

## Research Article

## Reproduction revisited – a decade of changes in the reproductive strategies of an invasive catfish, *Pterygoplichthys disjunctivus* (Weber, 1991), in Volusia Blue Spring, Florida

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### Abstract

The reproductive patterns of invasive species may undergo changes in response to the pressures of a novel environment. We tracked the reproductive strategies of *Pterygoplichthys disjunctivus* collected in Volusia Blue Spring, adjoining the St. Johns River, over a 10 year period from 2005 through 2014. After analyzing various measures of fecundity and reproductive seasonality, we found that during that time period, *P. disjunctivus* reduced investment in individual offspring, while increasing overall fecundity and GSI. In addition, its reproductive season had expanded, and seasonal differences in nearly all measures became significantly smaller. This species does not seem to fit into any one reproductive strategy, nor has it moved in a consistent direction within the Winemiller-Rose reproductive strategy scheme. We suggest that despite the value of such schemes in predicting responses to environmental parameters, they may not be able to adequately describe the strategies of invasive species that have access to ecosystems that are more benign than their native habitats.

**Key words:** loricariid catfish, reproductive strategy, invasive species

### Introduction

The invasion biology literature discusses many of the traits that make invaders successful (tolerance of harsh conditions, large investment in reproduction, rapid growth, generalist diet, etc. (Sakai et al. 2001)), but one of the most powerful traits may be plasticity in life history strategies (Olden et al. 2006; Kováč et al. 2009; Feiner et al. 2012; Gutkowsky and Fox 2012; Záhorská et al. 2013; Hôrková and Kováč 2015). To test this theory, long-term tracking of life-history traits in invasive populations is required. In this paper we describe the recent changes in life history patterns (since our original description (Gibbs et al. 2008)) in an invasive loricariid catfish, *Pterygoplichthys disjunctivus*. This species is native to a strongly periodic environment in South America which is seasonal rainfall based, has extreme annual hydrological variation in terms of temperature, dissolved

oxygen (DO), water flow, and a 12 m seasonal water level difference (Goulding 1981); and has a feast and famine food cycle (Junk 1985; Lowe-McConnell 1987) and high species diversity (>900 species (de Queiroz et al. 2013)). We know that *P. disjunctivus* has likely been in central Florida's St. Johns River for several decades, where it has experienced regular seasonal patterns in temperature and productivity (chlorophyll *a*). Compared to the Amazon basin, this river system has relatively stable DO, pH, and flow regimes (Kroening 2004). Here we discuss how this species is shifting within the classic Winemiller-Rose reproductive strategy scheme as it adjusts, over a 10 year period, to having ready access to an additional resource on the St. Johns River; Volusia Blue Spring, a much smaller, but strongly equilibrium environment that is aquifer-based, has virtually no annual hydrological variation in terms of temperature and dissolved oxygen, stable flow, low variability in

water level (1.5 m), consistent, plentiful food supply, and relatively low species diversity (Stevenson et al. 2007; Work et al. 2010).

Reproductive patterns in fish are usually relatively stable, since there is a finite amount of energy available that can be diverted away from maintenance and growth and toward reproduction (Smith and Fretwell 1974; Ware 1975). When exploring life history traits of fishes, there are a variety of traditional trade-offs to consider, with bases in physiology (e.g. growth rates, egg size vs. clutch size) and the environment (e.g. temperature, predator/prey pressures) (Elgar 1990; Hutchings 1991; Winemiller and Rose 1992; Johnston and Leggett 2002). Although species rarely fit neatly into one category or another, it can be valuable for predictive purposes to place them somewhere on the Winemiller-Rose (1992) periodic – opportunistic – equilibrium pyramidal continuum, based on environmental conditions and how fish respond reproductively to that environment (Winemiller 2005). Those species originally defined by Pianka (1970) as r-strategists (successful in an environment with a population below carrying capacity and little competition for resources) were split by Winemiller and Rose (1992) into either periodic or opportunistic strategists. Periodic strategists must deal with a habitat that goes through periods that are not optimal (food, water levels, etc.), thus delaying reproduction until they are larger, and produce a single large clutch with low juvenile survivorship. Opportunistic strategists tend to be found in somewhat more predictable environments than periodic strategists, are smaller, mature early in life, and produce multiple small clutches with low juvenile survivability. Equilibrium strategists (those species Pianka (1970) considered K strategists—successful in an environment with a population at or near carrying capacity with intense competition for resources) occupy the most stable environments, are small to medium sized fish, mature at an intermediate age, and although they produce multiple small clutches each season, are able to ensure high juvenile survivorship through some form of parental care.

Plasticity in reproductive strategy allows individuals to maximize fitness in the face of body size constraints and changing environmental conditions and food resources. An increase in something like egg size (investment in individual offspring), is usually paired with a trade-off decrease in something else, like clutch size, such that overall reproductive effort and relative energy allocation stay the same (Elgar 1990; Winemiller and Rose 1992; Mims and Olden 2012). Changes in egg size during the short term (one to several generations) can be strongly influenced by the environmental conditions experienced

by females; especially predation pressure and food resources (Reznick and Yang 1993; Jonsson et al. 1996; Reznick et al. 1997; Einum and Fleming 2000). When females experience reduced food supplies, for example, they may provision their eggs with more yolk to ensure offspring survival (Hutchings 1991; Reznick and Yang 1993; Johnston and Leggett 2002). The larger the yolk, the larger the offspring is at hatching and onset of feeding; a competitive edge that allows offspring to feed on a greater variety of prey items (Jonsson et al. 1996). On the other hand, when food resources for the female are plentiful, they are likely to also be plentiful for the offspring (even if their diets are different), and so fecundity can increase through a combination of decrease in egg size and increase in clutch size, without any decrease in offspring survival (Ware 1975; Duarte and Alcaraz 1989). These kinds of changes in egg size and number could be either due to simple plasticity during a single season, or more stable adaptive changes that occur over multiple generations in response to long-term shifts in environmental conditions.

Studies of shifts in reproductive life history in the context of biological invasions provide a natural experiment to test predictions based on life history theory. Invasive species often reveal their physiologic and phenotypic plasticity as they invade, and then become established in, novel habitats that are potentially less favorable (more stressful) than their native environment. During this period of stress, the invasive species may take on more generalized (opportunistic) life history strategies and produce more, small oocytes (less yolk), mature earlier, grow faster, and produce smaller batches of eggs over an expanded breeding season. Once they have established a stable population, however, it may be advantageous to revert back to the more specialized (equilibrium) strategies that were adaptive in their native habitats, and produce fewer, large (heavily yolked) oocytes, mature later, grow more slowly, and provide parental care (Winemiller and Rose 1992; Záhorská et al. 2013; Hórková and Kováč 2015).

*Pterygoplichthys disjunctivus*, is an algivorous loricariid catfish species native to the Madeira River drainage of the Amazon Basin in Brazil and Bolivia (Rubio et al. 2016). As an escapee from fish farms and the aquarium trade, this species has successfully invaded North America, the Caribbean, Asia, Africa, and Australia (Gibbs et al. 2013; Rueda-Jasso et al. 2013). Their success in their invaded habitats is due, in part, to the nature of their highly periodic native environment: the seasonally flooded forests of the Amazon. Many loricariids are adapted to large, regular, seasonal changes to their hydroperiod that result in feast or famine scenarios, periods of intense

competition, and exposure to extreme conditions (Schwassmann 1978; Arrington et al. 2006). As a result, *P. disjunctivus* evolved numerous survival-enhancing traits, including being a nest-guarder with relatively high fecundity (among loricariids), having large coelomic fat stores, heavy armor plating, and the ability to both breathe air in low-oxygen environments and to survive several days of desiccation in burrows (Suzuki et al. 2000; Hoover et al. 2004; Gibbs et al. 2008; Gibbs and Groff 2014). It is important to understand *P. disjunctivus*'s life history, because in addition to their simple presence in large numbers in invaded habitats, *P. disjunctivus* is known to disrupt invaded habitats through digging nesting burrows in riverbanks (Nico et al. 2009), harassing manatees (Gibbs et al. 2010), and creating nutrient hotspots (Rubio et al. 2016).

*Pterygoplichthys disjunctivus* has been found in Florida since the 1950s, and Volusia Blue Spring since 1999. We first described their reproductive patterns during 2005–2007 (Gibbs et al. 2008). Although we have no evidence that *P. disjunctivus* is spawning in the spring run, (all spawning/nesting appears to be in the adjoining St. Johns River (Nico et al. 2009)) and juveniles tend to avoid the clear water of the spring, the large numbers of adult *P. disjunctivus* that we have caught in the spring run over the years have allowed us to describe, in some detail, the age and growth patterns (Gibbs et al. 2013) and the reproductive strategies (Gibbs et al. 2008) of this species, and to quantify its significant impacts on nutrient loads in the spring run (Rubio et al. 2016). In 2005–7, we found evidence of a relatively fecund species with strong seasonal patterns in GSI and oocyte size class. We also noticed that *P. disjunctivus* displayed some characteristics that were periodic (large body relative to most other species in the spring run, and relatively high fecundity), opportunistic (high reproductive effort, relatively early maturity (age 2; maximum age is a little over 5 years (Gibbs et al. 2013)), and multiple batch spawns), and equilibrium (high parental investment by both females (eggs) and males (guarding nests)). Interestingly, during the course of the original study we also noticed that *P. disjunctivus* might be changing some of its life history strategies in response to its new habitat in terms of:

- (1) females became capable of spawning at significantly smaller sizes (more opportunistic);
- (2) a significantly greater proportions of fish were becoming spawning-ready at any given time (more opportunistic);
- (3) batch and relative fecundity increased significantly (more periodic);

- (4) male and female GSI increased significantly each year (more periodic); and
- (5) an initially strong seasonal GSI pattern was beginning to look less organized by 2007 (more opportunistic).

We concluded at the end of our 2008 study, that although *P. disjunctivus* captured in Volusia Blue Spring appeared to be getting more successful at reproducing, our three year study was not long enough to be sure the trajectory of their new reproductive trend would persist as they continued to live in the St. Johns River and have access to the rich resources and benign conditions of the spring run. We have continued to collect reproductive data on *P. disjunctivus*, and hypothesized that because of the spring's physical and environmental stability, additional data (2012–14) would either confirm the persistence of the reproductive strategies that *P. disjunctivus* was employing by the end of 2007, or provide evidence of change toward more equilibrium strategies; especially increased oocyte size (survivorship of juveniles), increased age at maturity (generation time), and lower fecundity.

## Methods

### Study location

Volusia Blue Spring, located in north central Florida (28°56'51"N; 81°20'22.5"W), is a first magnitude oligohaline spring, discharging an annual average of 4.2 m<sup>3</sup>/s of clear 23 °C water from the Floridan aquifer into a 650 m spring run and then into the St. Johns River (Scott et al. 2004). Water flow is strong and constant throughout the year: although influenced by some seasonal variation in discharge and recharge of the aquifer, surface water, and the broad connection to the St. Johns River, water level varies by less than 1.5 meters annually. With the exception of the mouth of the spring run, water temperature does not change throughout the year (Wetlands Solutions 2010). Water conditions measured in 2012–14 (e.g. pH, dissolved oxygen, flow, water level) were consistent with those measured in 2005–7 (Work et al. 2010; our unpublished data). All areas of the spring run are accessible to all aquatic life throughout the year, and nearly all of the spring run is surrounded by steep banks. The upper half of the spring run experiences heavy recreational use from March through October, while the lower half is maintained as a manatee refuge throughout the year. Although we do see changes in benthic algae during the course of the year (lowest in late fall, proliferation of large mats in the summer), algal coverage throughout the year is generally high (~80%) in the spring run (Stevenson

et al. 2007; Wetlands Solutions 2010) and we have noted that catfish have full guts and consistent intestinal fat stores at all times of the year (unpublished data). In addition to the effects of day length on algal productivity, the connection to the St. Johns River likely provides one of the strongest seasonal signals to the spring run ecosystem: it is considerably colder in winter and warmer in the summer, there are significant annual incursions of river water into the spring run during the winter, and large numbers of fish and manatee move in and out of the spring run annually (Wetlands Solutions 2010).

The St. Johns River is relatively stable slow-flowing blackwater system, with relatively small seasonal changes in flow, interspersed with episodic spikes in flow and level during strong hurricane years. The river experiences seasonal changes in chlorophyll *a* (5–30 µg/L) and temperature (16–30 °C: only rarely cold enough to lead to death of tropical fish), but experiences little variability in pH and DO (Kroening 2004). The river is hydrologically and chemically distinct from Volusia Blue Spring.

The spring is home to over 40 species of fish, about half of which are observed regularly throughout the year (Work et al. 2010). In addition to *Pterygoplichthys*, Volusia Blue Spring invasive species also include two species of tilapia (Hornet and Blue), Brown Hoplo, koi, pirapatinga, and grass carp. Although three species of *Pterygoplichthys* have been identified in central Florida waterways (*P. disjunctivus*, *P. multiradiatus* (Hancock, 1828), and *P. anisitsi* (Eigenmann and Kennedy, 1903) (Hoover et al. 2004)), which are likely to be interbreeding throughout their areas of overlap, those in Volusia Blue Spring appear to be most like *P. disjunctivus* (Gibbs et al. 2013). Numerous fish species (including larger predators like gar, bass, and juvenile tarpon) from the St. Johns River move in and out of the spring run on a daily or seasonal bases, utilizing the spring as a thermal refuge or to feed/avoid predators: the low oxygen levels in many areas of the run limit the amount of time large non-air-breathing predators can spend foraging (Work et al. 2010). Manatees, armored catfish, and tilapia all utilize the spring run as a thermal refuge once the adjoining St. Johns River temperature drops below 20°C (Gibbs et al. 2010). Unpublished tagging studies indicate that catfish and gar can be consistently found in similar areas of the spring run throughout the year, and yet may also spend some time outside of the spring run. Interestingly, in the current study, the density of catfish observed during the daytime was distinctly lower than in the original study, however, comparisons of fecal deposition across a similar time period (Rubio et al. 2016), indicated that large numbers of

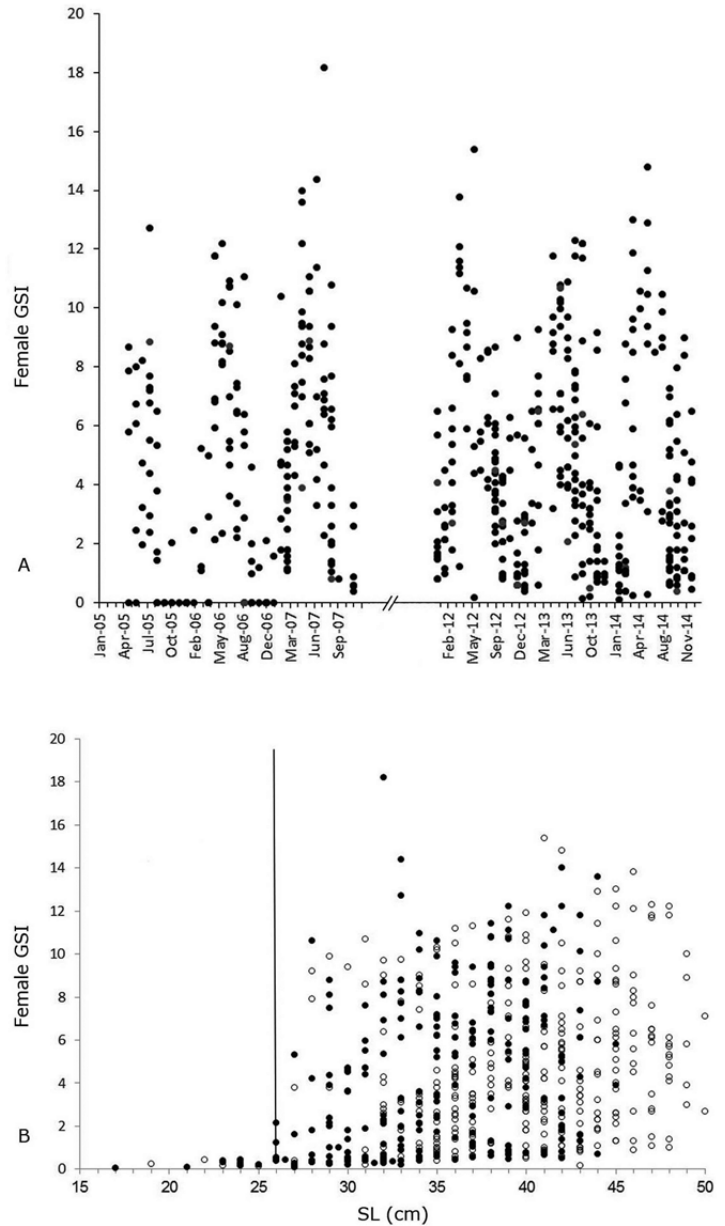
catfish were still spending considerable time in the spring run, and nighttime catfish density was probably similar to daytime density in the past. The tendency for catfish to be present in higher numbers at night has also been seen in Mexico (Rueda-Jasso et al. 2013).

Blue Spring is a stable, equilibrium system that has (1) a relatively unlimited food supply (algae); (2) a thermally stable, relatively benign, physical environment; and (3) a dearth of predators (adult catfish only have a small number of alligators, and even fewer otters as predators; no fish (gar, bass) or birds are capable of handling adult fish, and human predation other than this research is virtually non-existent). Although the adjoining St. Johns River is considerably more seasonal than the spring run, it is also considerably less seasonal than the native habitat of *P. disjunctivus*.

### Sample processing

The data for 2005–7 and 2012–14 were all collected in the same manner (see Gibbs et al. 2008). *Pterygoplichthys disjunctivus* were collected monthly from Volusia Blue Spring using pole spears (FL DEP Permits 1004113 and 05161323, Stetson University Institutional Animal Care and Use Committee (IACUC) approved), and brought back to the lab, where they were sacrificed with an overdose of MS222 (tricaine methanesulfonate). In addition to the May 2005–June 2007 data from Gibbs et al. (2008), we also included data that had been collected during the remainder of 2007 (55 females and 37 males). We examined *P. disjunctivus*'s recent reproductive patterns using data from 603 catfish (351 females and 252 males) collected between January 2012 and December 2014. Measurements included body mass (to the nearest 5 g), gonad mass (to the nearest 1 g for females, and 0.01 g for males), and Standard Length (SL) (to the nearest 1 cm). We preserved gonads in formalin for several days and then stored them in 70% ethanol before weighing, after which time we calculated gonadosomatic index (GSI = (gonad mass/body mass) × 100) for each fish. As in our 2005–7 study (Gibbs et al. 2008), reproductive maturity was defined as a GSI ≥ 1, and reproductive seasons were based on monthly plots of the GSI of reproductively mature fish (Figure 1).

Time and resource constraints necessitated a limitation of oocyte estimates to a representative sub-sample. To that end, for each month of each year, we randomly selected ovaries from at least 3 fish for detailed analysis: a subsample (usually containing 100–250 oocytes) was removed and weighed, all oocytes were counted, and the total number of oocytes in the pair of ovaries was extrapolated. The diameters



**Figure 1.** (A) Monthly female GSI patterns during the 2005–7 and 2012–14 studies. Each dot represents an individual fish; (B) Female GSI plotted against standard length. The vertical line represents the lower limits of length at reproductive maturity. ● = 2005–7; ○ = 2012–14.

of the first 100 oocytes pulled from each ovary were measured to the nearest 0.5 mm, and placed in one of three categories based on frequency distribution and appearance (Gibbs et al. 2008): immature (<1 mm, no yolk), maturing (1–2 mm, yolked), or mature (2.5–4 mm, yolked). The largest class of oocytes are assumed to be spawned together, and the smaller oocyte size classes are thought to remain in the ovaries and form the basis for the next batch of eggs (Suzuki et al. 2000; Jumawan and Herrera 2014; Samat et al. 2016). Batch fecundity was estimated as

the number of oocytes in the largest size class that would be laid at the same time (batch) (Hunter and Goldberg 1980; Gibbs et al. 2008). Relative Fecundity ( $RF = \text{batch fecundity} / (\text{body mass} - \text{ovary mass})$ ) estimates were made using the largest oocyte size class and then compared to the 2005–7 samples. We also calculated the average size of the largest 10% of oocytes (Top Decile) in each gonad for each month of the two study periods. Fish were determined to be spawning capable when they had yolky oocytes, a transparent ovarian wall, and a  $GSI > 1$  (Gibbs et al.

**Table 1.** Body condition and reproductive parameters for 2005–7 and 2012–14. (BS = breeding season; GSI = gonadosomatic index; NBS = non-breeding season; SL = standard body length).

	2005-7	2012-14
♀ Fish SL range	17–45 cm	19–50 cm
♂ Fish SL range	25–49 cm	21–53 cm
♀ Average Body Size	34.81 ± 0.33 cm (n = 251)	39.6 ± 0.28 cm (n = 348)
♂ Average Body Size	36.97 ± 0.44 cm (n = 180)	40.31 ± 0.39 cm (n = 252)
♀ Average Body Mass	869.4 ± 14.6 g (n = 251)	1097 ± 12.6 g (n = 348)
♂ Average Body Mass	908.5 ± 18.9 g (n = 180)	1077.8 ± 14.8 g (n = 252)
♀ Average Body Condition	0.0194 ± 0.00019 (n = 251)	0.0175 ± 0.00022 (n = 348)
♂ Average Body Condition	0.018 ± 0.0024 (n = 180)	0.0162 ± 0.00028 (n = 252)
♀ Spawning Capable BS	84% (n = 157)	94% (n = 166)
♀ Spawning Capable NBS	47% (n = 80)	75% (n = 173)
♀ GSI BS	5.41 ± 0.29 (n = 157)	5.98 ± 0.26 (n = 166)
♀ GSI NBS	2.35 ± 0.22 (n = 80)	3.50 ± 0.21 (n = 173)
♂ GSI BS	0.08 ± 0.003 (n = 108)	0.12 ± 0.005 (n = 70)
♂ GSI NBS	0.07 ± 0.003 (n = 62)	0.09 ± 0.003 (n = 160)
Relative Fecundity (BS)	5.03 ± 0.39 oocytes/g (n = 80)	7.95 ± 0.49 oocytes/g (n = 89)
TopD Oocyte Diameter BS	3.44 ± 0.092 mm (n = 31)	3.01 ± 0.031 mm (n = 47)
TopD Oocyte Diameter NBS	1.78 ± 0.21 mm (n = 34)	2.75 ± 0.082 mm (n = 47)

2008; Brown-Peterson et al. 2011). The description “spawning capable” was only a measure of ovarian condition (Brown-Peterson et al. 2011), not behavior; it did not mean, therefore, that the fish was actively spawning or about to spawn.

#### Statistical data analysis

We compared the length and weight of males and females from 2005–7 to those collected in 2012–2014 using two-tailed t-tests assuming unequal variance. In order to see the effect of reproduction on somatic body condition (BC), we calculated the condition of each individual using a modified Fulton’s Condition factor (Ricker 1987) that did not include the gonad mass ((body mass-gonad mass)/SL<sup>3</sup>; Le Cren 1951). We compared seasonal patterns in GSI and BC between studies by fitting a General Linear Model (GLM) in JMP<sup>®</sup>, version 11 (SAS institute Inc., Cary, NC). The model included the fixed effect of years varied at two levels (2005–7 vs. 2012–2014), the fixed effect of month and their interaction on either square root transformed GSI or Log transformed BC. Female GSI was also analyzed by season and years and their interaction to determine if elevated GSI was driven by breeding season elevation or elevation in the non-breeding season, or both. Response variables were transformed to correct deviations from normality. We compared the proportion of spawning capable fish in the breeding season and outside of the breeding season in 2005–7 and 2012–14 using a chi square test, followed by Fishers exact tests (FETs) with Bonferroni adjusted alpha value to account for multiple pairwise comparisons. Because relative fecundity (RF) and the diameter of the top 10% of oocytes

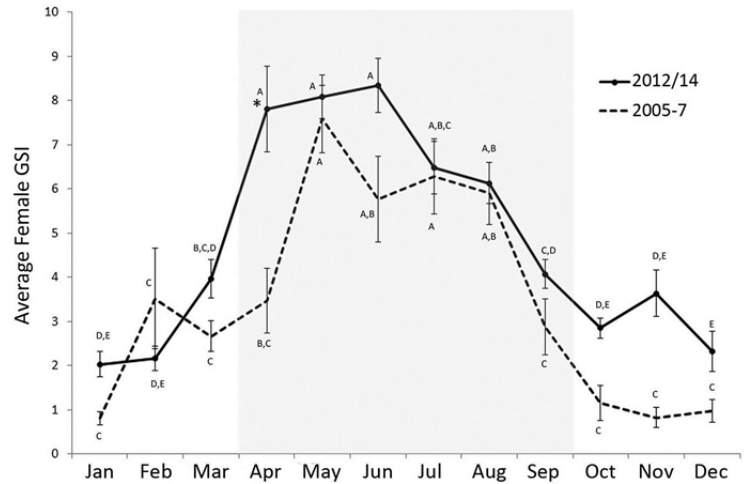
(TopD) were measured on a smaller sample of females, monthly comparisons were not possible, and we therefore binned months into those within the breeding season (April–September), and those months that fall outside of the breeding season (October–March). Season was then treated as a fixed effect varied at two levels (breeding and non-breeding) in a GLM including the effect of years and the interaction between years and season on relative fecundity and TopD. We used Tukey HSD post-hoc tests to correct for multiple pairwise comparisons. In the analysis of TopD, equal variance within each set of years was tested using Levene’s test. The proportion of females with oocytes in the top size class (2.5–4 mm) within each set of years was compared using a Fisher’s exact test. To ensure that any differences in relative fecundity were not driven by differences in female standard length in 2005–7 vs. 2012–14, we used an analysis of covariance (ANCOVA) with SL as a continuous covariate to compare RF between the two sets of years.

#### Results

Although the size ranges for fish were comparable between 2005–7 and 2012–14 (Table 1), on average both females and males were significantly longer and heavier in the new study compared to the old study (t test:  $P < 0.001$  for all comparisons).

There was a significant main effect of years (2005–7 vs. 2012–14), month, and their interaction on female GSI (Figure 2; Table 2). Post-hoc comparisons of all combinations of month and years revealed a significantly higher mean GSI in April in 2012–14 compared to 2005–7. When monthly female GSI

**Figure 2.** Average female GSI plotted against months of the year. The grey block represents the Breeding Season. Jan–Mar = Winter; Apr–Jun = Spring; Jul–Sep = Summer; Oct–Dec = Winter. Note that GSI patterns are less seasonal during 2012–14, due to increased GSIs during April, October, November, and December, relative to 2005–7. Two separate GLM analyses were run; one for each study. Months within a study that share a letter are not significantly different in post-hoc pairwise comparisons. The \* indicates the significantly higher GSI in April 2012–14 compared to 2005–7, indicating a pattern change, based on post-hoc comparisons between the two studies.



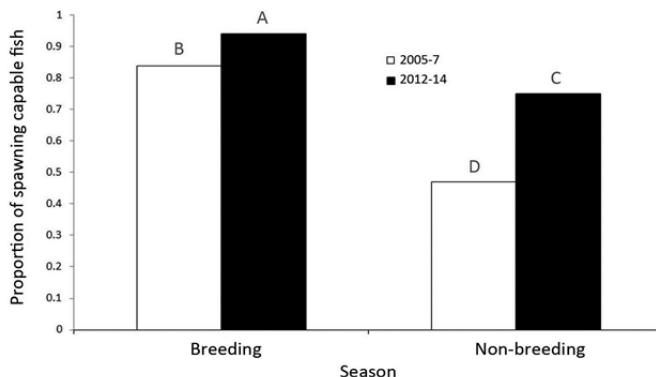
**Table 2.** Degrees of freedom, test statistics, and P values for each term in generalized linear statistical models for each response variable. Significant model effects are indicated in bold italics.

Response	Model Effect	Degrees Freedom (Numerator, Denominator)	F	P value
Female GSI	<i>Study</i>	<i>1, 584</i>	<i>41.59</i>	<i>&lt;0.001</i>
	<i>Month</i>	<i>11, 584</i>	<i>27.04</i>	<i>&lt;0.001</i>
	<i>Study x Month</i>	<i>11, 584</i>	<i>2.16</i>	<i>0.02</i>
Female GSI	<i>Study</i>	<i>1, 604</i>	<i>22.04</i>	<i>&lt;0.001</i>
	<i>Season</i>	<i>1, 604</i>	<i>239.46</i>	<i>&lt;0.001</i>
	Study x Season	1, 604	0.1003	0.75
Male GSI	<i>Study</i>	<i>1, 424</i>	<i>92.32</i>	<i>&lt;0.001</i>
	<i>Month</i>	<i>11, 424</i>	<i>4.73</i>	<i>&lt;0.001</i>
	<i>Study x Month</i>	<i>11, 424</i>	<i>1.12</i>	<i>&lt;0.001</i>
Female GSI	<i>Study</i>	<i>1, 604</i>	<i>12.14</i>	<i>&lt;0.001</i>
	<i>SL</i>	<i>1, 604</i>	<i>146.53</i>	<i>&lt;0.001</i>
	<i>Study x SL</i>	<i>1, 604</i>	<i>12.14</i>	<i>&lt;0.001</i>
Male GSI	Study	1, 444	1.062	0.3
	<i>SL</i>	<i>1, 444</i>	<i>26.18</i>	<i>&gt;0.001</i>
	Study x SL	1, 444	0.57	0.45
Female BC	<i>Study</i>	<i>1, 584</i>	<i>46.81</i>	<i>&lt;0.001</i>
	Month	11, 584	1.01	0.43
	Study x Month	11, 584	0.9	0.54
Male BC	<i>Study</i>	<i>1, 424</i>	<i>10.67</i>	<i>&lt;0.001</i>
	<i>Month</i>	<i>11, 424</i>	<i>7.29</i>	<i>&lt;0.001</i>
	<i>Study x Month</i>	<i>11, 424</i>	<i>2</i>	<i>0.03</i>
Relative fecundity	<i>Study</i>	<i>1, 166</i>	<i>80.68</i>	<i>&lt;0.001</i>
	<i>Season</i>	<i>1, 166</i>	<i>45.89</i>	<i>&lt;0.001</i>
	Study x Season	1, 166	0.13	0.72
Top 10 Oocyte Diameter	<i>Study</i>	<i>1, 172</i>	<i>67.65</i>	<i>&gt;0.001</i>
	<i>Season</i>	<i>1, 172</i>	<i>8.01</i>	<i>0.005</i>
	<i>Study x Season</i>	<i>1, 172</i>	<i>35.34</i>	<i>&gt;0.001</i>

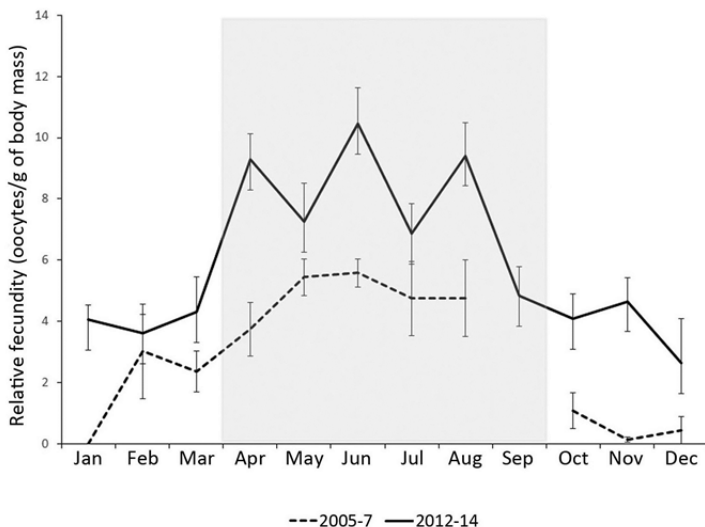
patterns were examined in 2005–7 and 2012–14 separately, seasonal patterns were significantly different (Figures 1, 2). However, when GSI was analyzed by month and season, results demonstrated that GSI was higher in 2012–14 compared to 2005–7 in both the breeding and non-breeding season (Table 2).

There was a significant effect of season and years in the analysis of the proportion of spawning capable females (Season: Chi Square = 49.16, P <0.001; Years: Chi square = 20.81, P <0.001). Post hoc pairwise comparisons showed that the proportion of spawning capable females was significantly higher during the

**Figure 3.** The proportion of spawning capable females increased significantly in the 2012–14 Non-Breeding season, and has become less seasonal than it was in the original study (the lack of shared letters indicate significant differences in post-hoc pairwise comparisons).



**Figure 4.** The relative fecundity is plotted against months of the year. The grey block represents the Breeding Season. Note that the relative fecundity has increased in 2012–14, and is also less seasonal (in the 2005–7 study, RF was often at 0 during the Fall and Winter).



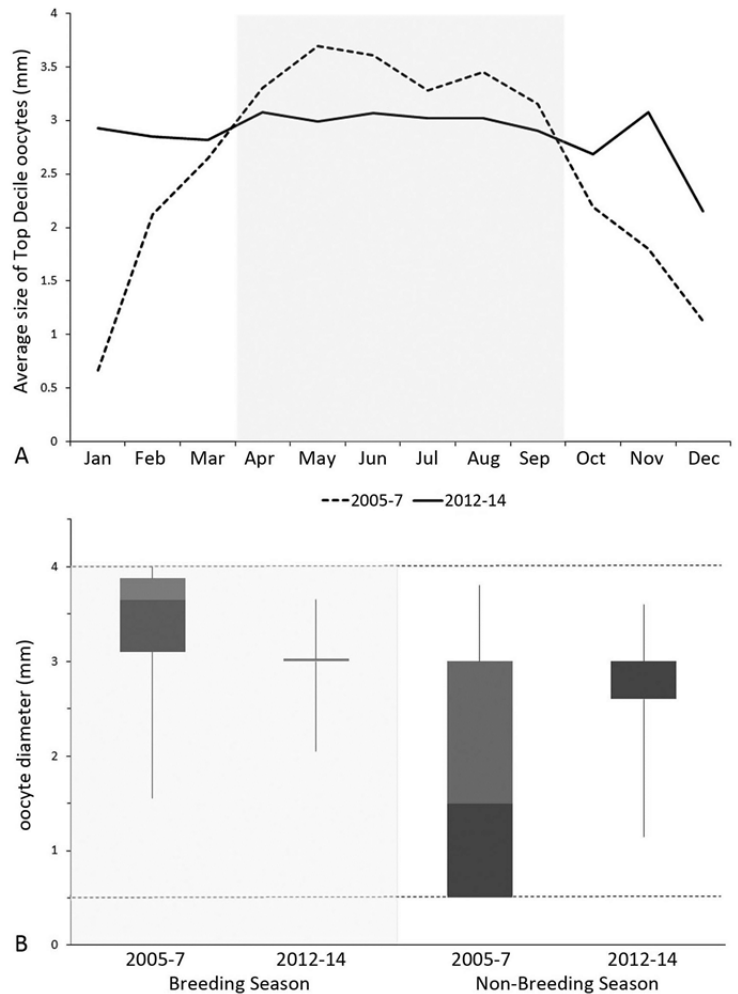
breeding season relative to non-breeding season in both 2005–7 and 2012–14 (Old FET,  $P < 0.001$ ; New FET,  $P < 0.001$ ) (Figure 3). The proportion of spawning capable females was higher in 2012–14 compared to 2005–7 in both the breeding (FET,  $P = 0.014$ ) and non-breeding (FET,  $P < 0.001$ ) season. However, the difference between breeding season proportions between 2005–7 and 2012–14 was not significant after adjusting for multiple comparisons.

There was a significant effect of season (breeding vs. non-breeding) and year on relative fecundity, although the interaction term was not significant (Figure 4, Table 2). Relative fecundity was higher during the breeding season compared to the non-breeding season in both years, and relative fecundity was consistently higher in 2012–14 (Figure 4). The effects of years on relative fecundity within each season were maintained after accounting for SL (ANCOVA: Breeding season,  $F_{1,91} = 6.08$ ,  $P = 0.006$ ; Non-breeding season,  $F_{1,73} = 12.31$ ,  $P = 0.001$ ).

There was a significant effect of years, season, and their interaction on TopD (Figure 5, Table 2). Post-hoc tests revealed that TopD was significantly higher in the breeding compared to the non-breeding season in 2005–7 only (Figure 5). The degree of variance in TopD oocyte diameter changed between 2005–7 and 2012–14 (Levene’s test,  $P < 0.0001$ ). In particular, the TopD in the 2012–14 Breeding Season became almost uniformly 3 mm with very little variance around the mean (Figure 5). The non-breeding TopD experienced a similar change by 2012–14: average TopD centered around 2.5–3 mm diameter and showed a lower variance compared to 2005–7 (Figure 5). Significantly fewer fish had TopD oocytes in 4 mm size classes in 2012–14 than in 2005–7 (FET,  $P < 0.0001$ ).

There was a significant effect of month and years on male GSI, although there was no significant interaction effect (Table 1). Similarly to females, male GSI was consistently higher in 2012–14 compared to





**Figure 5.** The average size of the Top Decile oocytes is plotted against months of the year (A) and Box-whisker plots of Top Decile oocyte size in Breeding and Non-Breeding seasons (B). Note the loss of seasonality in TopD monthly patterns (A). The maximum oocyte size (B) over the past 10 years was 4 mm, and the minimum was 0.5 mm (dotted lines). The upper whisker = maximum value – 3<sup>rd</sup> quartile, the bottom whisker is 1<sup>st</sup> quartile – minimum value. The light grey box = the 3<sup>rd</sup> quartile – the median value, and the dark grey box = median value – 3<sup>rd</sup> quartile. The 2012–14 Breeding Season box is small because the 1<sup>st</sup> quartile, median, and 3<sup>rd</sup> quartile were virtually the same. The 2012–14 Non-Breeding Season is small because the median and 3<sup>rd</sup> quartile values were the same.

2005–7. However, males differed from females in that their seasonal GSI patterns did not differ significantly between 2005–7 and 2012–14 (Figure 6).

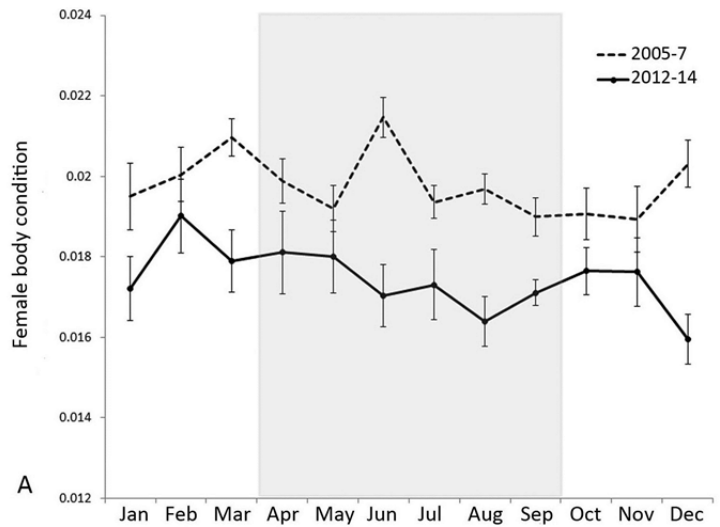
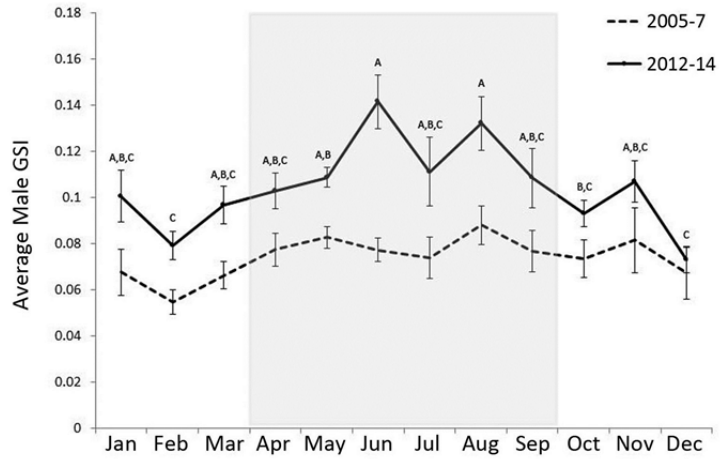
There was a significant effect of years on female BC, though female BC did not vary by month (Figure 7a, Table 2). Females in 2012–14 were in consistently lower BC compared to females in 2005–7. Analysis of male BC revealed a significant effect of years, season, and their interaction (Table 2). Males in 2012–14 were in lower body condition compared to 2005–7, and post-hoc comparisons revealed greater seasonality in 2012–14 compared to 2005–7 (Figure 7b).

## Discussion

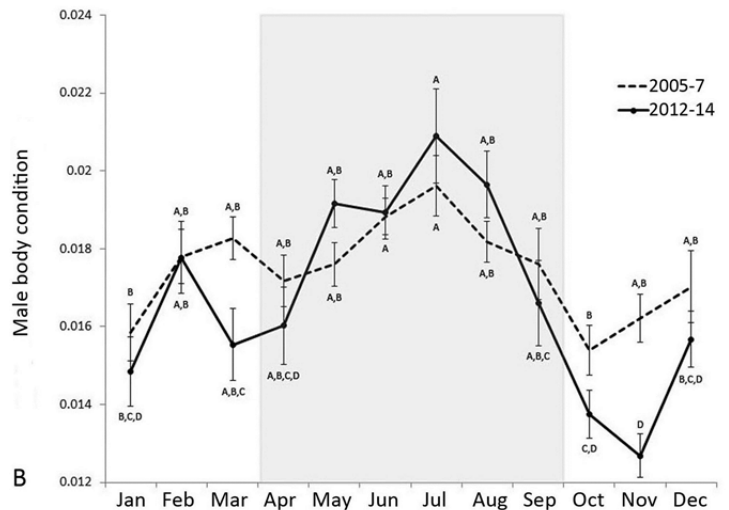
It is not often that we have the opportunity to track the rapid changes in reproductive patterns of an invasive species as it adapts to an ecosystem that is

substantially more benign than its native system. Our hypothesis that *P. disjunctivus* would have continued to expand its reproductive capabilities in its invaded Florida habitat was supported, although not by following all of the original trends we had seen in 2005–7 (there was no further reduction in size at first maturity) or by moving clearly toward an equilibrium reproductive strategy (oocytes got smaller instead of larger, there was no increase in age at maturity, fecundity increased instead of decreasing). Most interestingly, we documented significant increases in reproductive effort since 2005–7, in terms of increased numbers of reproductive-ready females throughout the year (particularly during the late fall and winter of the non-breeding season), increased relative fecundity, and a reduction in the maximum diameter of oocytes. The relatively quiescent period that we had seen in female ovaries during the 2005–7 non-breeding season was much less apparent in

**Figure 6.** The average male GSI is plotted against months of the year. Note that the 2012–14 GSI is higher overall than 2005–7, and has become more seasonal. Months that share a letter are not significantly different in post-hoc pairwise comparisons.



**Figure 7.** Female (A) and Male (B) body condition indices are plotted against months of the year. Note that female BCI has decreased throughout the year, while male BCI has only dropped significantly during October and November. Also, note the seasonality in the male pattern, and lack of seasonality in the female pattern. Months that share a letter are not significantly different in post-hoc pairwise comparisons.



2012–14, and, although we occasionally found females with spent ovaries in 2012–14, they were not found at any particular or predictable time of the year. The significant increase in 2012–14 spring (especially April) and slight increase in fall GSIs indicated an expansion of the original 2005–7 female breeding season.

Although we did not directly measure annual reproductive effort (sampling was terminal and spawning occurs outside of the spring run), our monthly measurements of reproductive parameters still allowed us to do much more than estimate individual clutch size. The GSI patterns, proportion of fish in reproductive-ready mode, oocyte size, and body condition together provide evidence that reproductive effort in this species has changed significantly since 2005–7. Females significantly increased their reproductive effort via increased relative fecundity and a decrease in maximum oocyte size in 2012–14. Our data fits well with that collected from this species in two tropical invasion locations: data collected in Mexico revealed a similar, although somewhat higher, relative fecundity (12.6 eggs/g (Rueda-Jasso et al. 2013)), and oocyte diameters in a Malaysian population were similar to the current study (max = 3.6 mm (Jumawan and Herrera 2014)). With the exception of the 4 mm oocyte size class, which had mostly disappeared from our data by 2012–14, all mature fish in this study, regardless of size, produced the full range of oocyte diameters. The pattern of Top Decile oocyte size we observed in 2005–7 became significantly less seasonal and less variable in 2012–14, both through an increase in non-breeding TopD oocyte size and a dramatic shift to near uniformity of breeding season TopD oocyte size. The statistical strength of the TopD oocyte size data suggests this could be an adaptive change in reproductive strategy, rather than simple ecophenotypic plasticity.

Female fish have maintained the same minimum size at first maturity we saw in 2005–7 (Gibbs et al. 2008); in the current study no fish under 26 cm SL (2 years old (Gibbs et al. 2013)) were caught in spawning-capable mode. Although we found that more fish were reproductive-ready during 2012–14 than in 2005–7, it is unlikely that catfish are spawning throughout the year. Despite 16 years of surveying the spring run for nests, we have yet to find a nest. Fish must still be dependent on summer temperatures in the St. Johns River for nesting sites that are warmer than anything available in the spring run, and perhaps closer to the temperature of nesting habitat in their native Madeira River. We suggest that the reproductive capability of *P. disjunctivus* has expanded not only to fit within the normal

seasonal temperature limitations of the St. Johns River, but continued access to the food-rich, benign Volusia Blue Spring has allowed this species to maintain reproductive readiness throughout much of the non-breeding season, and therefore take full advantage of early springs or otherwise warm years to extend their breeding season.

The increased reproductive effort we saw in 2012–14 is likely the reason that both male and female body condition indexes decreased relative to 2005–7 (Mazzoni and Caramaschi 1995). We found no evidence that suggested fish were in poor health in 2012–14; with rare exceptions, all individuals in both of our study periods had full guts and intestinal fat deposits, suggesting that this decrease in body condition (lower stored energy) might not be particularly harmful to the fish. In an attempt to put the body condition of *P. disjunctivus* into some context, we conducted a literature survey for loriciariids with similar body shapes, living in their native ecosystems, and estimated their body conditions using average standard lengths and body mass data. The average body condition of *P. disjunctivus*, even after the significant decline in 2012–2014 (2005–7 BC=0.0195; 2012–14 BC=0.017) was higher than the body condition of *Hypostomus auroguttatus* Kner, 1854 (BC = 0.0105) (Gomes et al. 2015), *H. albopunctatus* Regan, 1908 (BC=0.014), *H. regani* Ihering, 1905 (BC=0.011), *H. strigaticeps* Regan, 1908 (BC=0.013) (Silveira and Vaz-dos-Santos 2015), and *H. francisci* Lütken, 1874 (BC = 0.0104) (Sales et al. 2016). In its native boom or bust environment, *Pterygoplichthys* may have needed to store more energy to hedge their bets to increase survival through lean times. Because the invaded Blue Spring ecosystem is relatively stable and food is widely available, such bet hedging strategies may no longer be adaptive.

Our seasonal analyses of body condition revealed that male and female trends varied considerably, both in terms of monthly patterns and the amount of change between the two study periods. Although seasonal patterns for females were not significant in this study, female *P. disjunctivus* did appear to have a somewhat lower BCI in summer; in the middle of the reproductive season, after they have invested tremendously in egg production. The significant overall reduction in female BCI in 2012–14 is likely in response to an increased year-round reproductive effort. Male *P. disjunctivus* body condition was significantly more seasonal during both periods than females, and was significantly lower in November 2012–14 than 2005–7, which roughly corresponded to when the newly expanded spawning/nest guarding season should be complete. Indeed, the pattern of

gender variability in BC we saw for *P. disjunctivus* was similar to what was reported in *Loricariichthys melanocheilus* (Zardo and Behr 2015), which also had a relatively stable seasonal female body condition (when gonad mass was not included) and a less seasonally stable male body condition. Although there is no data available on egg mass defense in *P. disjunctivus*, since other nest-guarding males have been documented to contain multiple clutches of varying age or guard a series of clutches throughout the season, and some nest-guarding males have been reported to either not feed or not feed as frequently during the time they are guarding the egg masses (Moodie and Power 1982; Lowe-McConnell 1987; Ferreira et al. 2013), it is reasonable to expect something similar for *P. disjunctivus*. A prolonged nest guarding period would require both a greater testes investment during the reproductive season, and also cause a greater drain on body resources (Blumer 1979).

The food resources and predation pressures experienced by *P. disjunctivus* in Volusia Blue Spring and the St. Johns River could have had a significant effect on their reproductive strategies, even over a mere 10 year (4–5 generation) period. In lab experiments, female *Poecilia reticulata* (Peters, 1859) changed their subsequent brood size and average offspring weight on the basis of both past and current food regimes during a single season: a reduction in food during the interbrood intervals resulted in fewer larger offspring, while those females provided with increased food produced an increased number of smaller offspring (Reznick and Yang 1993). This trade-off between large eggs and high fecundity and a relationship with food resources has also been seen in captive bred (hatchery) Chinook salmon (*Oncorhynchus tshawytscha* (Walbaum, 1792)). In the hatchery environment, plentiful food and low predation rates removed some of the selection pressure to produce large eggs, but left the fecundity pressures in place (Heath et al. 2003). Thirteen years (3–5 generations) after a hatchery was established with wild stock, the captive-bred descendants were producing more, but significantly smaller, eggs than the founding population. Unfortunately, not only was survival of these smaller eggs lower than the larger eggs produced by wild fish, but small egg size persisted in subsequent generations even after hatchery fish were released into the wild and bred with the wild stocks (forming supplemented stocks), thus indicating a genetic component to this change in salmon (Heath et al. 2003). The guppy (single season study, short generation species, plastic response) and salmonid (multi-year study, longer generation species, genetic response) studies of reproductive

changes in response to changing environmental conditions provide an interesting comparison to what we have seen in Volusia Blue Spring with an invasive species acclimating or adapting to an ecosystem that contains resource-rich refuges that are far more benign and stable than its native environs.

The changes in reproductive patterns we have seen in *P. disjunctivus* over the past 10 years (smaller size of oocytes, increased relative fecundity, increased GSI, and expansion of breeding season) did not follow our predictions for a fish species that originated in a highly variable (periodic) environment, and was settling into a more stable equilibrium environment. We propose, therefore, that the increased reproductive effort and other seasonal changes we see in *P. disjunctivus* are not due to increased environmental risk/variability and a need to bet hedge (often the case described in invasion literature), but rather are due to a different selection gradient: the stability of their invaded habitat and that food and predation are less limiting. For example, the significant decrease we observed in the presence of the largest oocyte size reflects the plentiful food resources available to the female and offspring, which allows females to make a shift in their reproductive investment toward greater numbers of smaller oocytes, probably laid in more batches during the now expanded breeding season, rather than toward heavier provisioning of a smaller number of oocytes (Nussbaum and Schultz 1989; Rollinson and Hutchings 2013; Robertson and Collin 2015). We suggest that due to the resources available in Volusia Blue Spring, *P. disjunctivus* may have less need to heavily provision oocytes; parental care should ensure high proportions of hatchlings and plentiful food should ensure adequate juvenile survival rates.

We know that some other loricariids in their native habitats (e.g. *Hypostomus francisci*; Sales et al. 2016), fall between the equilibrium and opportunistic strategies of the Winemiller-Rose continuum, and another, *Hypostomus auroguttatus*, utilized an equilibrium strategy in its native river system (balanced sex ratio, total spawner, low fecundity, large eggs, and parental care), and switched to an opportunistic strategy (more small eggs) to deal with the environmental challenges of living in an artificial reservoir (algal blooms, extremes in dissolved oxygen, and variable temperatures and pH) (Mazzoni and Caramaschi 1997; Duarte et al. 2011; Gomes et al. 2015; Sales et al. 2016). We also know that it is typical for invasive fish in a new environment (often challenging or stressful) to shift toward opportunistic strategies (Záhorská et al. 2013; Hůrková and Kováč 2015), but that does not seem to be the case for *P. disjunctivus* in Volusia Blue Spring. We were curious

about how *P. disjunctivus* would shift strategy within the Winemiller-Rose scheme as it established itself in Volusia Blue Spring, and instead shifts in any one direction within the Winemiller-Rose reproductive scheme were not apparent. *Pterygoplichthys disjunctivus* (1) provides parental care to improve juvenile survival (equilibrium); (2) has relatively large eggs (equilibrium), but has reduced egg size over the course of the study (periodic/opportunistic); (3) age at maturity dropped during the 2005–7 study (moving from equilibrium to opportunistic/periodic), but has since remained stable; (4) fecundity and GSI were high in the 2005–7 study (opportunistic/periodic) and have become even higher (periodic); (5) the increase in breeding season length is likely to result in additional spawning events (opportunistic); and (6) food is plentiful and environmental conditions are both stable and predictable (equilibrium).

As *P. disjunctivus* established itself in Volusia Blue Spring during the past 10 years, we watched oocyte size decrease, age at maturity decrease and then stabilize, and fecundity increase in a variety of measures. None of this was expected, especially the reduced variance in TopD oocyte size and reduced size of oocytes. We suggest that these changes are due to reductions in annual environmental variability along with reduced food and predation pressures, and since Volusia Blue Spring conditions have not changed significantly since 2005–7, and the oocyte size trends we saw were remarkably constant across a large sample size, these changes could be adaptive, much like that seen in hatchery salmon and their descendants (Heath et al. 2003). The example of *P. disjunctivus* and its invasion of Volusia Blue Spring is particularly valuable as we look for ways to manage the increasing numbers of invasive species throughout the world. Invasive species are known for their ability to successfully adapt to a variety of environmental conditions, and so classic life history schemes may not be as relevant for invasive species, or at least invasive species inhabiting relatively benign, stable environments.

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