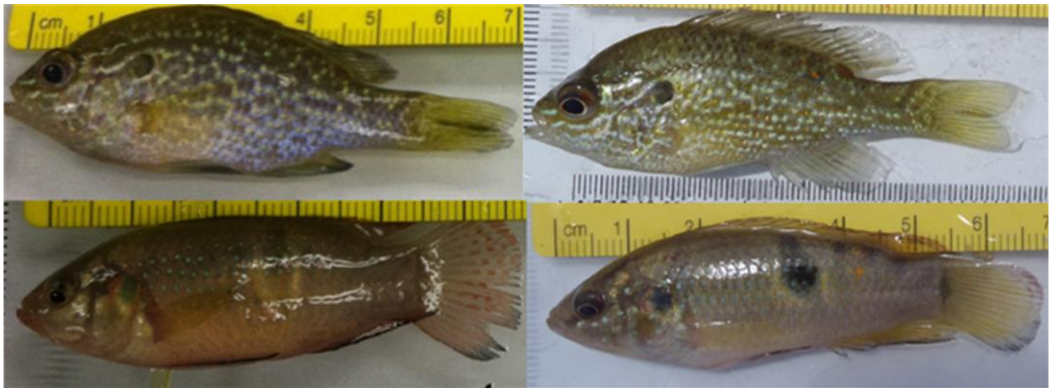

Figure 3: Photos of African Jewelfish and Dollar Sunfish at beginning and end of study. Elastomer tag seen on fishes at the end of study.

were followed by Tukey’s post-hoc comparisons to examine patters of significance. Analyses were performed using SYSTAT 13®.

Results

Overall, I created representative isolated aquatic taxa communities that began with the same quantity of resources which became limited over time and successfully mimicked a stressful solution hole environment. Nonnative African Jewelfish survived harsh conditions better than the native Dollar Sunfish. While only 66 of the 144 Dollar Sunfish stocked at the onset of the study survived, 110 of the 144 stocked African Jewelfish survived to the 5-week endpoint of the study. Across treatments, survival was significantly higher for African Jewelfish that Dollar Sunfish (Table 2a, Figure 4). The nonnative African Jewelfish averaged almost 90% survivorship, whereas survivorship for native Dollar Sunfish averaged near 50%. Contrary to expectations, however, survival did not vary across treatments, nor did the treatments affect each species’ survival differently (Table 2a). Most notably, survival of native Dollar Sunfish was similar in the presence and absence of the nonnative African Jewelfish.

For the surviving fish, I noted significant variation in body condition over the course of the experiment. Both species lost condition across all experimental treatments but the loss in condition was greater for the native Dollar Sunfish (Table 2b, Fig. 5). Dollar Sunfish declined 33% in body condition over the 5 weeks, whereas African Jewelfish declined only 18% in body condition. Changing the relative or total abundance of the two species (treatment effect) did not affect body condition in either species (Table

a. Survivorship

Source	**SS**	**df**	**MS**	**F-ratio**	**p-value**
Constant	**11.63**	**1**	**11.63**	**146.19**	**0.001**
Treatment	**0.39**	**3**	**0.13**	**1.64**	**0.195**
Species	**0.69**	**1**	**0.69**	**8.64**	**0.005***
Treatment*Species	**0.21**	**4**	**0.05**	**0.65**	**0.628**
Error	**3.42**	**43**	**0.08**		

b. Body condition

Source	**SS**	**df**	**MS**	**F-ratio**	**p-value**
Constant	**0.00**	**1**	**0.00**	**0.07**	**0.791**
Treatment	**0.03**	**4**	**0.01**	**1.27**	**0.281**
Time	**0.30**	**1**	**0.30**	**56.23**	**0.001***
Treatment*Time	**0.02**	**4**	**0.00**	**0.77**	**0.545**
Treatment*Species	**0.02**	**4**	**0.00**	**0.84**	**0.502**
Time*Species	**0.02**	**1**	**0.02**	**4.15**	**0.042***
Treatment*Time*Species	**0.02**	**3**	**0.01**	**1.04**	**0.375**
Error	**1.80**	**338**	**0.01**		

Table 2 General linear model statistics for survivorship and body condition of focal fishes across treatments and time

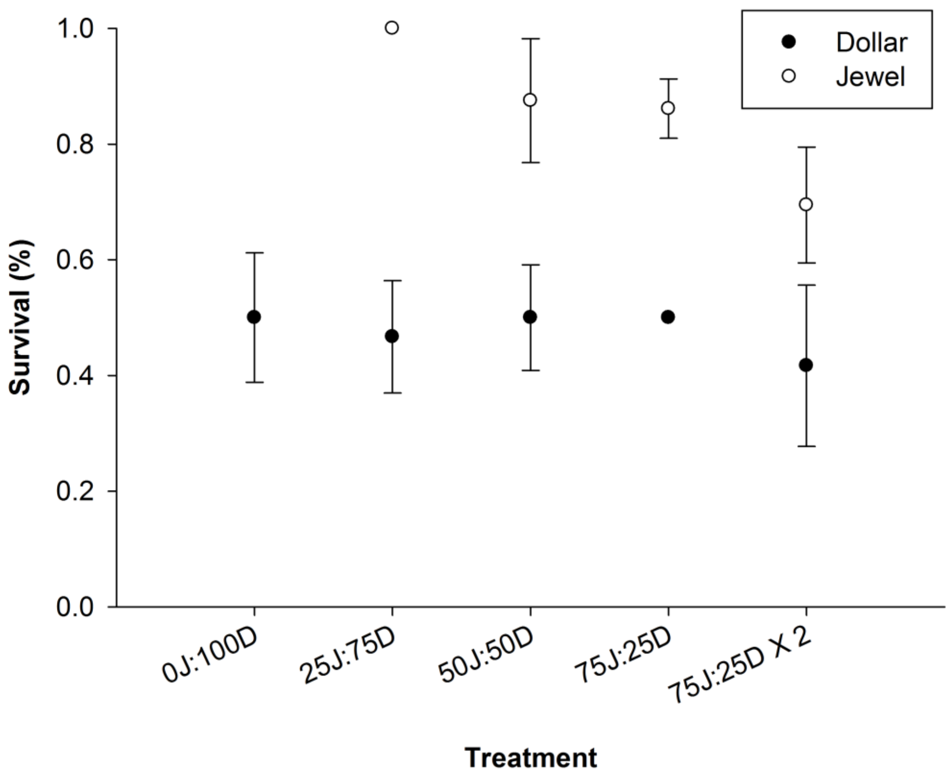

Figure 4 Scatter plot of percent survivorship across treatments for Dollar Sunfish and African Jewelfish. Dollar Sunfish had a 50 ± 3 percent survivorship while African Jewelfish had an 89 ± 3 percent survivorship. Filled in circles are native (Dollar Sunfish) averages and empty circles are nonnative (African Jewelfish) averages

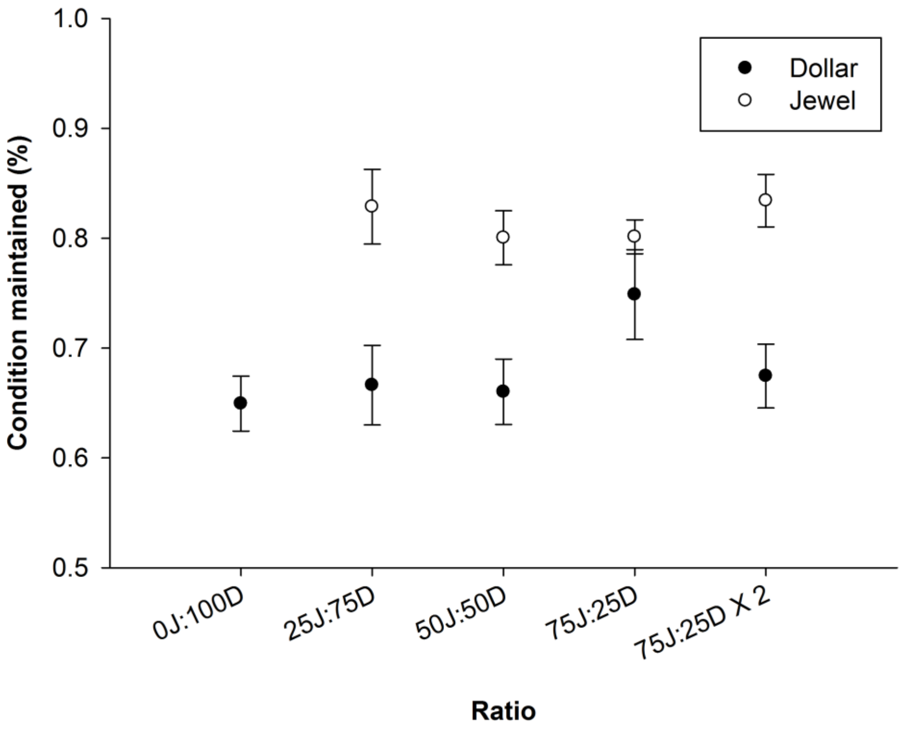

Figure 5: Scatter plot of body condition maintained across treatments for Dollar Sunfish and African Jewelfish. Filled in circles are native (Dollar Sunfish) averages and empty circles are nonnative (African Jewelfish) averages. Natives maintained around 66 ± 0.01 percent of their beginning body condition where nonnatives maintained around 82 ± 0.01 percent across treatments. Changes in species density or ratio had no significant effect on body condition.

2b). Similar to my survival results, the loss in condition experienced by the native Dollar Sunfish was similar in the presence and absence of the nonnative African Jewelfish.

Discussion

Native and nonnative species often respond differently to disturbances (e.g., harsh dry down conditions); patterns that may influence how species interact during competition following an invasion. In this study, I examined the effect of harsh environmental conditions associated with dry season refuge habitats on a native vs. nonnative Everglades' fish and whether presence of the nonnative had a negative effect on the native species. My results showed that at the end of five weeks, the native Dollar Sunfish experienced higher mortality (50% vs. 90%) and condition loss than the nonnative African Jewelfish. Contrary to my expectations, I detected only species effects and no effect from increasing the ratio or density of the nonnative species in the experimental treatments meaning that they probably do not compete. Both survival and condition loss were similar across varying number and/or density of the nonnative African Jewelfish. Importantly, for the native Dollar Sunfish, condition loss and survival were comparable in the absence vs. presence of African Jewelfish. These results suggest that African Jewelfish are better able to cope with harsh environmental conditions than the native species, and that for the native species; the effect of these conditions may overwhelm potential negative interactions with the nonnative species.

In my study, nonnatives were able to survive and maintain a higher body condition than the native fish. High numbers of nonnative freshwater fish, originating from releases of pets and escape from aquaculture farms (Hardin 2007; Fuller, Nico and

Williams 1999), have been able to survive and spread in the Everglades (Kline et al. 2013; USGS-NAS 2013; Schofield and Loftus 2014). Nonnatives proliferate in an ecosystem may attribute their success to character traits like aggression, boldness, broad diet, exhibition of a wide range of physical tolerances, and having some form of paternal care (Schofield et al. 2013). Previous studies conducted in solution holes of the Rocky Glades are similarly reported nonnatives having a higher survivorship as compared to natives (Trexler et al. 2000; Kobza et al. 2004; Kline et al. 2013). Nonnatives like the African Jewelfish exhibit traits found in invasive species like aggression, bi-parental care and being dietary generalists (Parkos, Ruetz and Trexler 2011; Schofield et al. 2013), consuming invertebrates as part of their diet, and competing for refugia, potentially making the Dollar Sunfish a poor competitor in dry down situations.

Nonnative survival and establishment is contrary to the perception that native taxa are preadapted to the native disturbance regime and should be expected to do better than nonnatives in their introduced ranges (Kiernan, Moyle and Crain 2012). As observed in a California stream, where native fishes recovered dominance after restoration of historic hydrological regimes while nonnative fishes were displaced (Kiernan, Moyle and Crain 2012). Historic hydrology of the Everglades has been disrupted under current water and flood management, which has become harsh for native aquatic fauna (McVoy et al. 2011). Nonnatives, like the African Jewelfish, may be adapted to handle the stress of the disturbed ephemeral landscapes, possibly because of similar competitive habitats within their native range (Seehausen and Schluter 2004). Replacement of native Dollar Sunfish with nonnative African Jewelfish should have community wide implications due to their different roles as consumers.

The African Jewelfish is an aggressive and territorial cichlid that I expected to compete for resources with Dollar Sunfish. Literature indicated that as resources become limited, competition increases and species with higher competitive ability persist (Cain and Langmore 2016). Therefore, as I decreased the ratio of natives to nonnatives I expected to see higher mortality and loss of condition for the natives but I did not. African Jewelfish are diet generalists (Parkos, Ruetz and Trexler 2011; Schofield et al. 2013), consuming a varied diet of invertebrates, algae, and fishes (Hickley and Bailey 1987; Rehage et al. 2013). Contrary to my predictions of increased mortality and decreased body condition in natives, I observed that natives did poorly across all treatments, regardless of nonnative numbers. Dollar Sunfish are gape-limited, and the diet consists mainly of shrimp and copepods (Warren 2009; Etnier and Starnes 1993). Native Dollar Sunfish and African Jewelfish avoid competition for food because they eat different prey and may not interact as much as was expected prior to my experimental study. African Jewelfish may affect natives, such as Dollar Sunfish, not through competition but perhaps via predation of juveniles since they are a small bodied piscivores and novel to the ecosystem. Alternatively, I might have failed to detect competition because of low statistical power (power=5%) or the five week study was not long enough to detect differences.

Communities are shaped by their environment and how well taxa match their trait characteristics (Lhotsky et al. 2016). Favorable environmental conditions often promote taxa dissimilarity, while harsh conditions cause selection of favorable traits that supports trait convergence (Lhotsky et al. 2016). My findings that Jewelfish had no measurable effect on native Dollar Sunfish suggest that the effects of species interactions (e.g., competition) can be damped or swamped by the effect of harsh environmental conditions. As environmental conditions become more severe, a focal species may experience a shift from negative competitive effects to neutral or positive facilitative effects, called the stress gradient hypothesis (Barrio et al. 2013). For example, an aquatic plant located in a stressful zone with low oxygen, benefited from having crabs present because they helped aerate the sediment. But when the plant was located in highly aerated sediment, the presence of crabs decreased plant productivity (Daleo et al. 2009). Therefore, harsh environmental conditions in the Everglades may shift competitive effects that may have been found between native and nonnative taxa under less stressful dry downs.

Historically, the Rocky Glades experienced a less severe dry season and only 35 native freshwater fishes were present in the system (McVoy et al. 2011). As a result of prolonged drying, the Rocky Glades may now function as a sink for native fishes, and a source of nonnative fishes that may be better adapted to these chronically stressful conditions (Rehage et al. 2013). Dollar Sunfish may be more affected by current water management that has caused degradation of the Rocky Glades ecosystem. As habitat quality decreases so may native species numbers (Fraser, Banks and Water 2014), which may than open niches to be colonized by nonnative species (Fraser, Banks and Walter 2014; Didham, Watts and Norton 2005; Chollet et al. 2014). Once natives have been displaced and nonnatives have become established, natives may have difficulty regaining lost resources (Manea, Sloane and Leishman 2016; Bradley et al. 2012). The anthropogenic changes occurring in the eastern Everglades may ultimately lead to an ecological trap for the Dollar Sunfish and other native aquatic species.

In summary, I found that the nonnative African Jewelfish show greater resistance than a native centrarchid sunfish in post-drainage conditions of simulated Everglades' solution holes. African Jewelfish have been in ENP since 2000, so natives may have already adjusted to their presence. Adaptation of sunfish to the invader over the 15 years since the initial invasion could be the reason why I did not find survivorship or body condition differences between treatments. Future research will explore how allopatric versus sympatric natives react to the presence of the nonnative African Jewelfish to assess reasons why I saw no treatment effects in survivorship or body condition in my experiment. Nonnatives species do not always have the same influences on each of the communities in which they are introduced, and effects of these species are often context dependent and can vary over time and season, and are therefore hard to predict (Ricciardi and MacIsaac 2011; Biswas and Wagner 2014; Strayer et al. 2006). Predictions of nonnative effects can be better assessed through long-term datasets that include times before and after invasion to be able to document change and establish effects.

By restoring and increasing habitat quality and quantity, managers may be able to increase native numbers while simultaneously decreasing nonnatives' competitive ability (Didham et al. 2007; Kiernan, Moyle and Crain 2012; Ringler, Hodl and Ringler 2015). As climate change becomes more severe, which could counteract restoration; it is important to discover the unknown role harsh environmental conditions play in native species persistence and whether drier conditions do in fact favor nonnatives.

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CHAPTER III

SURVIVORSHIP OUTCOMES: NATIVE AND NONNATIVE FRESHWATER FISHES TRAPPED IN A COMPETITIVE DRY DOWN ENVIRONMENT

Introduction

South Florida's subtropical climate attracted suburban residents, tourists, and farmers, and underwent much hydrological change to make the landscape suitable for urbanization introducing many nonnatives (Harvey et al. 2010). The Everglades ecosystem is relatively young, only around 5,000 years old (Gleason and Stone 1994), with a low species diversity of 35 native freshwater fish in Everglades National Park (Loftus 2000). Low diversity, along with disturbance, may have made the system vulnerable to invaders with its low biotic resistance (Stachowicz et al. 2002). Everglades National Park (ENP) has 17 nonnative fishes that have spread and become established in the park (Kline 2006; Loftus 2000; Kline and Fratto 2008; Shafland, Gestring and Stanford 2008; Kline et al. 2013). Recognizing whether nonnatives do or do not influence native species composition and abundances, is imperative for managers to make knowledgeable decisions that lead to native species persistence and nonnative species control.

Worldwide, anthropogenic disturbances have drastically changed the landscape and will continue at the expense of natural ecosystems (Palmer et al. 2004). The most disruptive anthropogenic disturbances include global climate change, introduction of invasive species, and changes in land use (e.g., agriculture and urbanization; Vitousek et al. 1997). Climate change has brought rising temperatures and droughts which are expected to become more frequent and erratic in the future (Bradley et al. 2012). In conjunction with climate change, disturbances such as alteration of hydrology for freshwater management can affect the persistence of native and nonnative species in ecosystems (Nosakhare et al. 2012; Milliman et al. 2008; Godfray and Garnett 2014;

Maree et al. 2013). Nonnative flora and fauna which have been released through the exotic pet and ornamental plant trades can lead to secondary effects on native species (Hardin 2007; Loftus 2000). A warming climate has furthered the ability of many tropical nonnative species to survive and spread (Hardin 2007; Loftus 2000). Novel disturbances such as the ones described above can put natives at a disadvantage relative to nonnatives through changes in dispersal opportunities and resource availability (Bradley et al. 2012).

Water management for flood control, drinking water, and agriculture has drastically altered hydrology of the landscape (Oki and Kanae 2006). The management of the land has made agricultural, industrial and residential development possible through the creation of canals, levees, and dams. Hydrological changes have degraded the system by serving as barriers for natives along with conduits of nutrients, endocrine disrupters, and invasive species (Bronstert 2004; Light and Dineen 1994; Harvey et al. 2010; Davis and Ogden 1994; Clotfelter, Bell and Levering 2004). Areas especially affected, concerning decreases in endemic native species numbers, are those found in the lower reaches of the watershed, downstream of urban development (Cervantes-Yoshida, Leidy and Carlson 2015). Changes to hydrology that decrease water-flow often free nonnative species from competition with natives, doing so by decreasing quality of native habitat and native species numbers (Osmundson and Burnham 1999). Native species frequently benefit after restoration of habitat or hydrology, while reversing the gains made by nonnative populations (Kiernen et al. 2012; Gido and Propst 2012). Water management that deviates from the natural hydrology of the system can therefore have many negative effects at both abiotic and biotic levels that include changes to the physical habitat, connectivity, native species and proliferation of nonnatives (Ostrom 1999; Grantham, Merenlender and Resh 2010; Bunn and Arthington 2002).

Nonnative species often have the advantage upon arrival to a degraded ecosystem because of the depression of native populations already created by the disturbance (Didham, Watts and Norton 2005; Cholet et al. 2015; MacDougall and Turkington 2005). Not only do nonnatives have the benefit of open niches that they can monopolize, nonnatives often have traits known to improve fitness in competitive environments and disturbed habitats, including high foraging rates (Pintor and Sih 2009), generalist diets, and aggressive behavior (Pintor, Sih and Kerby 2009). A nonnative can cause competitive displacement of inferior individuals from resources such as food (Hasegawa 2016; Mooney and Cleland 2001) and refuge (Brooks and Jordan 2010) potentially decreasing native survival. Direct competition can displace native species, as seen in a nonnative ant that is responsible for native ant nest raids (LeBrun, Abbott and Gilbert 2013). Competition may also be indirect by way of exploitation competition, where native and nonnatives consume the same limited food sources (Howe et al. 2016). Nonnatives have been able to spread based on their pre-adapted physiological traits along with the aid of human introductions into tropical and subtropical areas (Verbrugge et al. 2012; Hou et al. 2014; Schofield, Loftus and Brown 2007; Hardin 2007).

The Rocky Glades region located in ENP experiences seasonal changes in water levels (Figure 1; Kline et al. 2013). Over the past 100 years these fluctuations have been enhanced in the extreme because of water being held back for seasonal agriculture, flood management, and urban use (Davis and Ogden 1994; McVoy et al. 2011). Today, at the onset of the dry season, fishes in the Rocky Glades are forced to move into deeper water

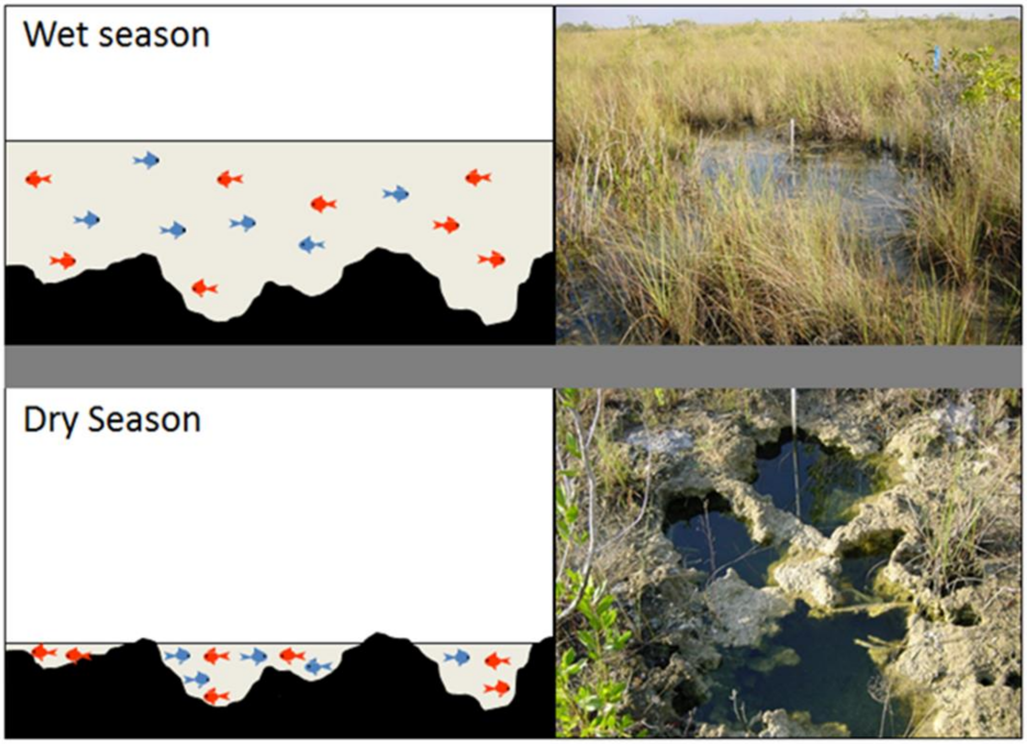

Figure 1: Ephemeral landscape depicting marsh and solution holes during the wet and dry season

sloughs, canals, or karst solution holes that serve as refuges for up to half of the year (McVoy et al. 2011; Harvey et al. 2010; Kobza et al. 2004). If fishes choose a solution hole as a refuge: environmental variables, such as water quality, species composition and density are affected by the size, complexity, and aquatic vegetation within that refuge once that hole becomes hydrologically isolated from the rest of the marsh (Kobza et al. 2004). Estimates show that over 80% of solution holes are shallow (<0.5 m), with most refuges desiccating yearly under the current water management regime (Kobza et al. 2004). Over the duration of the dry season, resources for fishes in solution holes (e.g., water and food) become further limited, while habitat quality continually degrades (e.g., decreased dissolved oxygen and increased ammonia) (Rehage et al. 2014; Kobza et al. 2004). The extended stressful conditions of the Rocky Glades, exacerbated by current water management practices, may now cause the Rocky Glades' solution hole complex to simultaneously function as a trap for native fishes and a refuge for nonnative fishes that may be better adapted to these conditions (Rehage et al. 2014).

The primary objective of my study was to examine the individual and community effects that nonnative fishes may have on solution hole community structure. From my previous findings, I can predict a series of outcomes from the interaction between the altered hydroperiod and invaded fish communities: solution holes should have a high abundance of small individuals when first disconnected from the marsh. Once disconnected, body size should shift to larger-bodied fishes because smaller fishes will likely be consumed by piscivores over the duration of the dry season. Species composition should begin as a native-biased fish community and later shift to a nonnative-biased community by the end of the dry season, because nonnatives are often better adapted to competitive stressful conditions (Verbrugge et al. 2012; Hou et al. 2014; Schofield, Loftus and Brown 2007). Fish that are omnivores should have a greater survivorship because they can switch food types when their preferred food is depleted (Schreber 1997; Volterra 1928). Body condition should decrease for all fishes as resources become limited but should be maintained better by nonnatives. To test these hypotheses, I asked the following questions: (1) How is size structure and community assembly changed from the beginning to the end of the dry season? (2) Does the ratio of natives to nonnatives change over the dry season? and (3) How does body condition of natives versus nonnatives change from the beginning to the end of the dry season? To address these questions, I monitored aquatic communities in Rocky Glades' solution holes across two consecutive dry seasons. I quantified community assembly, survivorship and body condition of native and nonnative species at the beginning and end of the dry season.

Methods

The effects of season on survivorship and body condition of taxa in the Rocky Glades were compared. Select solution holes across the dry seasons, located along Boundary Road and Main Park Road were surveyed. Twenty-eight solution holes were surveyed in 2012-13 and 38 solution holes in 2013-2014. Solution holes based on sites with a long hydroperiod, at a depth of ≥ 70 cm and low occurrence of vegetation to aid in sampling ease were chosen. Sites with high vegetation could not be sampled effectively for species composition and abundance; fish become entangled in vegetation affecting accurate surveys (Penczak 2013; Killgore et al. 1988). Data collection began when the solution holes became disconnected from the marsh. After the solution holes were chosen, backpack electrofishing surveys were conducted to determine assemblages and body condition of taxa at the onset of the dry season. Fish were collected using a Smith-Root, Inc. LR-24 Electrofisher backpack electroshocker. Fish were stunned using a 7Ah battery at 60Hz with a 5 ms pulse width. The anode consisted of a metal ring with a 28cm diameter and the cathode was a 3 m stainless steel cable. Two people with a 2 mm mesh dip net collected the stunned fish. The solution holes were considered depleted of fish once five passes were conducted with the absence of any new fish surfacing. Abiotic readings of solution hole conditions (temperature, conductivity, salinity, turbidity and dissolved oxygen) and water level measurements were taken at the beginning and end of the dry season. Any mortality was noted and excluded from the beginning species assemblage.

Survival and average body condition of all fish taxa were compared at the beginning and end of study. All fish species in a solution hole were counted and a subset were weighed and measured and then returned to the solution hole. To compare body condition of individual species at the beginning and end of the dry season, residuals of transformed log(body mass) adjusted for log(body length) were tested (Jakob et al., 1996; Kotiaho, 1999; Marshall et al., 1999).

Statistical analyses

Variations were examined using three-way ANOVAs that tested the effects of season, year, and species on response variables (survivorship and body condition). To satisfy assumptions of parametric tests, fish abundances and species richness values were checked with Shapiro-Wilks' test for normality prior to analysis. Analyzes were conducted in SYSTAT 13® and Sigmaplot 11.0®. Correlation coefficients were calculated for all species pairs per solution hole site. All species pairs were analyzed for residuals of number of individual species going in adjusted for individual species proportional survivorship.

Results

Size structure and community assembly

Median length of all fish species except the native Yellow Bullhead Catfish were smaller at the beginning of the dry season than at the end (Table 1). No difference in native versus nonnative survivorship with respect to size were found (Figure 2, p-value 0.123). Fish guilds that survived until the end of the dry season were ones that incorporated invertebrates and fish into their diets (Figure 3). Average number of fish caught across all solution holes decreased over the course of the dry season ($p < 0.001$). Overall survivorship did not differ between years (2012-2013: 22%-22%) ($p = 0.997$) with no season-by-year interaction ($p = 0.99$). Average survivorship within each solution hole also decreased in both years ($p < 0.01$) and did not differ between years ($p = 0.83$) (Figure 4). Average species richness within each solution hole also decreased ($p <0.01$) and did not differ between years ($p = 0.31$), (Figure 5).

Native and nonnative assembly

At the beginning of the dry season, native taxa made up a greater proportion of community members in solution holes, accounting for ~80% and ~74% of all individuals

Common name **Nonnative** **Native**	**Scientific name**	**Median length Early dry (cm)**	**Late dry % change (cm)**	**Feeding guild**
African Jewelfish	*Hemichromis letourneuxi*	3.95	+5.06	P/I
Black Acara	*Cichlasoma bimaculatum*	4.95	+2.02	P/I
Brown Hoplo	*Hoplosternum littorale*	7.60	+7.89	I/D
Jaguar Guapote	*Parachromis managuensis*	6.15	+88.62	P/I
Mayan Cichlid	*Mayaheros urophthalmus*	4.85	+7.22	P/I
Pike Killifish	*Belonesox belizanus*	6.90	+7.22	P
Spotted Tilapia	*Pelmatolapia mariae*	9.30	+18.84	H
Walking Catfish	*Clarias batrachus*	11.50	+2.15	P/I/H/D
Bluefin Killifish	*Lucania goodei*	1.95	-	I/H
Dollar Sunfish	*Lepomis marginatus*	4.40	-9.09	I
Eastern Mosquitofish	*Gambusia holbrooki*	2.45	+18.37	I
Florida Flagfish	*Jordanella floridae*	2.10	-	I/H
Golden Topminnow	*Fundulus chrysotus*	3.50	-	I
Least Killifish	*Heterandria formosa*	1.30	-	I/H
Marsh Killifish	*Fundulus confluentus*	4.10	+4.88	P/I/H
Redear Sunfish	*Lepomis microlophus*	6.60	-	I
Sailfin Molly	*Poecilia latipinna*	4.85	+8.25	I/H
Spotted Sunfish	*Lepomis punctatus*	4.65	+44.09	I
Yellow Bullhead	*Ameiurus natalis*	6.45	+0.00	P/I
Warmouth	*Lepomis gulosus*	6.70	+8.96	P/I

Table 1: Species breakdown, scientific name, median length and feeding guild.

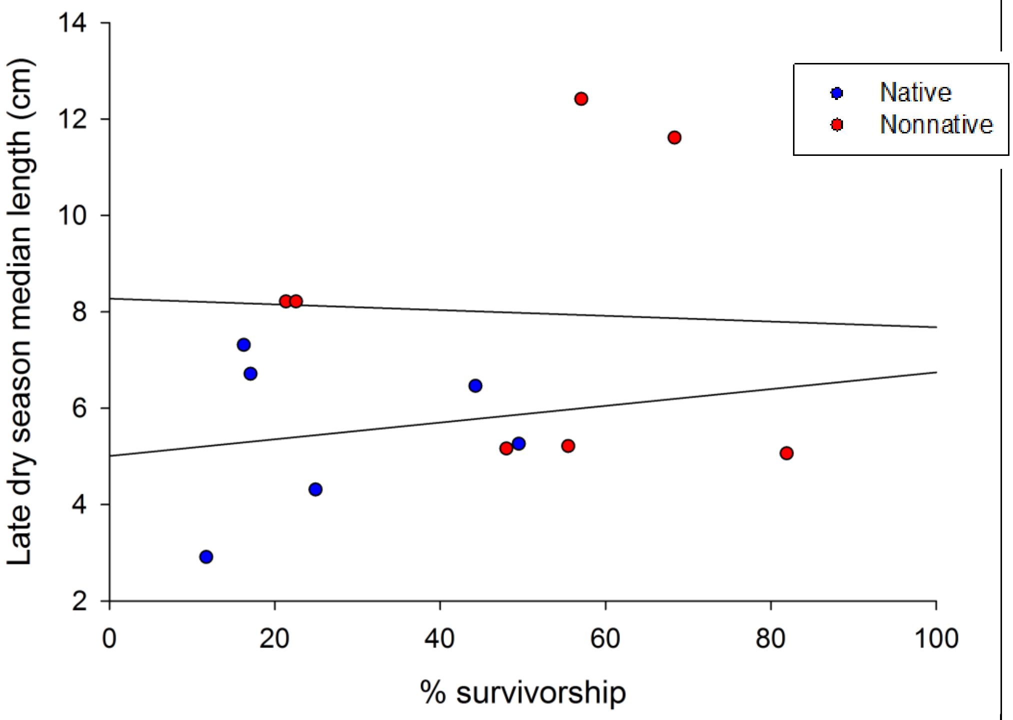

Figure 2: Scatter plot of percent survivorship versus median length (cm) of natives versus nonnatives. I found no difference in native versus nonnative survivorship with respect to size, p-value, 0.123.

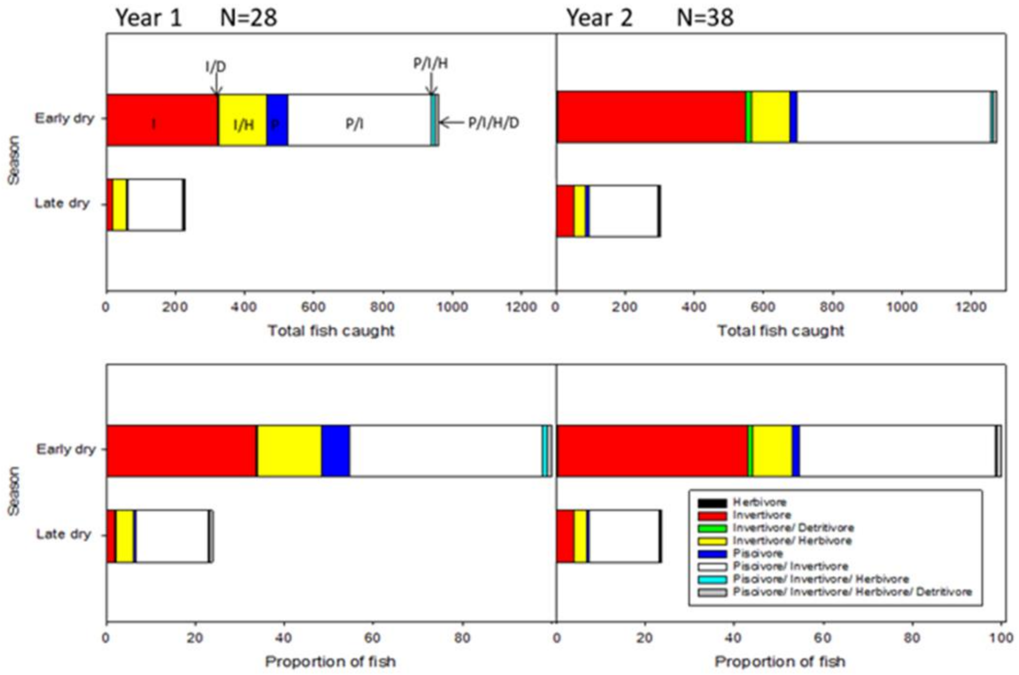

Figure 3: Total counts and proportion to survive of fish guilds across year and season for both native and nonnatives fishes added together. P/I survive best because they can feed at multiple guilds, including fishes. P: Piscivore; I: Invertivore; H: Herbivore; D: Detritivore

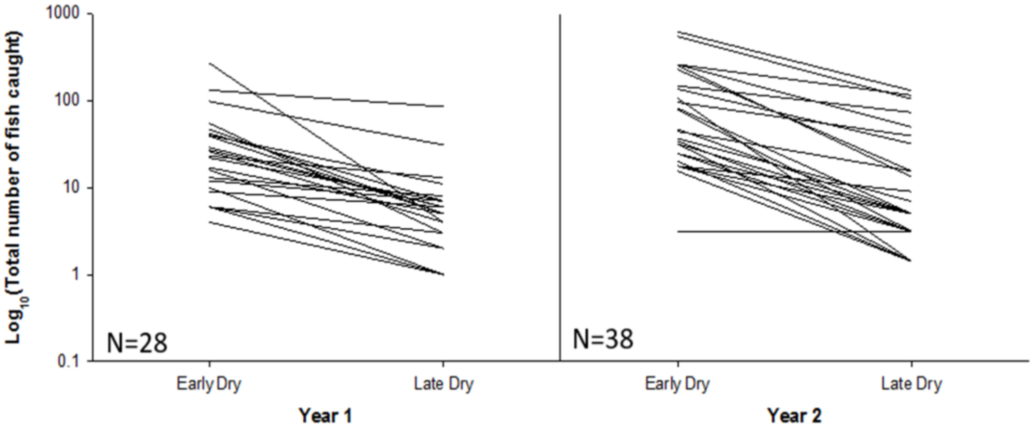

Figure 4: Average number of fish caught among solution holes decreased consistently from the early to late dry season across years. Total number of fish decreased from early to dry season for both years ($p<0.01$) and did not differ across years ($p=0.83$). Each point represents a solution hole.

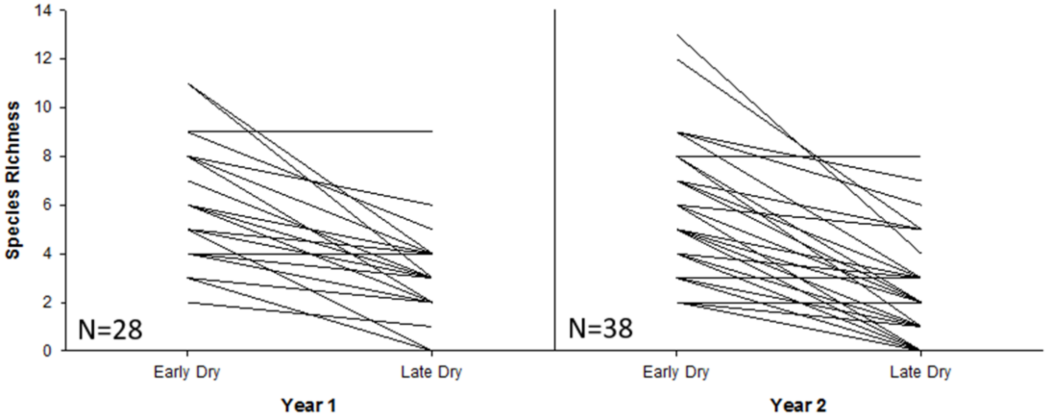

Figure 5: Average species richness among solution holes decreased consistently from the early to late dry season across years. Species richness decreased from early to dry season for both years ($p<0.01$) and did not differ across years ($p=0.31$).

while nonnatives began at 20% and 26% for both years, respectively. By the end of the dry season, native numbers dropped by 26% and 31%, and nonnatives made up 41% and 51% of individuals in the community in both years, respectively

(Figure 6). Nonnative species had a higher survivorship than native species across years (Figure 7, p-value, 0.004, 0.012, respectively).

Species that were part of the Piscivore/ Invertivore (P/I) guild were more likely to survive (p-value, 0.006, Figure 8). Nonnatives that incorporated fish and invertebrates in their diet were more likely to survive than natives who did not (p-value, 0.001, Figure 8). Four species were always the most prevalent natives at the beginning and end of the dry season for both years and only differed in order of abundance: Eastern Mosquitofish (*Gambusia holbrooki*), Yellow Bullhead Catfish (*Ameiurus natalis*), Warmouth (*Lepomis gulosus*), and Sailfin Molly (*Poecilia latipinna*) (Table 2).

Three nonnative species were the most prevalent at the beginning and end of the dry season for both years: African Jewelfish (*Hemichromis letourneuxi*), Pike Killifish (*Belonesox belizanus*), and Black Acara (*Cichlasoma bimaculatum*) (Table 2).

Positive correlation coefficients were only found when looking at species pairs. Jaguar Guapote have a higher proportion of survival when small-bodied fishes are present in higher numbers (Table 3, Figure 9). The Jaguar Guapote is part of the carnivorous P/I guild. Other positive species associations were ones that did not have completely overlapping diets; native Yellow Bullheads (P/I): nonnative Brown Hoplos (Invertivore/ Detritivore, I/D), nonnative Black Acara (P/I): nonnative Brown Hoplos (I/D), native Dollar Sunfish (I): nonnative Mayan Cichlids (P/I), nonnative Pike Killifish (Piscivore, P): nonnative Black Acara (P/I) or nonnative Mayan Cichlids (P/I) and nonnative Brown

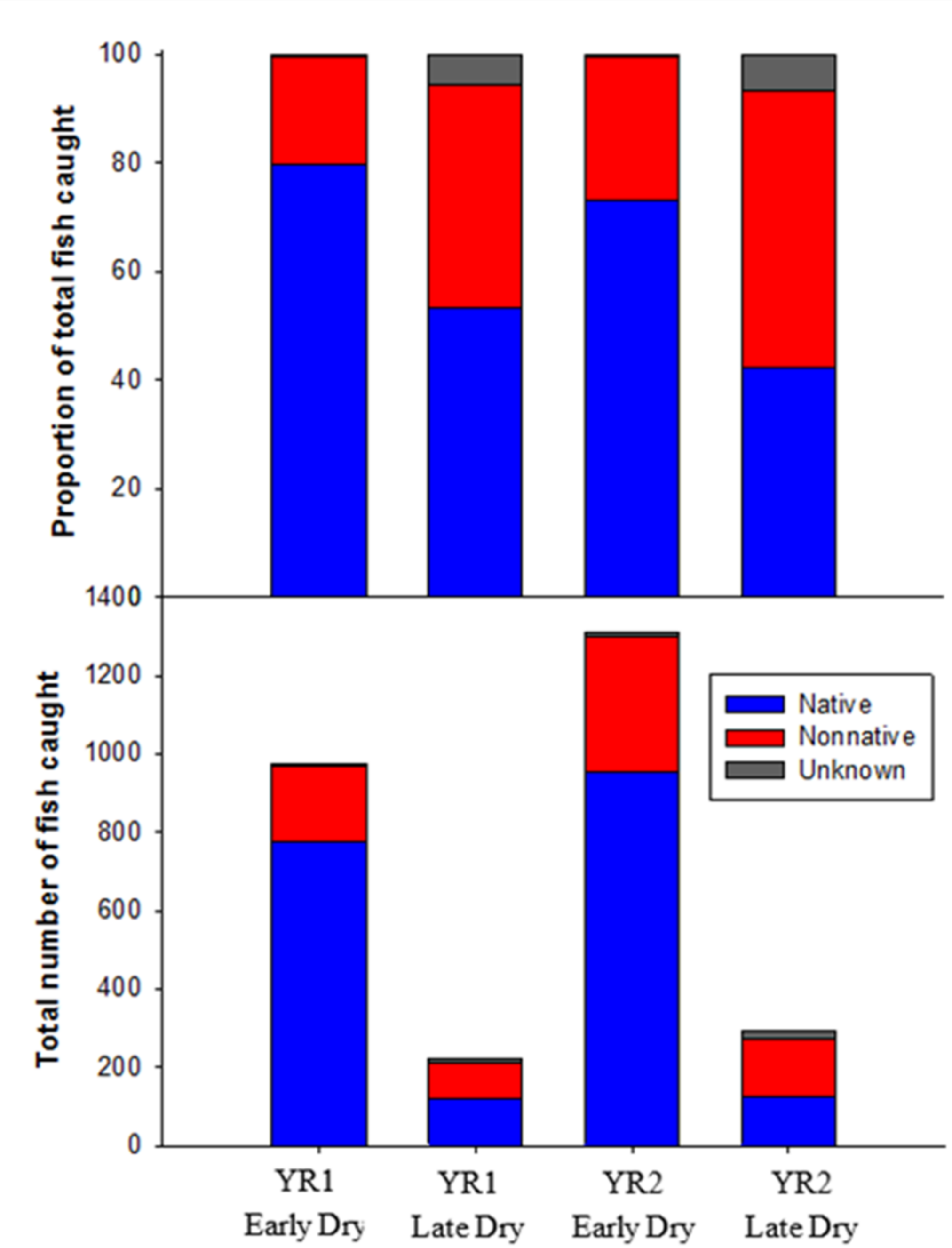

Figure 6: Nonnatives survive better than natives from early dry (ED) to late dry (LD) season

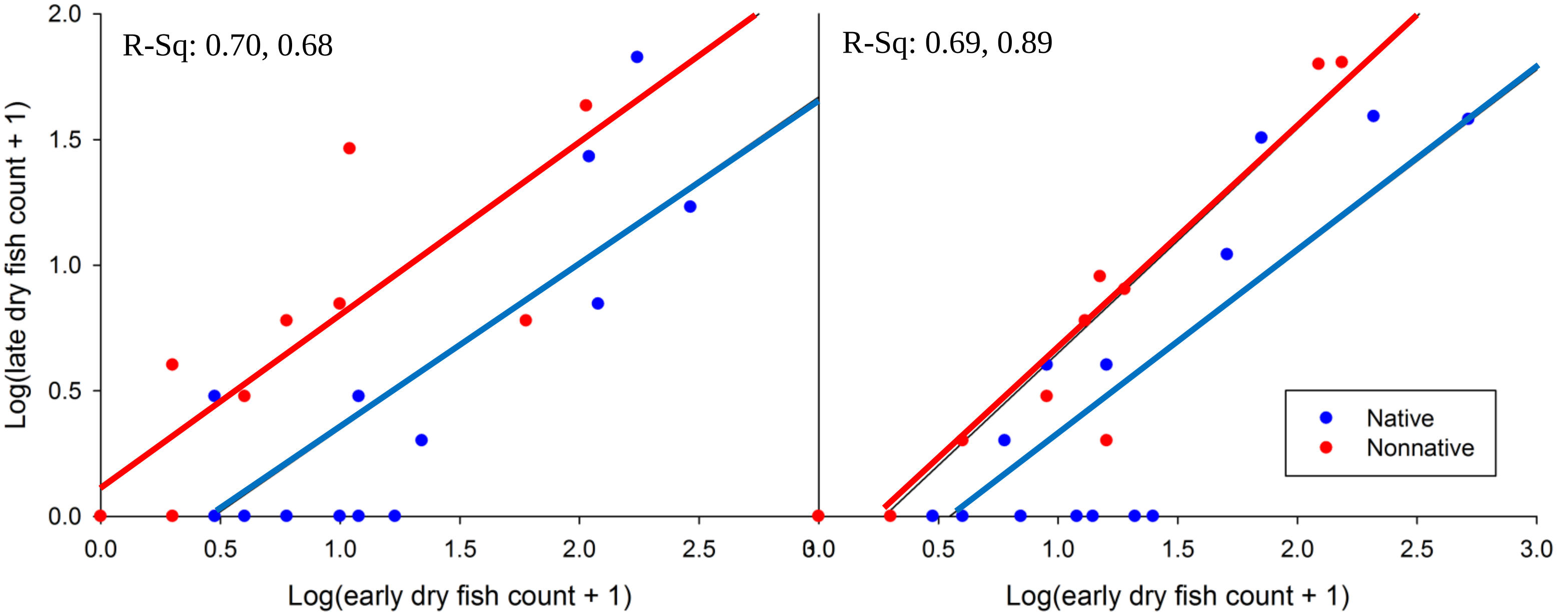

Figure 7: Total number of fish caught decreased consistently from the early to late dry season across years. Native species (blue), nonnative species (red). Many natives dropped in abundance while more nonnatives survived. YR1 p-value, 0.004 and YR2 p-value, 0.012

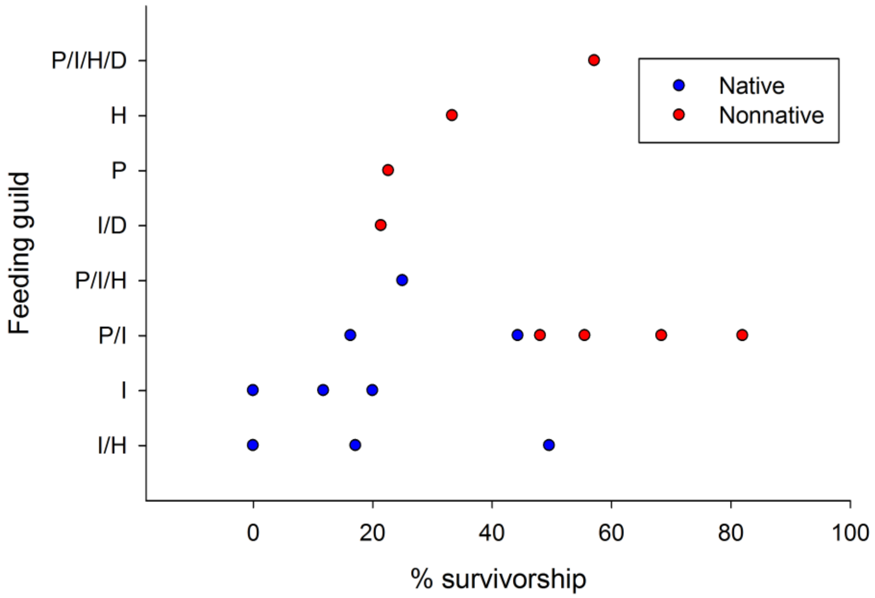

Figure 8: Percent survivorship versus feeding guild comparing natives to nonnatives. Species with > 40% survivorship fed on at least fish and invertebrates. Nonnatives have a higher survivorship than natives, p-value, 0.012

Common name Nonnative Native	YR1 Early Dry Count	~ %	YR1 Late Dry Count	~ %	YR2 Early Dry Count	~ %	YR2 Late Dry Count	~ %
Eastern Mosquitofish	291	30	16	7	519	40	37	13
Yellow Bullhead	174	18	66	30	208	16	38	13
Warmouth	119	12	6	3	50	4	10	3
Sailfin Molly	109	11	26	12	70	5	31	11
African Jewelfish	106	11	42	19	153	12	63	22
Pike Killifish	59	6	5	2	18	1	7	2
Spotted Sunfish	21	2	1	0.45	15	1	3	1
Golden Topminnow	16	2	0	0	6	0.46	0	0
Dollar Sunfish	11	1	0	0	8	0.61	3	1
Marsh Killifish	11	1	2	0.90	5	0.38	1	0.34
Black Acara	10	1	28	13	122	9	62	21
Walking Catfish	9	0.92	6	3	12	0.92	5	2
Jaguar Guapote	5	0.51	5	2	14	1	8	3
Brown Hoplo	3	0.31	2	0.90	15	1	1	0.34
Redear Sunfish	3	0.31	0	0	0	0	0	0
Florida Flagfish	2	0.21	0	0	3	0.23	0	0
Mayan Cichlid	1	0.10	3	1	8	0.61	2	0.68
Bluefin Killifish	1	0.10	0	0	2	0.15	0	0
Least Killifish	1	0.10	0	0	24	2	0	0
Spotted Tilapia	0	0	0	0	3	0.23	1	0.34
Bluegill Sunfish	0	0	0	1	0.08	0	0	0

Table 2: Native (blue) and nonnative (red) species survivorship counts and percentage breakdown. Early and late dry season across years.

Increased proportional survival	Median length Late dry (cm)	Feeding guild	As species numbers going in increased	Median length Early dry (cm)	Feeding guild	R-value	P-value	N
Jaguar Guapote	11.6	P/I	Dollar Sunfish	4.40	I	0.570	0.034	14
			Eastern	2.45	I	0.832	0.001	14
			Mosquitofish	4.10	P/I/H	0.821	0.001	14
			Marsh Killifish	4.65	I	0.536	0.048	14
			Spotted Sunfish	1.30	I/H	0.690	0.006	14
			Least Killifish					
Yellow Bullhead	6.45	P/I	Brown Hoplo	7.60	I/D	0.472	0.031	21
Black Acara	5.05	P/I	Brown Hoplo	7.60	I/D	0.564	0.003	29
Pike Killifish	8.20	P	Black Acara	4.95	P/I	0.536	0.001	24
Brown Hoplo	8.20	I/D	Sailfin Molly	4.85	I/H	0.740	0.015	10
			Mayan Cichlid	4.85	P/I	0.667	0.035	10
Dollar Sunfish	4	I	Mayan Cichlid	4.85	P/I	0.530	0.029	17

Table 3: Positive species pair associations.

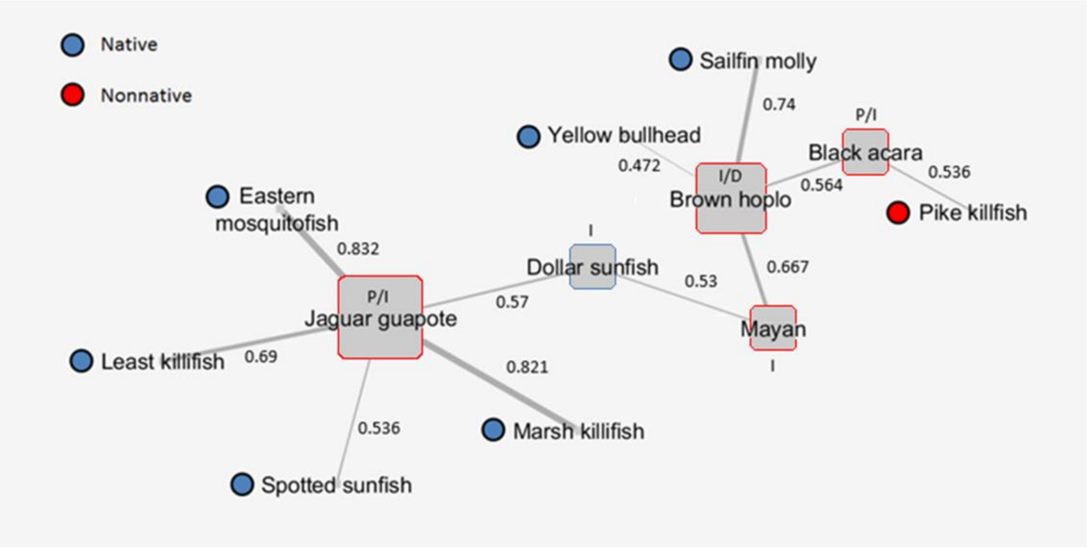

Figure 9: Species pair associations. Thickness of the line represents R-value, correlation coefficient. Species with red circles are nonnatives and species with blue circles are natives. Species with grey boxes are ones with positive associations with species surrounding them. Nonnatives that are part of the Invertivore guild plus another guild (e.g., Detritivore or Piscivore) are at the center of species associations.

Hoplos (I/D): native Sailfin Mollies (I/H) or nonnative Mayan Cichlids (P/I) (Table 3, Figure 9).

Body condition

Body condition of each individual species at the beginning and end of the dry season was compared. Species were excluded from analyses if they did not have at least three individuals to run a regression at both the early and dry season time point. No species increased their body condition from beginning to end of the dry season (Figure 10). Species that maintained body condition from beginning to end of the dry season were the nonnative Mayan Cichlid, Jaguar Guapote, Brown Hoplo, Walking Catfish and the native Sailfin Molly, Eastern Mosquitofish, Spotted Sunfish, Warmouth and Marsh Killifish (Figure 10). Species that decreased in body condition from the beginning to end of the dry season were the nonnative Black Acara, Pike Killifish, and African Jewelfish (Figure 10). The only native that decreased in body condition was the Yellow Bullhead Catfish (Figure 10). There was no difference in body condition and survivorship when comparing native to nonnative species (Figure 11, p-value, 0.077).

Discussion

Throughout my solution hole sites in the Rocky Glades, the total number of fish caught declined by ~80% from the beginning to the end of the dry season. Native species, which made up the majority of species richness and abundance at the onset of the dry season, showed higher mortality rates than nonnatives. Body condition varied across individuals for both native and nonnative species. Species that incorporated invertebrates

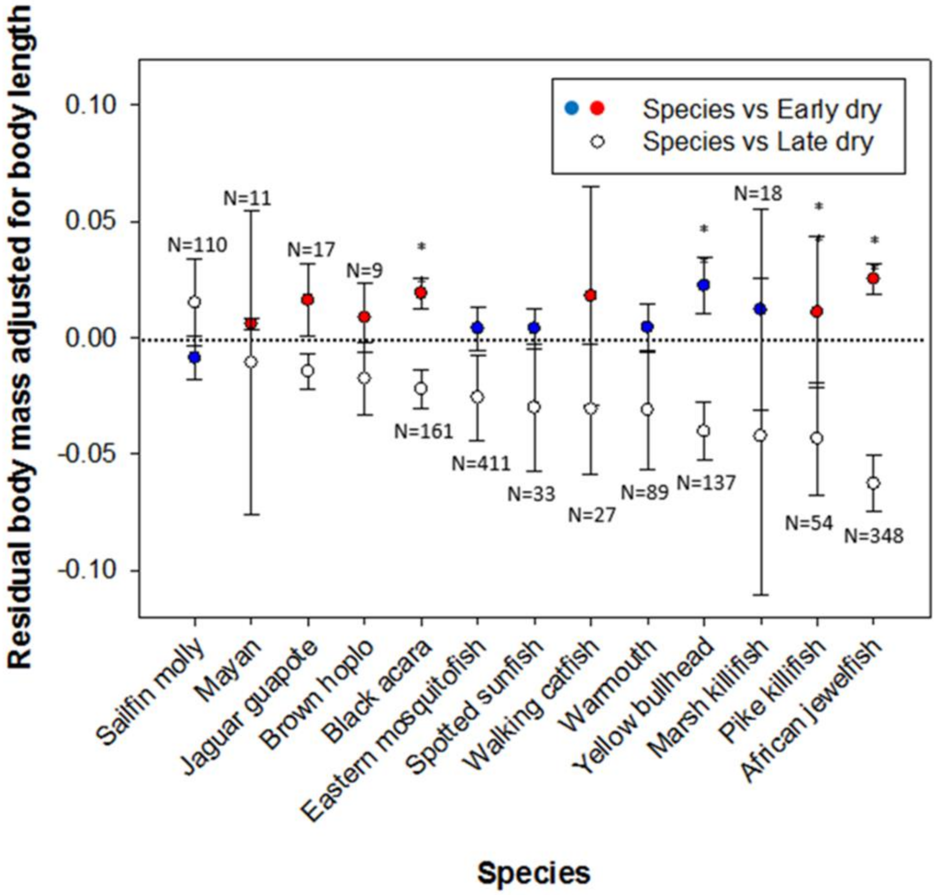

Figure 10: Body condition of nonnative (red) and native (blue) species from early to late dry season for both years. Error bars represent standard error. Large error bars can be indicative of large individual variability or lower sample size (N). Species that are in the best condition are the ones typically at the centers of positive associations in Figure 9.

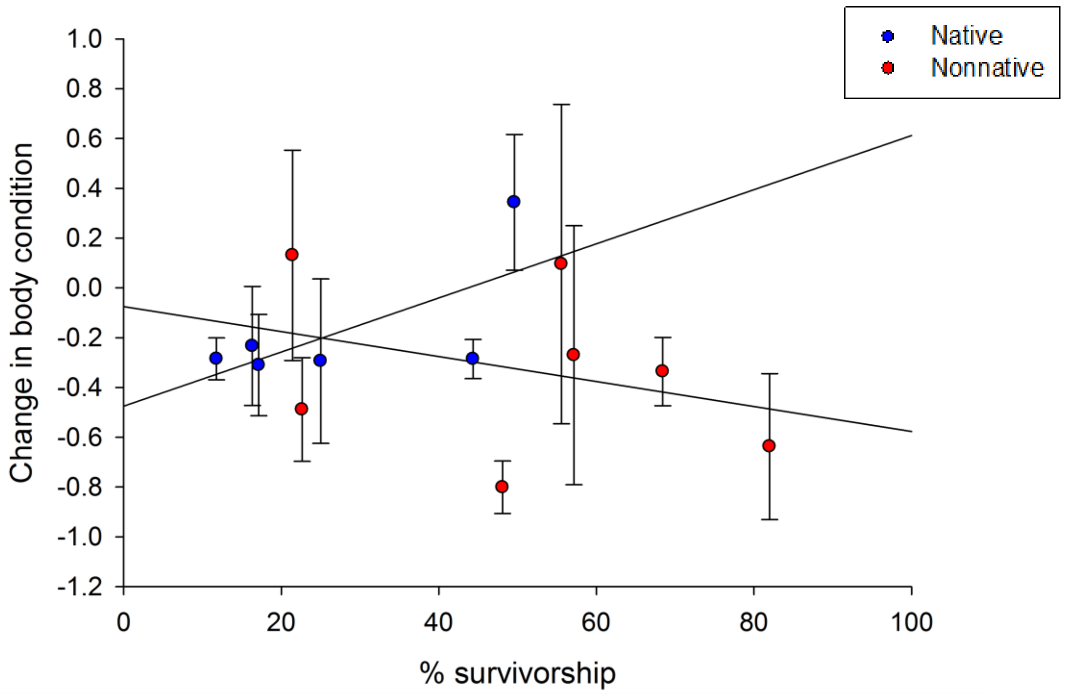

Figure 11: Change and body condition of native versus nonnatives. There was no difference in native versus nonnative species when comparing body condition to survivorship, p-value, 0.077

and fishes into their diets were the most likely to survive. One of the most abundant natives at the end the dry season was the Yellow Bullhead Catfish, but it was also the only native to lose body condition. The most abundant nonnative to survive was the African Jewelfish and was one of three nonnatives to be in the poorest condition by the end of the dry season Over the past 100 years, the Rocky Glades has rapidly been altered in its function as a native fish dry season refuge (McVoy et al. 2011). This study found that nonnatives have higher survivorship compared to natives, providing further evidence that the Rocky Glades serves as a trap for natives and a refuge for nonnative fishes (Rehage et al. 2014).

Size structure and community assembly

Small individuals typically survive better under low food conditions because they require less food. The survival of larger fish in this study supports my prediction of changing size structure, shifting from small to larger individuals from the beginning to end of the dry season. Presumably, larger fish survive better because they can eat a wider size range of prey (Szabo 2002). I was correct in my prediction that fish that fed within multiple guilds were the species that had the greatest survivorship. Fish may have benefited from initially following other aquatic taxa to a suitable refuge (Hamilton 1971). Once trapped in a solution hole, individuals may be better at surviving based on their size, but experiences may help (Grand 1997). Beneficial traits may include an individual’s personality (Sgoifo et al. 2005) which may explain the large standard error in body condition within species. Survivorship may be an indicator of an individual’s competitive ability (Parker and Sutherland 1986) and not merely based on a species guild.

Another competitive advantage nonnatives may have over natives is the evolutionary mismatch between local parasites providing an enemy release (Mitchell and Power 2003; Torchin et al. 2003). Native Dollar Sunfish were found to have more parasites and a higher incidence of infection than did African Jewelfish (p-value, 0.001 and 0.001, respectively, Trujillo et al. unpublished data).

Native and nonnative assembly

During the onset of the wet season, natives migrate from source populations (e.g., sloughs and canals, Rehage et al. 2014; Goss, Loftus and Trexler 2013) in larger numbers than nonnatives but have decreased survivorship at the end of the dry season when compared to nonnatives. Native and nonnative community ratios therefore changed from a native-biased to a nonnative-biased assembly from the beginning to the end of the dry season. I was correct in my prediction of a shift to a nonnative-biased community. Heightened competition between native and nonnative species may be driving the shift because most native and nonnative fishes are part of the P/I guilds. Nonnatives that are part of the invertivore guild plus another guild (e.g., detritivore or piscivore) were the ones at the center of positive species associations. Nonnatives that have been added to the system and succeeded are small predatory fishes (African Jewelfish and Pike Killifish), larger herbivores (Spotted Tilapia) and detritivores (Brown Hoplo and Walking Catfish), guilds that were not previously found. My positive association analyses suggest that nonnative species may have community-wide effects because of the roles they play in native consumer/prey community competition and survivorship in these stressful dry down conditions. Nonnative species are resilient to disturbance and have been found to recolonize sites even after their removal (Gallagher et al. 2016). Yet, native species of the Rocky Glades return in high numbers from source population during the wet season. Suggesting the rebound in large native numbers is caused by their migration ability during the wet season.

Body condition

Maintaining body condition did not always predict high survival frequency, nor did native/nonnative status. Species with positive associations had dietary overlap but also dietary differences, as in the native Sailfin Molly (I/H) and the nonnative Jaguar Guapote (P/I). Food partitioning may allow for these positive associations to occur which leads to survivorship of multiple species (Stephens and Krebs 1986; Perry and Pianka 1997). In concordance with optimal foraging theory, species are expected to specialize in diet when resources are abundant and segregate by trophic niche as resources become limited (Correa and Winemiller 2014; Stephens and Krebs 1986; Perry and Pianka 1997). Circumstances that may affect species persistence during a disturbance event are the severity of the event and/or quality of the refuge (Magoulick and Kobza 2003). Survival would be favored when the disturbance is mild and the quality of the refuge is high (Rehage et al. 2014; Magoulick and Kobza 2003). In the case of solution holes of the Rocky Glades, the dry season is severe and refuges are typically shallow and often dry over the course of dry season (Kobza et al. 2004). Fish persist in the Rocky Glades because of annual replenishment during the wet season by fish migrating into the marsh habitat from deeper refugia (Goss, Loftus and Trexler 2013; Magoulick and Kobza 2003). Survival of individuals is also affected by degradation of water quality across the dry season, noted by increases in ammonia and chlorophyll *a* as water levels decline (Kobza et al. 2004). If more water was allowed into the system, the dry season would be less severe and refuges would be better in quality for natives (Rehage et al. 2014). However, the consequences of water management are unknown and may further benefit nonnative spread (Kline et al. 2014). Disturbance often favors the spread and establishment of nonnatives (Pinto and Ortega 2016) which has been seen in the Rocky Glades system. In a mesocosm study of undisturbed and disturbed plots, nonnative plants established themselves in all disturbed plots regardless of native plant richness level (Pinto and Ortega 2016). Some native species may also benefit from the removal of nonnatives, such as in the case of the native Brook Trout, which did better after removal of the nonnative Brown Trout (Hoxmeier and Dieterman 2016).

In summary, nonnatives are better at surviving the chronic stressful dry season under the current water management regime but natives reappeared the next season in greater numbers. The Everglades watershed has experienced marked changes to the amount and distribution of the water flowing through the system, starting from the Kissimmee River and extending down to Florida Bay (Marshall et al. 2004). Along with hydrological changes, South Florida has had an increase in the number of nonnative species, whose effects on the ecosystem is largely unknown (Hardin 2007; Shafland 1996; Trexler et al. 2000). Nonnatives survive and leave solution holes in higher numbers than natives which may allow them to monopolize resources (e.g., nesting sites) at the onset of the wet season until high numbers of migrating natives arrive. Nonnatives that become established and spread are often aggressive, have a broad diet and high physiological tolerances that may ultimately be their reason for success (Verbrugge et al. 2012; Hou et al. 2014; Schofield, Loftus and Brown 2007; Hardin 2007). Future studies should focus on the reasons behind positive species associations found in this study. Along with determining physiological tolerances of nonnatives that have entered the system (Schofield, Loftus and Brown 2007; Schofield, Loftus and Fontaine 2009), examining the migratory abilities (Goss, Loftus and Trexler 2014) of native versus nonnatives through the use of tags at source sites. And investigate which behavioral types (Schofield, Loftus and Brown 2007; Schofield, Loftus and Fontaine 2009) do best in the stressful dry down environment of the Rocky Glades. With the addition of water into the system from the Comprehensive Everglades Restoration Project we will hopefully see shorter, less extreme dry seasons that may benefit natives as seen in other restoration studies (Lo Galbo et al. 2013; McVoy et al. 2011).

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CHAPTER IV

BEHAVIORAL INTERACTIONS BETWEEN A NONNATIVE CICHLID AND A SYMPATRIC VERSUS AN ALLOPATRIC NATIVE

Introduction

The introduction of a nonnative species can modify traits and behaviors of native species, alter how ecosystems function, and impose socioeconomic costs (Smith, Hewitt and Klenk 2012; Loope 2004; Coutenay 1986). Damaging effects produced by nonnatives include, but are not limited to displacement of natives from preferable habitats (Houser, Ginsberg and Jakob 2014; Brooks and Jordan 2010), changes in native behavior, reduction or loss of native populations (Dorcas et al. 2012; Kaufman 1992) along with changes to native communities and key ecosystem processes (Capps and Flecker 2013; Koehn 2004; Starling et al. 2002). In an experimental setting, nonnative tilapia aggressively ejected native sunfish from a refuge (Brooks and Jordan 2010). Examples like this one show the importance of learning how natives are affected by the presence of nonnatives. Linking nonnative monitoring efforts to native survivorship alone may mask indirect effects caused by introductions. Determining the behavioral mechanisms by which nonnatives reshape communities can lead to better management strategies for nonnative taxa (Catford, Jansson and Nilsson 2008).

Behavioral traits that affect survivorship and reproductive output are likely targets of natural selection (Sih 2013; Wingfield 2013; Werner and Peacor 2003) with populations sometimes evolving quickly (Wright et al. 2010) in both invader (Holway and Suarez 1999) and native communities (Stuart et al. 2014; Strauss, Lau and Carroll 2006; Vermeij 1982). The introduction of a nonnative can increase apparent competition (indirect competition between prey that share a predator) in a system and modify native predator behavior causing native prey to be more readily consumed (Brenneis, Sih and de Rivera 2011). Changes in behavior have been previously documented in native mollusks, where, in response to a nonnative crab predator, the mollusk dug itself deeper into the substrate (Strauss, Lau and Carroll 2006). Alterations in resource levels may also induce trait changes (Peacor and Werner 1997) where a reduction in availability following from increased competition may force native consumers to partake in riskier acts (Werner and Peacor 2003). While naïveté of prey has been well studied (Sih et al. 2010), naiveté of competitors has not.

To explore naiveté of native species to nonnative invaders, this study focuses on South Florida where the successful invasion of 17 nonnative fish species have been documented over the past 50 years (Kline et al. 2013; Shafland, Gestring and Stanford 2008; Loftus 2000). Although nonnative fish have increased species richness by 50%, relatively few studies have recognized any significant ecological effects from these fish introductions, a finding which has led to contradictory perceptions on the overall effects of nonnative aquatic taxa in the ecosystem (Schofield et al. 2013; Trexler et al. 2000; Shafland 1996). Managers need to understand the behavioral dynamics, particularly in those habitats where nonnative species are abundant (e.g., Rocky Glades and canals). This understanding requires empirical approaches that manipulate the presence of nonnatives and closely examines how natives and nonnatives interact and thus quantify the mechanisms for interaction (e.g., Porter-Whitaker et al. 2012; Brooks and Jordan 2010; Rehage, Dunlop and Loftus 2009).

To examine behavioral interactions between native and nonnative taxa, I focus on the highly invaded region of South Florida (Kline et al. 2013; Harvey et al. 2010) and areas in Central and North Florida where nonnatives are often cold limited and cannot yet invade. Historically, the eastern Everglades region experienced a short dry season where water levels lowered but remained high enough in solution holes for fish to survive in this refuge until the wet season (McVoy et al. 2011; Harvey et al. 2010). Because of the drainage and impoundment of the entire ecosystem for reasons of flood management, this area now experiences a long and extremely dry winter that is not suitable for aquatic life (McVoy et al. 2011; Rehage et al. 2013; Harvey et al. 2010). In a region of the Everglades called the Rocky Glades, fish attempt to wait out the dry season using karst solution holes for refuge. This area may now be a sink instead of a source for natives who no longer survive the dry season (Rehage et al. 2013) and a source of nonnatives that may be both better adapted for chronically stressful conditions and better at obtaining and acquiring resources in these competitive environments. Because of similarities in size and niche occupancy, African Jewelfish (*Hemichromis letourneuxi*) have been predicted to compete heavily with native Dollar sunfish (*Lepomis marginatus*) (Rehage, Dunlop and Loftus 2009). By examining behavioral responses invoked by African Jewelfish upon Dollar Sunfish from populations with and without a prior history of African Jewelfish co-residency, this study shows whether invasion by nonnative African Jewelfish has induced compensatory adaptation in the behavior of native Sunfish.

In my study, I asked (1) how behavioral responses to the presence of Jewelfish differ between native Dollar Sunfish from allopatric populations and versus those within the invasion range of African Jewelfish? and (2) are allopatric or sympatric native populations of Dollar Sunfish are better able to acquire food when competing with the nonnative competitor? To address these questions, I performed behavioral assays between native Dollar Sunfish from sympatric and allopatric populations with the nonnative African Jewelfish. I quantified aggression, distance between fish, first fish to recruit to food, and number of worms eaten. Because fish in these isolated Rocky Glades' solution hole communities display strong competition for resources, I hypothesized that allopatric sunfish will interact more aggressively than sympatric natives, while sunfish from sympatric populations will have learned or evolved to avoid African Jewelfish, and keep their distance, and will obtain less food than allopatric sunfish.

Methods

The aim of this study was to look for plastic vs. static responses of two native populations of Dollar Sunfish. The sympatric population of Dollar Sunfish has been previously exposed to the nonnative African Jewelfish since the 1960s and therefore has had 56 years of potential interactions and adaptation, whether through phenotypic plasticity in behavior or through microevolution. The allopatric populations of Central and Northern Florida are outside of the range of this nonnative and are therefore naïve to this invader. In order to explore adaptation in sympatric vs. allopatric native sunfish populations, differences in behavioral trials and interactions with the African Jewelfish were compared. An inconsistent response difference between the Dollar Sunfish populations would indicate that natives have adapted to the presence of the nonnative Jewelfish.

Behavioral trials were adapted from Bell 2005; Bell and Stamps 2004. All fish were collected via un-baited minnow traps (30 Dollar Sunfish from each population and 60 African Jewelfish from ENP). Fish were transported to Florida International University inside coolers with air stones and StressCoat® to minimize stress. Fish were fed live blackworms or frozen brine shrimp once every two days, ad libitum, and kept on a 12:12 hour light:dark cycle at 20°C in ten 20 gallon tanks with sand substrate, filter and air stone. 5-10% water changes were conducted every two days.

Trials were run in individual 20 gallon tanks partitioned into 2 equal sections with an opaque mesh divider to prevent fish from interacting physically before the trail. Tanks had sand substrate and water levels were kept at a constant 15cm. One side of the tank (random choice) had a Dollar Sunfish (from an allopatric population or sympatric population) and the other side had an African Jewelfish. One side of the tank (random choice) had a clear PVC pipe and the other side was bare to elicit a dominance response between the individuals when the partition was lifted. Each fish was weighed and measured at the end of each trial.

Behavioral assays

Fishes were fed *ad lib.* before the start of the trial. Fishes were then placed in observation tanks and allowed to acclimate over two nights with the barrier in place. Observation tanks had the same water parameters as holding tanks. On the 5th day I gently removed the barrier and recorded each individual's behavior for 20 minutes. I then introduced food, oligochaete "blackworms", into the tank and recorded behavior for another 5 minutes. All behavioral trials were conducted between 08:00 and 14:00. I observed fish continuously for 1 minute after first interaction and then again for 1 minute once food was introduced and the fish recruited to the food. Videos were scored manually using JWatcher® for this portion of the behavioral trail. These 1-minute interactions and 1-minute food trials were then scored using Ethovision® to estimated average distance between fish. I scored behaviors such as lateral displays, bites and chases manually.

All assays were video recorded with no observer in the room. I recorded the number of times that each fish interacted (e.g., biting, chasing, lateral displays) with each other. After 20 minutes, live blackworms were introduced into the tank. The first fish to consume the food and amount of food consumed was recorded.

Feeding trials

Feeding trials were conducted to determine how many worms were eaten on average across species when no other competitor was present. All trials were video recorded with no observer in the room. I began recording as soon as live worms were placed in the tank. Videos were scored by hand in JWatcher, noting the number of live worms each fish ate during the first minute.

Statistical Analysis

To examine variation in behaviors, I used Generalized Linear Models (GLMs) that test for the effect of differing populations, species and the interaction along with Cohen's d to test for effect size. Values for behavioral counts were $\sqrt{(x+1)}$ transformed and checked with Shapiro-Wilks' test for normality. Average distance between fish were Log10(x) transformed and checked with Shapiro-Wilks' test for normality. GLMs were followed by Tukey's post hoc tests for population comparisons. Fisher's exact test was performed for approach data. Analyses were performed using SYSTAT 13®.

Results

Dollar Sunfish from the sympatric population were twice as likely to approach African Jewelfish as those from the allopatric population (Figure 1). There was no difference in the distances between fish kept by sunfishes from the difference populations (data not shown). African Jewelfish bit Dollar Sunfish more than the reverse (data not shown, p-value=0.009) but there was no difference in number of bites given by African Jewelfish on allopatric or sympatric dollar sunfish, p-value, 0.836, 0.825, respectively). Specifically, sympatric Dollar Sunfish populations had an average of 3.1±0.7 bites on the African Jewelfish while allopatric populations had 3.67±1.1 bites (Figure 2A). In contrast, African Jewelfish had an average of 5.92±1.2 bites on sympatric sunfish and 5.19±0.88 bites on allopatric populations. Number of chases by African Jewelfish on Dollar Sunfish was greater than the number of chases by Dollar Sunfish on African Jewelfish (data not shown, p-value, 0.001). There was no difference in the number of chases by either allopatric or sympatric Dollar Sunfish on African Jewelfish (Figure 2B; p-value, 0.824) but there was a trend of more chases on sympatric Dollar Sunfish by African Jewelfish (p-value, 0.081). Specifically, the average number of chases by sympatric Dollar Sunfish on African Jewelfish was 2±0.61 while allopatric populations had 2.22±0.63 chases (Figure 2B). African Jewelfish chased sympatric sunfish an average of 6.8±1.4 times and chased allopatric sunfish 3.78±0.79 times. Dollar Sunfish overall displayed more than African Jewelfish (Figure 2C, p-value= 0.001). There was no difference in the number of displays by allopatric or sympatric Dollar Sunfish or African Jewelfish (p-value=0.677, 0.916, respectively). Sympatric Dollar Sunfish had an average of 6.71±0.94 lateral displays while allopatric Dollar Sunfish had an average of 5.29±0.85

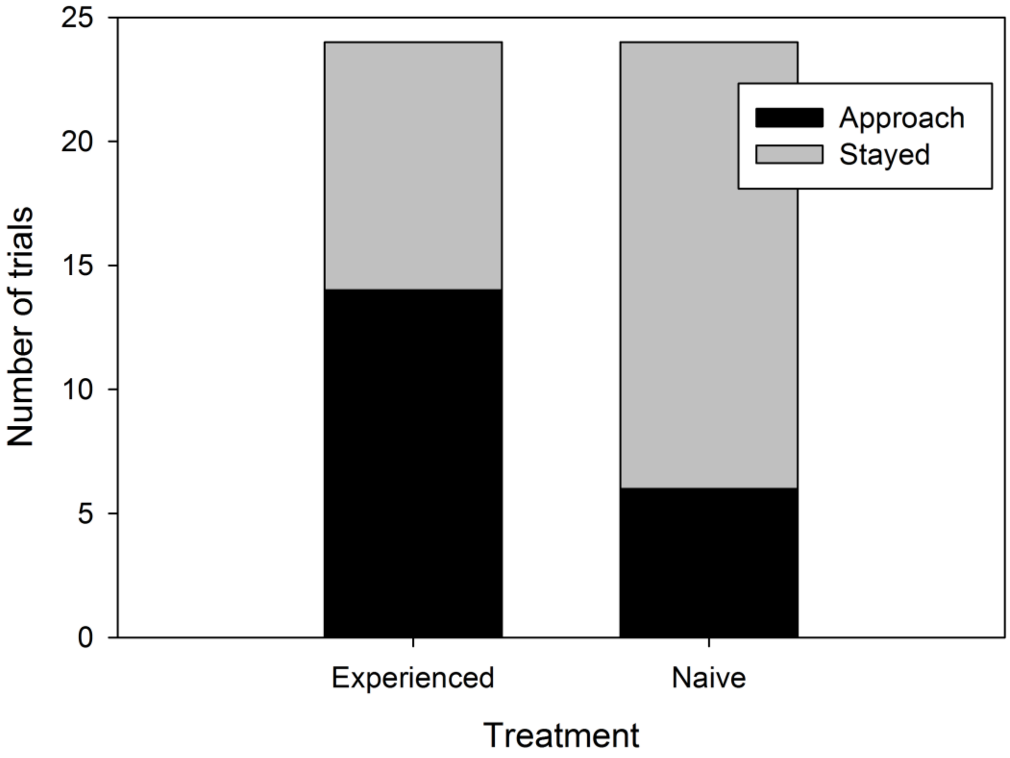

Figure 1: First fish to approach across sympatric and allopatric populations. Sympatric Dollar Sunfish approach twice as often as Dollar Sunfish from allopatric populations.

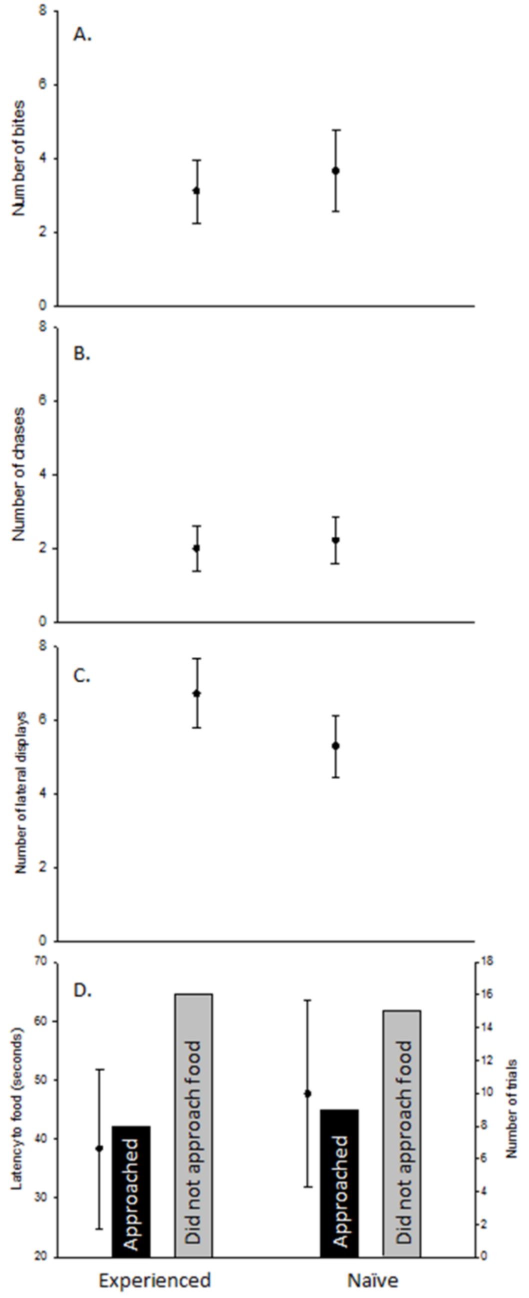

Figure 2: Average number of behavioral interaction between native species across populations. A. Bites, B. Chases, C. Lateral displays and D. Latency to food and number of trials. Bars represent standard error.

lateral displays. African Jewelfish had an average of 3.57±0.8 displays on sympatric sunfish and 2.57±0.43 displays on allopatric populations. Latency to approach food did not differ across dollar sunfish populations (Figure 2D; p-value, 0.587).

African Jewelfish were more often the first to feed than Dollar Sunfish in either population (p-value, 0.001). African Jewelfish recruited to food greater than 70 percent of the time across all populations. Average number of worms eaten was greater for African Jewelfish (p-value, 0.001, Figure 3B). Dollar Sunfish from the sympatric population ate closer to the number of worms eaten by competing Jewelfish than did sunfish from the allopatric population (p-value, 0.05, Figure 3, medium effect size: Cohen's d=0.50).

Discussion

Overall, the African Jewelfish is bolder than Dollar Sunfish and better at acquiring food which may make this species more likely to survive in chronically stressful environments. Sympatric Dollar Sunfish were more tolerant of the nonnative and able to preoccupy the African Jewelfish and therefore making the nonnative acquire less food in the experienced populations than naïve populations.

The eastern Everglades was once a region that remained flooded for the majority of the year but with current water management the system dries nearly every year. The marsh drying forces fish to move into competitive karst refugia, which often desiccate before the start of the next wet season, killing most of the inhabitants (McVoy et al. 2011; Rehage et al. 2013; Harvey et al. 2010). For those refugia that remain wet, competition is great for the increasingly limited resources, such as food and areas with higher dissolved

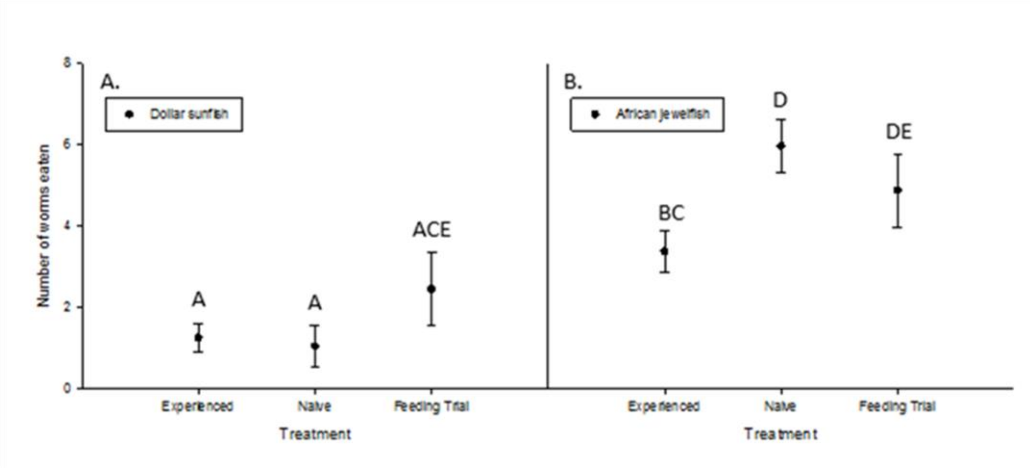

Figure 3: Average number of worms eaten between native and nonnative across populations and feeding trials. African Jewelfish ate more worms than did Dollar Sunfish. Bars represent standard error.

oxygen (Kobza et al. 2004). One trait that may be beneficial is tolerance of other competitors (Dudley, Murphy and File 2013). Nonnatives often are more aggressive, including the African Jewelfish (Schofield et al. 2013). Sympatric Dollar Sunfish approached African Jewelfish twice as often as allopatric Dollar Sunfish, which likely caused the trend toward a higher number of chases. African Jewelfish could have also perceived sympatric dollars as a greater threat caused by their bolder approach. A study that shows similar findings in sympatric native tolerance found that native salamanders had an increased number of responses to nonnatives if they were from the invaded community rather than the naïve community (Cunningham and Rissler 2013). Another study also found that experienced crayfish were more aggressive than naïve crayfish to a nonnative competitor (Hayes et al. 2009). A study that revealed a better depiction of native tolerance was a predator-prey study, which found that experienced tadpoles were less active without a predator cue but had a smaller decrease in activity with the cue, possibly to help increase foraging (Hartman and Lawler 2014). Looking at activity levels of sympatric and allopatric natives may be an area of further study. Higher activity levels may make Dollar Sunfish more prone to African Jewelfish chases but may increase their foraging potential. However, increased activity may also bring negative effects such as increased risk of predation (Brenneis, Sih and Rivera 2011). The population differences I found may be caused by phenotypic plasticity of Dollar Sunfish or through the evolution of behavior produced by natural selection.

The African Jewelfish is a picivorous cichlid that has spread quickly through south Florida (Schofield 2013; Dunlop-Hayden and Rehage 2011; Rehage, Dunlop and Loftus 2009). While native Dollar Sunfish were once the most abundant sunfish species caught in solution holes (Rehage et al. 2013) that number has since decreased while African Jewelfish are now the 2nd most abundant fish caught in solution holes (Trujillo et al. unpublished data). Dollar Sunfish are gape limited and have a narrow diet mainly of aquatic invertebrates (e.g. shrimp, copepods) (Warren 2009; Etnier and Starnes 1993) which may have played in part in their decline. Nonnatives often succeed in survival and spread because they are bold to explore new territories (Schofield et al. 2013). Nonnatives also typically have broad, generalist diets (Schofield et al. 2013) and these are traits of the African Jewelfish (Parkos, Ruetz and Trexler 2011; Schofield et al. 2013; Hickley and Bailey 1987; Rehage et al. 2013). Consistent with findings in the present study, bold individuals often feed more on prey out in the open (Sih, Bell and Johnson 2004; Coleman and Wilson 1996). African Jewelfish were the first to recruit to a new food source and ate more live worms than native species which could explain why traits such as higher growth rates and increased body mass of nonnatives have been shown in previous studies (Pintor and Sih 2009; Hayes et al. 2009). African Jewelfish faced with sympatric sunfish ate fewer worms than with allopatric sunfish. Differences in the sympatric sunfish’s behavior likely resulted in the African jewelfish being unable to eat as much as when in the presence of allopatric sunfish. The nonnative African Jewelfish may be both better adapted for chronically stressful conditions and better at acquiring resources in competitive dry down environments (Rehage et al. 2013) but sympatric natives may be learning or evolving traits to help them deal with their opponents.

In summary, Dollar Sunfish from sympatric populations may be better adapted to living with the nonnative African Jewelfish because of learned or evolved tolerance from the exposure to this nonnative. Dollar Sunfish from sympatric populations may be more likely to acquire food from worms overlooked by the African Jewelfish but at the cost of being bolder to the nonnative, which may prove to be the critical factor when it comes to survival in resource-limited refuges. African Jewelfish are aggressive, bold and territorial, which may be the reason for its success in acquiring resources through the displacement of native sunfish. Follow up experiments should focus on breeding Dollar Sunfish, in captivity, from allopatric and sympatric populations and testing if offspring responses to African Jewelfish are in fact heritable or learned. Experiments observing whether Dollar Sunfish can forget African Jewelfish interactions and how long does it takes to learn aggressive behaviors would also provide further insight of trait changes in native populations. Changes in traits are products of natural selection and can sometimes develop quickly in both invader and native communities. Furthermore, behavioral plasticity may provide a range of traits that both native and nonnatives may exploit to persist in the world's rapidly changing environment.

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CHAPTER V

GENERAL CONCLUSIONS

Anthropogenic disturbances are becoming more frequent stressors of native species populations (Wong and Candolin 2015; Vitousek et al. 1997). Sources of disturbance include global climate change, urbanization, and the introduction of nonnative species (Vitousek et al. 1997). Nonnative species interactions may have effects on the individual level, which can then spread to the community and ecosystem levels if not regulated. Published studies have concentrated on measuring prey naiveté (Sih et al. 2010) but have not explored consequences of novel nonnative competitors. Through direct and indirect interactions (LeBrun, Abbott and Gilbert 2013; Howe et al. 2016), nonnatives can act as novel competitive stressors to native species. My research provides another connection to demonstrate how a nonnative competitor alters native responses (Hasegawa 2016; Short and Petren 2008; Petren and Case 1996; Petren, Bolger and Case 1993) and demonstrate that natives have adapted to the presence of a nonnative after multiple generations. Everglades National Park has experienced a large establishment and proliferation of nonnative fish species, but with inconsistent evidence of their influence on the system and native species (Schofield et al. 2013; Trexler et al. 2000; Shafland 1996). To help fill this knowledge gap of how nonnatives may or may not affect native species, I investigated how survivorship, body condition and behavior change across differing ratios, density and co-occupancy of nonnatives. My results have further provided evidence that the Rocky Glades serves as a sink for native and a source for nonnatives under current water management regimes (Rehage et al. 2014).

In Chapter 2, I conducted an empirical study, in which I simulated Rocky Glades' solution holes during the dry season to carefully determine the effects of competition between native and nonnative species on survivorship and body condition. I used a nonnative replacement design to investigate the response of native Dollar Sunfish to the presence of African Jewelfish. Previous literature suggests that competition increases as resources become more limited (Cain and Langmore 2016) and increasing numbers of nonnatives have negative effects on the survival of native species (Anderson 2006; Gruner 2005; Louda et al. 1997). Disturbance is especially great if those nonnatives have invasive characteristics, like high aggression and a broad diet (Schofield et al. 2013). In agreement with other literature on the Rocky Glades region (Trexler et al. 2000; Kobza et al. 2004; Kline et al. 2013), I found that nonnative species did have a higher survivorship and body condition than native species. However, I found no effect of density between or within either species. African Jewelfish averaged close to a 90 percent survivorship, whereas native sunfish averaged around 50 percent survivorship. Dollar Sunfish maintained around 67 percent of their original condition and African Jewelfish maintained 82 percent of their early dry season condition. My data suggest that nonnative African Jewelfish do not compete, but are more resilient in environmentally stressful conditions than native Dollar Sunfish. African Jewelfish occupy ephemeral habitats in their native range and may cope better with the Rocky Glades annual dry down (Seehausen and Schluter 2004).

In Chapter 3, I used survey techniques to investigate the differential survival of native and nonnative fish taxa in Everglades’ solution holes across the dry season. Previous literature found that nonnatives experience higher survivorship than native fish taxa (Trexler et al. 2000; Kobza et al. 2004; Kline et al. 2013). I found that close to 80 percent of all fish died in my solution hole sites. Bigger species survived better, possibly because their larger gape size allowed them to eat a broader range of prey (Szabo 2002).

Small species with higher mass-specific metabolic rates may confer a disadvantage in maintaining biological functions under high stress and low food (Beamish, Mahnken and Neville 2004). In addition, feeding guilds that survived until the end of the dry season were often species that consumed both invertebrates and fishes. At the onset of the dry season native fishes made up around 77 percent of the community while nonnatives were close to 23 percent. However, by the end of the dry season, natives constituted 28 percent and nonnatives 46 percent, a result of greater mortality among native species. Maintaining body condition was not always an indicator of survivorship, in fact, species with a decreased body condition were some of the most abundant species at the end of the dry season (e.g., nonnative African Jewelfish and native yellow bullhead catfish). Species pairs with positive associations were those with differences in their diet. Species that partitioned food resources may have coexisted with less competition, leading to higher survival (Stephens and Krebs 1986; Perry and Pianka 1997). Competitive ability may be a better indicator of survival, such as personality and experiences, than just the feeding guild alone (Parker and Sutherland 1986; Sgoifo et al. 2005; Grand 1997).

In Chapter 4, I used behavioral assays to assess the different responses of native fish from invaded versus naïve communities to a nonnative competitor or antagonist. Previous literature suggests that natives increase their responses to nonnatives in invaded versus naïve communities (Cunningham and Rissler 2013; Hayes et al. 2009). I found that Dollar Sunfish from an invaded community were twice as likely to approach the nonnative as compared to the allopatric population of Dollar Sunfish. Dollar Sunfish populations did not differ in their aggressive interactions to African Jewelfish (e.g., bites, chases and lateral displays). African Jewelfish were the first to approach food when it was introduced into the tank, a characteristic of boldness (Sih, Bell and Johnson 2004). African Jewelfish also ate more worms than either population of sunfish, which may provide further support as superior survivors in stressful competitive dry down environments. Despite nonnatives acquiring more resources than natives, nonnatives ate less in the presence of natives from invaded communities, possibly caused by increased responsiveness to the Dollar Sunfish. Increased responsiveness by the nonnative could be caused by increased activity of the fish from the invaded community (Hartman and Lawler 2014), which was not measured in my behavioral assay. Decreased consumption of food by the nonnative may leave more resources for experienced natives to benefit from and survive. I found that Dollar Sunfish, after more than 60 years of sympatric interactions, are more tolerant of African Jewelfish than their uninvaded counterparts. Population differences in the likelihood of approaching an aggressive nonnative may be caused by phenotypic plasticity of learned behavior produced by natural selection.

Overall, I found that nonnatives are better able to cope with stressful dry down environments than are native species. In both experimental and field settings, nonnatives had a higher survivorship than many native species, which are ideally pre-adapted to native environmental conditions. Disturbances that alter historic conditions may be the main reason for decreases in native survivorship (Fraser, Banks and Water 2014), which then open niches for pre-adapted nonnatives to invade (Fraser, Banks and Walter 2014; Didham, Watts and Norton 2005; Chollet et al. 2014). Nonnatives often have broad physiological tolerances along with traits that aide in proliferation and establishment in a disturbed ecosystem, like parental care, aggression and generalist diet that make them better competitors (Schofield et al. 2013). Natives are not completely lost and have been able to adapt to the presence of nonnatives like the African Jewelfish. Dollar Sunfish have heightened responses to the presence of African Jewelfish when it comes to territoriality. Sympatric Dolar Sunfish may also be able to distract nonnatives from food long enough for them to acquire some resources to help them survive the stressful dry down.

Disturbance differentially affects native and nonnative species. Nonnatives have often been found to resist disturbance, settling back into disturbed areas after restoration (Gallagher et al. 2016). The hydrology of the Everglades has been disrupted by current water and flood management practices (McVoy et al. 2011) while habitat quality continues to degrade at the expense of native species, further favoring nonnative establishment and spread (Pinto and Ortega 2016; Manea, Sloane and Leishman 2016; Bradley et al. 2012). If the Everglades were ever to lose the annual replenishment of migrating fish from deeper refugia during the wet season, South Florida would not only lose a population of native fish species (Goss, Loftus and Trexler 2013; Magoulick and Kobza 2003) but also a major food source for native wading birds (Gawlik and Boston 2008). As the climate continues to warm, we expect to see further range expansions of nonnative species (Rehage and Blanchard 2017) which may counteract many restoration efforts. Behavioral plasticity may be the only option that offers the fastest trait changes for both native and nonnatives to continue to survive in this rapidly changing world.

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VITA

VANESSA TRUJILLO

Born, Hialeah, Florida

2006-2010	B.S., Biology University of Florida Gainesville, Florida
2011 -2017	Doctoral Candidate Florida International University Miami, Florida
	Teaching Assistant Florida International University Miami, Florida

PUBLICATIONS AND PRESENTATIONS

Trujillo, V. & Rehage, J.S. (2012) Physiological Stress Effects induced by the Non-Native African Jewelfish on Native Dollar Sunfish. Poster presented at the meeting INTECOL International Wetlands Conference, Orlando, Florida.

Rehage, J.S., Gandy, D.A. & Trujillo, V. (2013) Assessing the Impact & Potential for Containment of Nonnative Fishes Across Everglades Habitats. Annual Report to Everglades National Park.

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Trujillo, V. & Rehage, J.S. (2013) Jewels for Dollars: Native and Non-Native Interactions in an Already Stressful Dry Down Environment. Poster presented at the meeting Florida Coastal Everglades All Scientist Meeting, Miami, Florida.

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