

Research Article

Age and growth of the loricariid catfish *Pterygoplichthys disjunctivus* in Volusia Blue Spring, Florida

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Abstract

Little is known of age and growth patterns in loricariid armored catfish living either in their native or invasive ranges. For this first study of age and growth patterns in a loricariid invasive to the US, we collected 185 lapillar otoliths from vermiculated sailfin catfish, *Pterygoplichthys disjunctivus*, in Volusia Blue Spring, Florida and used them for age determination. Age estimates were generated and compared with reproductive, standard length (SL), and body mass data collected over a seven year period. Otolith band-pair counts yielded high precision age estimates (Average Percent Error = 4.3, Coefficient of Variation = 5.8, Precision = 3.36), which indicated the oldest catfish were no more than 5.25 years old. Standard length-frequency analysis and a linear growth model both supported a growth rate of approximately 10 cm/year. The von Bertalanffy Growth model did not provide a better fit, and was therefore discarded. Since none of the 185 otoliths was estimated to be from catfish older than 5.25 years, and none of the 5,800 fish caught in the past ten years was longer than 51.5 cm SL, it appears that *P. disjunctivus* in this Florida spring and river environment grows rapidly for about five years, but the cohort dies out due to high natural mortality rates.

Key words: armored catfish; otoliths; growth rates; ageing

Introduction

Over the past 20 years, at least seven species of South American loricariid catfishes have become established in tropical and sub-tropical systems around the world, including the southern United States, the Caribbean, Mexico, South Africa, the Philippines, Taiwan, and other parts of southeast Asia (Bunkley-Williams et al. 1994; Fuller et al. 1999; Chavez et al. 2006; Page and Robins 2006; Jones et al. 2013). *Pterygoplichthys disjunctivus* (Weber, 1991) is a native of the Madeira River drainage of Bolivia and Brazil and appears to have been in Florida since the late 1950s, when loricariid catfish were first described in the Tampa Bay - Gulf Coast region (Courtenay et al. 1974; Ludlow and Walsh 1991; Page 1994). It has become established in several large river systems in Florida, including the Hillsborough, Kissimmee, Oklawaha, Peace, St. Johns, and Withlacoochee (Fuller et al. 1999). Like some

other Florida tropical fish invaders [e.g. *Tilapia Oreochromis aureus* (Steindachner, 1864)], *P. disjunctivus* utilizes warm water springs as thermal refuges from cold winter river temperatures (Gibbs et al. 2010). Unfortunately, despite the large numbers of armored catfish reported in invasive populations, very little research has been conducted on the life history or ecosystem impacts of *P. disjunctivus*, making it difficult to effectively evaluate the impacts of invasion (Courtenay 1997; Simberloff 1997; Hoover et al. 2004; Liang et al. 2005; Gibbs et al. 2008; Gibbs et al. 2010).

Loricariids are popular in the aquarium trade, and, like other loricariids in the United States, *P. disjunctivus* probably colonized from fish farm escapes and aquarium releases (Page 1994; Greene and Lee 2009). Tropical non-indigenous fish have become commonplace in Florida and Gulf Coast regions of the United States, and may cause a myriad of ill effects on their new environments, particularly since their diet and

reproductive habits may harm or out-compete native species and physically alter the ecosystem. We do know that *P. disjunctivus* disturb resting endangered Florida Manatees in springs by grazing algae from the manatee's skin (Nico et al. 2009; Gibbs et al. 2010), and that catfish graze large amounts of algae from rocky and woody substrates (Hoover et al. 2004; Gibbs, personal observation). Male *P. disjunctivus* also damage river banks by digging extensive nesting burrows (Hoover et al. 2004; Nico et al. 2009), and females are prolific, iteroparous reproducers. Finally, Florida *P. disjunctivus* appear to be increasing their reproductive output, expanding the length of their reproductive season, and extending their period of reproductive readiness (Gibbs et al. 2008; unpublished data). All of these effects and the ease with which *P. disjunctivus* has invaded ecosystems around the world, adds increased urgency to our need for a better understanding of their life history patterns.

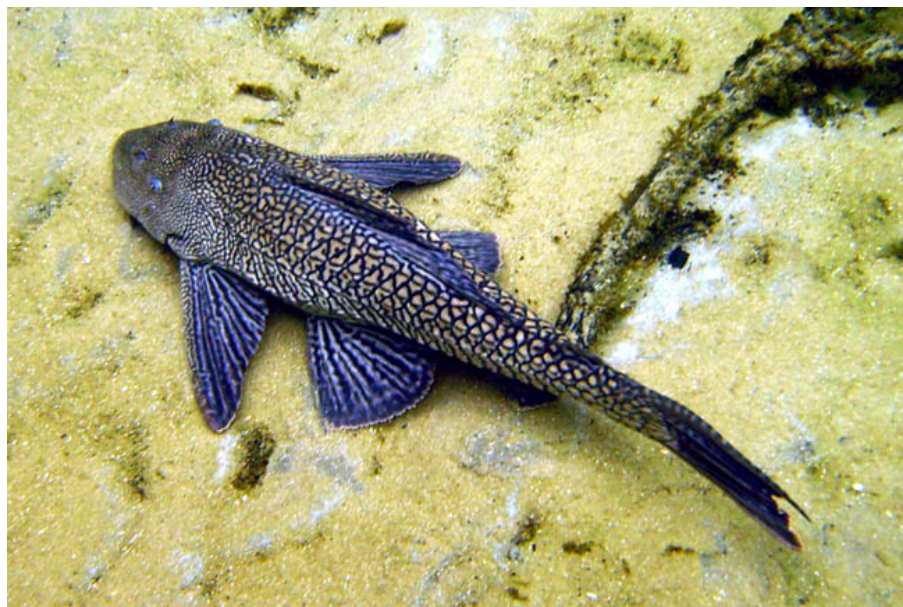
Relatively few age and growth studies have been conducted on South American tropical freshwater fish, and the one study that has been published in English on growth patterns for an armored catfish, only covered daily otolith microincrements in a juvenile callichthyid [*Hoplosternum littorale* (Hancock, 1828)] (Ponton et al. 2001). Subtropical Florida and its large numbers of invasive species provide us an opportunity for studying age and growth patterns in many previously unstudied species. The goals of the study were to (1) report on age and growth patterns of *Pterygoplichthys disjunctivus* in Volusia Blue Spring; (2) correlate otolith band pair patterns with seasonal events; and (3) use otolith band patterns and size frequency distributions to estimate annual growth rates and age at maturity. We expected that growth patterns of *P. disjunctivus*, like those of other tropical fishes, would be tied to a physiological winter associated with seasonal reproductive costs or relatively small seasonal drops in temperature, water levels, and/or food availability (Lowe-McConnell 1975; Bagenal and Tesch 1978; Brothers 1979; Boujard et al. 1991; Booth et al. 1995; Grammer et al. 2012). Based on previous reproductive studies (Gibbs et al. 2008) and observations from the field and lab, we hypothesized that age and growth parameters for a population of *P. disjunctivus* living in sub-tropical central Florida would include rapid growth, a short generation time, and be tied to the summer reproductive season.

Methods

The study site was Volusia Blue Spring in north-central Florida, located within Blue Spring State Park, and connected to the St. Johns River (28°56'51.0"N, 81°20'22.5"W). Volusia Blue Spring is a 650 meter, 1st magnitude spring (>2.8 m³/sec of water flows from the Floridan Aquifer), with a constant temperature of 23°C (Scott et al. 2004). The upper half of the spring run is heavily utilized for human recreation, except during the winter, when the entire run is protected as a thermal refuge for the Florida Manatee. We have observed 35 native and seven exotic fish species utilizing the run, most permanently and several seasonally (Work et al. 2010). Three species of *Pterygoplichthys* are found in central Florida [*P. anisitsi* (Eigenmann & Kennedy, 1903), *P. disjunctivus*, and *P. multiradiatus* (Hancock, 1828)] (Hoover et al. 2004). Although these congeners are likely to be interbreeding, the catfish in Volusia Blue Spring have been identified as most like *Pterygoplichthys disjunctivus* (J. Armbruster, pers. comm.) (Figure 1). We find *P. disjunctivus* in the spring run throughout the year, but its numbers increase rapidly at the onset of colder winter season, when it uses the spring run as a thermal refuge and human disturbance is at a minimum (Gibbs et al. 2010).

We caught over 5,800 catfish in Volusia Blue Spring between 2005 and 2011, primarily using pole spears (Florida Dept. Environmental Protection Permit 1004113, Stetson University Institutional Animal Care and Use Committee (IACUC) approved). Catfish were caught throughout the year, but our sampling effort was reduced during the winter to avoid disturbing the manatees. We brought a maximum of 20 fish from each daily catch back to the lab for further processing. On the days when more than 20 fish were removed from the spring, standard length (SL) data (measured from the tip of the rostrum to the tip of the caudal peduncle, after Boeseman (1968)) were collected in the field from the remaining catch using an Aquatic Ecosystems Fish Measuring Board. When more than 100 catfish were caught, we took SL data from a haphazard sample that included the full size range of fish caught. Although most of the 20 fish taken back to the lab were haphazardly chosen from the day's catch, once again, we always included some of the largest and smallest fish to ensure that the full range of body sizes was represented in the study. The fish we

Figure 1. *Pterygoplichthys disjunctivus* in the Volusia Blue Spring run. Photograph by M. Gibbs.



brought back to the lab were sacrificed with an overdose of tricaine methansulfonate (MS222), and then SL was measured to the nearest 0.5 cm, and body mass to the nearest 5 g using an Ohaus triple beam balance. Gonads were removed, preserved in 10% formalin, and then stored in 70% ethanol for later processing. Between 2008 and 2011, we removed at least one lapillal otolith [the largest otolith in loriciid catfish (personal observation; Ponton et al. 2001)] from each fish in a subsample of 150 catfish. The hindbrain and semicircular canals were exposed by vertically sawing through the cranium about level with the operculum. Catfish from which otoliths were removed, were selected to evenly represent the full range of catfish SL. Male and female data were not separated for this study, but will be compared in a larger study that is currently underway.

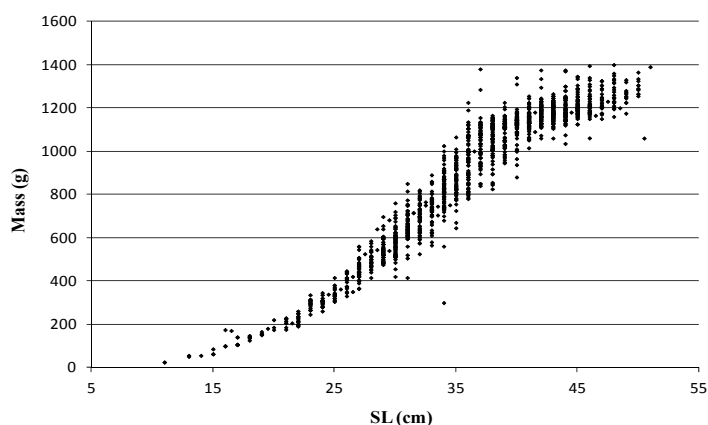
We plotted length-frequency data against date, and used comparisons of both 6- and 12-month length-frequency mode progression to establish cohort growth rates (Peterson Method; Brothers 1979). The length-frequency results were then used to support age estimates based on otolith analyses (Brothers 1979; Campana 2001; Morales-Nin and Panfili 2002).

After removal from the catfish, each otolith was stored in a separate envelope and assigned a unique otolith number to remove any cue to the original fish number that might influence the

otolith reader as to gender, SL, and season of capture. All otolith data were recorded under this otolith number. The length, mass, and thickness of otoliths were measured and later correlated with fish SL. After mounting each otolith on a glass slide with cyanoacrylate cement, we sectioned them by grinding each otolith on one or both sides using a modified turntable and ultra-fine grit sand- and polishing paper (Karakiri and Westernhagen 1988). The resulting otolith sections were viewed with transmitted light with a Zeiss Axiostar Plus compound microscope at 50–100× total magnification. Although it is traditional to make transverse otolith sections, in our case sagittal sections were more practical. We made both transverse and sagittal sections from ten pairs of otoliths and compared the growth band patterns and counts from the two different planes in order to determine whether either or both planes lent themselves to ageing; finding no differences, we ultimately used 185 otoliths sectioned in the sagittal plane for the ageing analysis.

We estimated age by counting otolith growth band pairs (pairs of translucent and opaque growth zones). Opaque zones consisted of increments laid close together, and were, therefore, defined as periods of slow growth. Translucent zones, which consisted of increments laid further apart, were defined as periods of faster growth. All 185 otoliths were read three times each by a single

Figure 2. Mass (g) vs. standard length (cm) of *Pterygoplichthys disjunctivus* collected in Volusia Blue Spring, Florida between 2005 and 2013 (n=1378).



reader (voucher specimens were independently confirmed), and we measured the precision of age estimates with a Coefficient of Variation (CV), Average Percent Error (APE) and Index of Precision (D) (Cailliet et al. 2006). The width of each band pair was measured with a calibrated ocular micrometer (Zeiss Axiostar Plus compound microscope), and trends in band pair width from one age class to the next were fit to a 2nd order polynomial trend line.

When determining the status of the otolith margins (whether the fish was currently in fast growth, slow growth, etc.), we followed the recommendations of Cailliet et al. (2006), and assigned the outermost otolith marginal increment to one of four grades based on how far the growth phase had progressed from the last slow growth zone towards the next. Otolith margins were scored in intervals of 0.25, from 0 (at the beginning of the translucent (fast growth) zone) to 1 (when the margin transitioned into an opaque (slow growth) zone) (Jepsen et al. 1999; Pajuelo and Lorenzo 2003). We used Marginal Increment Analysis (MIA) to validate seasonal deposition of the growth band pattern by scoring the state of the otolith margin according to the four grades described above, and correlating that grade with month of capture (Campana 2001). A Kruskal-Wallis analysis of variance was used to determine the MIA likelihood ratio (whether there was a significant difference in MIA among months) (Cailliet et al. 2006). We also compared each otolith's marginal increment status to the fish's body condition [assessed using Fulton's

Condition Factor (Nash et al. 2006)] and a long term data set on reproductive seasonal patterns (Gibbs et al. 2008; Gibbs, unpublished data).

We plotted estimated age against both SL and body mass for all fish. Due to the dearth of published studies of age and growth patterns in loricariid catfish, we fit the SL versus estimated age data for all individuals to both the linear model (which the data appeared to fit), and the commonly used Von Bertalanffy Growth Formula (VBGF) (Cope and Punt 2007). The fit of the data to both models was assessed with a linear regression and residual mean square error analysis (MSE) (Perez et al. 2011).

Results

The largest of the 5,800 fish caught during the seven years of data collection was 51.5 cm SL, the smallest was a 0.5 cm hatchling; small (less than 25 cm SL) catfish were rarely found in the spring run (Figure 2). An unusual, tropical storm-induced flooding event (lasting 3–4 weeks) during the early fall of 2008 is likely to have increased survival of young fish by creating additional nursery habitat, and thus resulted in an unusually large size cohort in the mid 20 cms in the fall of 2009 (Figure 3). The length-frequency data clearly showed similar progressions of SL cohorts over the next several six month intervals. The large cohort at 22 cm in September 2009, progressed to 27 cm in March 2010, and then to 32 cm in Sept. 2010, thus supporting a cohort growth rate of about 10 cm/year. Seasonal body

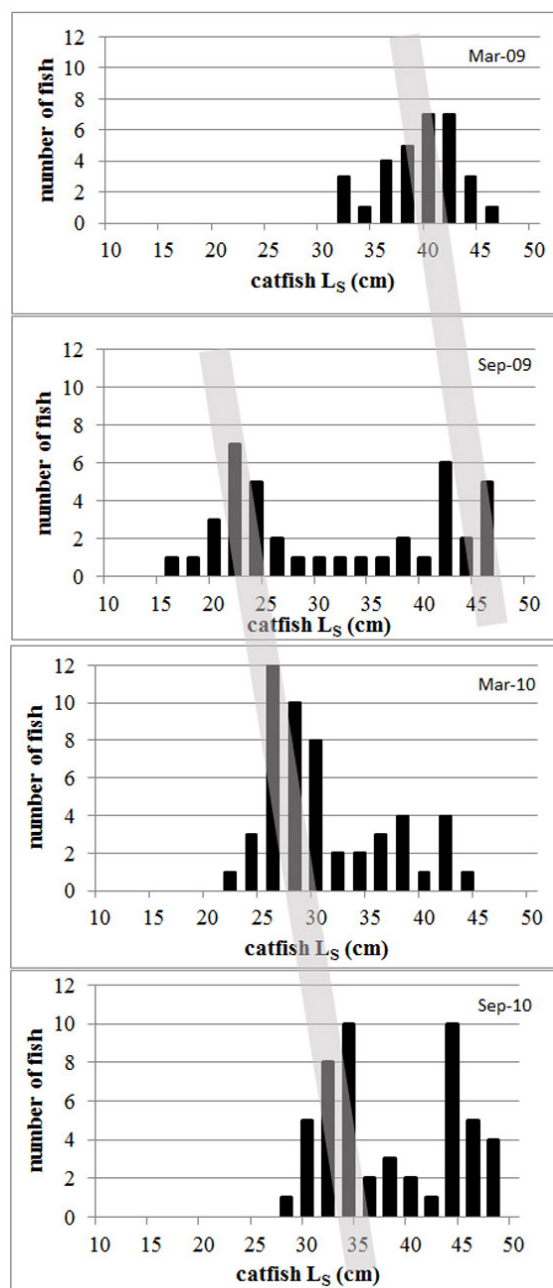


Figure 3. Representative length frequency mode progression shows a regular, steady growth rate of about 10 cm/year. The September 2009 peak at 23 cm SL is followed by a 28 cm SL peak in March 2010, and then a 33 cm SL peak in September 2010. A larger mode at 39 cm SL in March 2009 is also seen in September 2009 at 44 cm SL. Tracking lines (wide grey bars) based on the mean SL within each mode highlight the progression of length modes over time.

condition [(body mass - gonad mass at length)/SL³] comparisons revealed that male body condition peaked sharply during the early summer, correlating strongly with the onset of slow growth and the very beginning of the broad female gonadosomatic index (GSI) peak (linear regression, $r^2 = 0.889$, $p < 0.001$) (Figure 4). Female body condition (calculated with body mass - gonad mass) was highest during the winter, and dropped during the summer GSI peak before recovering in October/November. Female body condition (calculated including gonad mass) exaggerated the body condition peak that coincided with the onset of peak GSI, but there was no significant correlation between seasonal female GSI and body condition or otolith MIA (linear regression, $r^2 = 0.05$). Body condition in both males and females dropped off rapidly as soon as the GSI peak began in June/July, and catfish did not shift into faster growth until after the GSI peak was over.

There was a significant positive relationship between otolith length and SL (linear regression, $r^2 = 0.81$, $p < 0.001$, $n = 178$) and between otolith mass and SL (linear regression, $r^2 = 0.79$, $p < 0.001$, $n = 95$). At the same SL that otolith length deposition started to slow down (~ 40 cm), the otolith mass increased, reflecting the increased deposition in the otolith's dorsum [ANOVA regression F-value was significant ($p < 0.001$, $n = 66$)]. This change in deposition pattern was also reflected by our comparisons of transverse and sagittal sectioning (Figure 5). Otolith band pairs were clearly visible and precision of band pair counts was high (APE = 4.3, CV = 5.8, and D = 3.36). Although band pairs 3-5 were narrower than bands 1-3, there was no apparent crowding of microincrements that might suggest a rapid decrease in growth rate and ageing resolution. The maximum number of band pairs for *P. disjunctivus* sampled was just over five. Age estimates from paired otoliths using both sagittal and transverse planes were the same; the thinner 3rd, 4th and 5th band pairs were clearly distinguishable in both otolith planes and thus either transverse or sagittal planes could be used to make accurate age estimates.

The timing of deposition of the annual opaque (slow growth) zone matched well with the peak in GSI (linear regression, $r^2 = 0.89$) and the MIA likelihood ratio was significant (Kruskal Wallis, $p = 0.0079$, $n = 114$, Figure 4), so we defined one year as the combination of a translucent fast growth and an opaque slow growth zone. For each otolith, we estimated age to the nearest

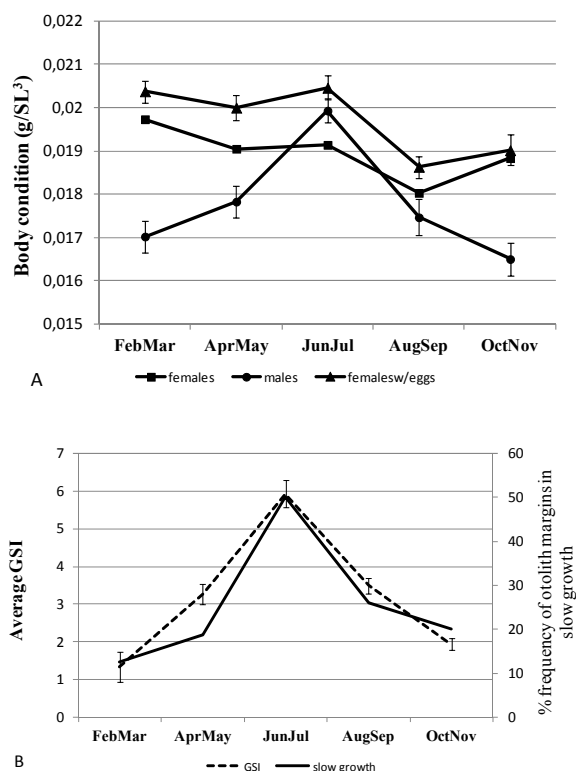


Figure 4. A. Seasonal body condition in male and female *P. disjunctivus* as measured by Fulton's condition factor ((body mass – ovary mass)/SL³) with standard error bars (error bars were too small to be visible for female data). B. Mean female GSI (n = 272) is plotted against the percent frequency of otoliths in slow growth.

quarter year based on our MIA status grades, and found the maximum estimated age for *P. disjunctivus* sampled here to be 5.25 years.

Like the length-frequency data, SL plotted against otolith-based estimated age indicated a highly predictable linear cohort growth rate of about 10 cm/year (linear regression, $p < 0.001$; $r^2 = 0.8$, $n = 179$) (Figure 6A) (Table 1). Our comparisons of estimated age to body mass, on the other hand, were less linear; particularly after age two when it became more variable (Figure 6B). When the estimated age and standard body length data were fitted to a VBGF, we only found a close fit to the linear component of the VBGF (Table 1), not for the asymptotic parts of the VBGF curve typical of older fish. In fact, our data did not exhibit any of the asymptotic growth characteristically modeled by the VBGF, and the maximum size (L_∞ of 75 cm SL) and age (age at L_∞ of 18 years) predicted with the VBGF far exceeded the maximal data from this study.

The maximum observed age of *P. disjunctivus* was used, along with MSE data, to estimate a population mortality rate of 43.5% ($\ln M = a + b \ln(t_{\max})$, where M = mortality rate, a = y-intercept from MSE data, b = slope from MSE data, and t_{\max} = maximum observed age) (Hoenig 1983).

Discussion

Otolith slow growth (opaque) bands in *Pterygoplichthys disjunctivus* collected from Volusia Blue Spring had a strong positive correlation with maximal body condition and gonad development (GSI) in June/July. Slow otolith growth coincident with peak summer GSI indicated that high reproductive demands (nest guarding for males and egg production for females) were the likely cause of the primary growth check for reproductively mature catfish. Catfish somatic growth was steady all through the Fall/Winter/Spring seasons, most likely due to the stable temperature and food conditions of the spring run. Our hypothesis that *P. disjunctivus* is a fast growing species was supported both by the small otolith size (2–4 mm diameter) compared to sea catfish (Ariidae) of similar size (16 mm diameter, Gibbs, unpublished data) (Templeman and Squires 1956) and the rapid progression of SL cohorts throughout the year. Our otolith analyses, combined with reproductive data (Gibbs et al. 2008), indicated that catfish first mature at age two, continue to produce gametes throughout each year of their lives, live to just over five years, and reach a maximum size of 51.5 cm SL. The otolith growth band patterns observed in Volusia Blue Spring *P. disjunctivus* may not be identical to age and growth patterns in the fish's native Amazon basin, however, *P. disjunctivus* has successfully invaded habitats throughout the subtropical/tropical world, making it important that we have at least some understanding of its age and growth patterns in or out of its native habitat. The lack of seasonal water level extremes that likely limit food supplies and reproduction in *P. disjunctivus*'s native habitat (Winemiller 1987) seems to be allowing *P. disjunctivus* to capitalize on a long nesting-appropriate season in the St. Johns River. An in depth study of actual nesting activity in the St. Johns near the Blue Spring run would be valuable in furthering our understanding of catfish life history patterns. Discussions of adaptive plasticity in growth and other life

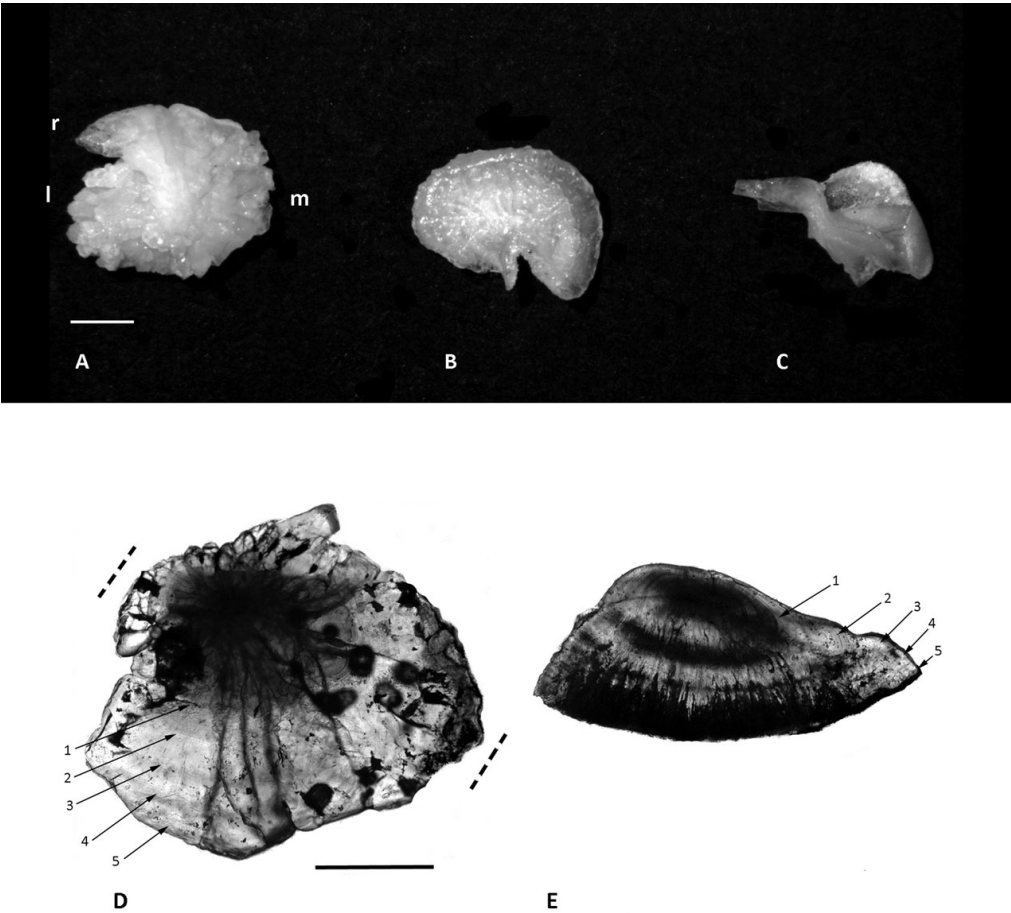


Figure 5. Dorsal view of lapillus (A), and lateral views of asteriscus (B) and sagittal (C) otoliths. Sagittal (D) and transverse (E) sections of a 5 year old catfish. Band pair boundaries are indicated with arrows. r = rostrum; l = lateral; m = medial. Dashed lines indicate the boundaries of the long axis used to measure otolith length (Figure 3). Scale bars = 1 mm. Photographs by M. Gibbs.

Table 1. Goodness of fit from the Linear and Von Bertalanffy Growth Formula models fitted to observed data for male and female *P. disjunctivus*. k = instantaneous growth rate. F, p-value and r^2 are from a linear regression of expected and actual data for each model. MSE = mean square error. The standard deviation (SD) of the residuals is calculated from a standard residuals analysis. Maximum SL (L_{∞}) and age (at L_{∞}) were estimated for VBGF, and observed for the Linear model.

Model	maximum SL (cm)	maximum age (yrs)	k	F	P	r^2	MSE	SD of residuals
Linear	52	5.25	0.257	605.54	<0.001	0.76	20.35	4.5
VBGF	75	18	0.223	615.65	<0.001	0.76	30.67	5.53

history patterns, like we appear to be seeing in *P. disjunctivus*, usually compare warm environments favorably to cold environments, however in this case, the more favorable system (Florida) is colder (albeit more stable) than the catfish's native tropical habitat (Heibo et al. 2005; Benjam et al. 2009).

In the tropics, reduced body condition in most fish species coincides with the end of peak spawning activity, after resources were diverted to gonad development, nest guarding, brooding, etc. (Morales-Nin and Ralston 1990; Jepsen et al. 1999). In Volusia Blue Spring, however, we did not see fish in poor body condition at any time of

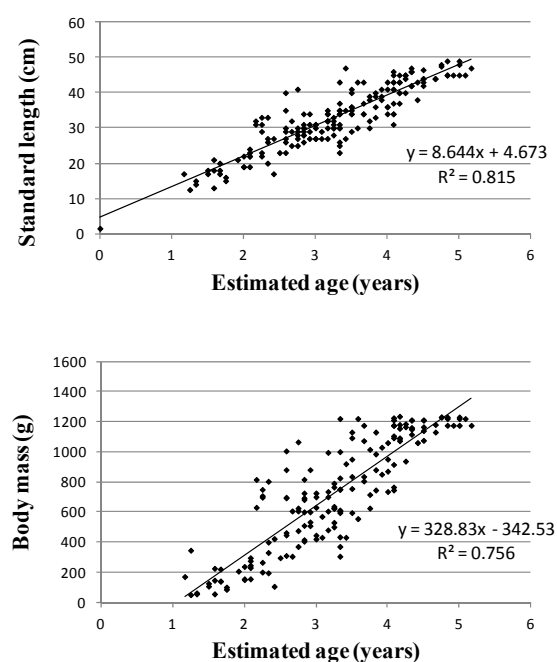


Figure 6. Standard length (top) and body mass (bottom) compared to estimated age. Note how much more variable body mass is relative to estimated age after year two.

the year. Instead, we saw a sharp peak in male *P. disjunctivus* body condition just prior to peak spawning, which began to drop off during the peak spawning period, (correlating strongly with when most fish were in a brief otolith slow growth mode) and then returned to pre-spawning levels. We know that nest guarding males invest a considerable amount of energy into guarding their eggs (Suzuki et al. 2000), and so an increase in body condition is likely to reflect preparation for prolonged nest guarding. Female and male peak body condition occurred just prior to the peak in GSI, however, the female peak was not as striking as that seen in males. Female body condition dropped off during August/September, as peak spawning ended, reflecting the energetic demands of preparing one last batch of eggs for the winter (*P. disjunctivus* often retain spawning ready ovaries through the winter months). The availability of plentiful food in the spring run throughout the year may allow the catfish to minimize some of the usual negative impacts of reproduction on body growth and, particularly, to maintain fairly consistent

cohort somatic growth rates throughout the year. We do, in fact, see that *Pterygoplichthys disjunctivus* maintained consistently full guts and intestinal fat stores throughout the year (Gibbs, unpublished data). The relatively short period of time catfish spend in their annual otolith slow growth period during the height of their prolonged summer reproductive season is likely a significant factor in the continuity of cohort somatic growth rates throughout the year.

We only rarely observed or caught fish less than 20 cm SL in the spring run, and these 30 small fish were all between 1 and 2 years old. Nico (2010) reported seeing more small catfish in the Volusia Blue Spring run at night than during daytime. His observations, however, are not comparable to the current data because he did not measure the fish. Although we regularly caught large spawning-ready females, in 10 years of sampling no evidence was seen of large-scale nesting by armored catfish in the Volusia Blue Spring run. During the summertime, the river is considerably warmer than the spring run, making it a better nesting/nursery location. Given the dearth of small specimens in the spring run, we think it likely that most armored catfish migrated into the spring run from hatching sites in the river. The thinner armor and smaller body size of juveniles make them more susceptible to predation by birds (e.g. Double-breasted Cormorants and Great Blue Herons) and Longnose Gar (all of which we have observed consuming small catfish), and this vulnerability may result in more cryptic habitat selection and activity periods for juveniles, especially in the clear waters of the spring run. The likelihood that juveniles are hiding, nocturnal, or living primarily in the tannin-stained river, would explain the low sampling numbers of small size classes in the spring run. The likely transition from juvenile to adult habitat (river into the spring) after their first year, and concurrent changes in anti-predator behavior (less cryptic habits) may be responsible for the striking difference between the first annual otolith band pair and the second. Campana (2001) suggested that growth rates of immature fish usually differ from those of mature individuals, but our observations of somatic growth rates in *P. disjunctivus* indicated that they were rapid (10 cm/year), predictable, and nearly linear for most of the fish's life.

It is curious that the largest *P. disjunctivus* we captured in Volusia Blue Spring was just under 52 cm SL, and the maximum reported size of *P. disjunctivus* in the US was 70 cm total length

(TL) [roughly 60 cm SL, however, collection data were not provided (Fuller et al. 1999)]. No other studies of *P. disjunctivus* or its congeners outside of its native Amazon basin have reported a maximum SL greater than 45 cm SL (Devick 1988; Ludlow and Walsh 1991; Bunkley-Williams et al. 1994; Liang et al. 2005; Hubilla et al. 2007). Studies from *P. disjunctivus*'s native habitat merely suggest that members of the genus may reach 60 cm, however, that length was not defined as SL or TL (Fink and Fink 1979). It is possible that *P. disjunctivus* larger than 52 cm SL are not observed in the spring run because they abandon the spring run in favor of the St. Johns River, however, besides the single record provided by Fuller et al. (1999) we are not aware of any specific data showing larger *P. disjunctivus* being collected or caught elsewhere. The failure to observe such large fish might simply be due to large fish permanently leaving the spring run, however, the plentiful food and benign conditions of the spring make that scenario seem less likely than our hypothesis that *P. disjunctivus* simply grows rapidly and steadily for five years and then dies out due to predicted accumulated high natural mortality rates (e.g. predation by otters and alligators (personal observation)). We pose this hypothesis for the following reasons: (1) Our ageing estimates were equally easy to establish for the oldest and youngest fish (no extreme compression of otolith increments was seen in older fish); (2) There was no evidence in the literature or our personal experience that fish larger than those caught in Volusia Blue Spring exist outside the spring; (3) Nearly all reproductively mature catfish have been caught at or above average body mass, with substantial coelomic fat stores, and no obvious signs of senescence; (4) The reproductive effort (represented by relative GSI) of the oldest females (>4 years) does not decline with age (the youngest and oldest females are equally likely to have similarly high GSI) (Gibbs, unpublished data); (5) There is no indication that females die after reproduction, as healthy mature catfish of all sizes are commonly found after the reproductive season with ovaries that are replenishing with maturing or mature ova; and finally (6) estimated mortality rates are high (43.5%).

The strategy of rapid growth and intensive reproductive effort utilized by this invasive species might maximize reproductive success (Simberloff 1997). The age and growth data we present here indicate that Blue Spring *P. disjunctivus*, a member of a widespread,

invasive family (Loricariidae), could be described as "opportunistic" [in the middle of Winemiller and Rose's triangle scheme (1992)] and/or r-selected (Pianka 1970; Olden et al. 2006). *Pterygoplichthys disjunctivus* has rapid linear growth rates (10 cm/year), relatively high fecundity (~30,000 eggs per season), maintains mature ovaries throughout the year, has a short lifespan (5 years), is tolerant of a range of environmental challenges, including hypoxia and desiccation, and appears to be phenotypically plastic in its reproductive patterns (Sakai et al. 2001; Gibbs et al. 2008). The likely persistence of a rapid growth rate through most of the *P. disjunctivus* life span, maximal GSI at all ages, and the lack of any fish in poor condition, all suggest that this species may be growing at maximal speed and then, due to high natural mortality rates, dying out with minimal signs of senescence. Goodness of fit measurements for all otolith data and the two models (linear and linear portion of VBGF) were virtually identical, and as such, the data presented here are best described by the linear model, until such time that conflicting data are found. We are not ruling out VBGF for this species, but currently have no data to support it.

We emphasize again that although there will likely be differences between age and growth patterns for *P. disjunctivus* in Florida springs and their native habitat, the worldwide extent of successful *P. disjunctivus* invasions, makes any kind of data on its life history patterns useful. Species that have successfully invaded a new habitat or country may be more successful than they were in their native habitat for a variety of reasons [e.g. a lack of specialized predators, good food supplies, lack of resistance by the ecosystem, etc. (Simberloff 1997)], and as such, the age and growth data we present here is likely to be as applicable to scientists studying the effect of loricariids in other parts of the world as would data from their native Amazon basin habitat. Plasticity in life history patterns should be expected in a species that successfully invades new environments, as it optimizes their fitness in the new system (Reznick 1990). Temperature is usually described as the most important environmental factor in determining growth rates, and this has been illustrated in several studies of clinal variation in life history traits (Heibo et al 2005; Benejam et al. 2009; Britton et al. 2010). Fish living in warmer environs tend to have faster growth, smaller bodies at maturity, mature earlier, increased

reproductive investment and shorter lives when compared to populations living in colder environs (Heibo et al 2005). We point out that colder environments tend to be more seasonal, thus creating a literal or physiological winter for their inhabitants that constrains growth and reproduction. Freshwater springs like Volusia Blue, however, are unusually stable environments; they have relatively stable water levels, high nutrient concentrations, moderate biodiversity and plentiful algal growth (Scott et al. 2004; Heffernan et al. 2010; Work et al. 2010). In the case of *P. disjunctivus*, Volusia Blue Spring, although colder than the fish's native Madeira River Basin, is substantially more conducive to maximal growth and reproduction. We think it unlikely that catfish in their native habitat would grow as steadily and rapidly as they do in the relatively benign conditions of Volusia Blue Spring (Secor and Dean 1989); fish in other invaded systems may experience growth patterns similar to what we describe here. It will, however, be interesting to compare catfish growth patterns in other invaded ecosystems that are less stable in terms of seasonal temperature, water quality and food availability.

If invasive species like *P. disjunctivus* are changing ecosystems and reducing native biodiversity around the world, it is increasingly important that their basic biology is understood so that they can be better managed or prevented from making further invasions (Sakai et al. 2001). For the most part, when a new species is introduced (intentionally or accidentally), both scientists and the public have little understanding of that species' capabilities (Chadderton 2003). Although it may be possible to eradicate an invasive species early on in an invasion, without much knowledge of their biology, once a species has become established, knowledge of life history traits (especially fecundity, generation time, and reproductive patterns) is crucial to managing a species or predicting which new species will invade in the future (Ricciardi and Rasmussen 1998; Simberloff 2003; Sivakumaran et al. 2003; Olden et al. 2006). Furthermore, as invasive species are quite capable of modifying their life history patterns to take advantage of their new habitat, it may not be possible to make precise predictions of how a species will behave in an invaded ecosystem based on information from a fish's native habitat.

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