Reproductive cycle and spatiotemporal variation in abundance of the one-sided livebearer *Jenynsia multidentata*, in Patos Lagoon, Brazil

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Abstract

Jenynsia multidentata is an important component of the fish assemblage of the Patos Lagoon estuary in southern South Brazil. In order to investigate its reproductive cycle and abundance patterns, standardized sampling was conducted over large spatial (marine, estuary and lagoon) and temporal (1996–2003) scales. Both females and males were significantly more abundant during summer (December–March) than winter (June–August). Total abundance was significantly positively correlated with water temperature (R=0.91), but not with salinity and Secchi depth. Females achieved higher average (49.1 mm $L_{\rm T}$) and maximum size (91 mm) than males (37.7 mm; 66 mm), and average sex ratio was female-biased (3.2:1) across all months. An annual reproductive cycle composed of two cohorts was proposed: individuals born from December to March started reproducing during late winter and spring and individuals born from September to November started reproducing during late summer and fall. A 12-month survey conducted throughout the longitudinal gradient of the lagoon indicated that the species was only present in the estuary, and was absent from marine and upper lagoon areas. The abiotic factors analyzed could not explain this spatial distribution. Inter-annual variation in abundance was great, with higher abundance during drier years. A 'dilution effect' was proposed to explain the low abundance of the species in the estuary during high-rainfall trigged by $El\ Niño$ episodes.

Introduction

Due to their diverse modes of reproduction and mating, livebearing fishes have contributed significantly to the understanding of the evolution of viviparity, internal fertilization, growth and maturation, courtship, and life-history parameters (Farr, 1977; Reznick, 1983; Constantz, 1984; Meyer & Lydeard, 1993; Endler, 1995). Most studies, however, have focused on poeciliids (Meffe & Snelson, 1989), and much less information is available for other livebearing fishes (Helfman et al., 1997; Guedotti, 1998). Research on the reproductive cycle and ecology of other livebearing fish families, such as Neotropical anablepids, would allow interspecific comparisons of reproductive

cycles and life-history strategies among livebearing fishes.

The family Anablepidae is composed of 13 species in three genera; two distributed in Central America and northern South America (*Anableps* and *Oxyzygonectes*), and one restricted to southern South Brazil (*Jenynsia*) (Ghedotti, 1998). The one-sided livebearer *Jenynsia multidentata* (Jenyns) shows the broadest distribution of its genus, ranging from the Atlantic coastal drainages from the Rio Negro Province (Argentina) to the city of Rio de Janeiro (Brazil) (Ghedotti & Weitzman, 1996). This specie is encountered year-round in the mixohaline waters of Patos Lagoon, a large coastal lagoon located in southern Brazil (Chao et al., 1985).

Previous studies about the life history of *J. multidentata* are scarce. Betito (1984) studied aspects of its reproduction and life-history patterns in Patos Lagoon estuary, and Fontoura et al. (1994) and Aranha & Caramaschi (1999) provided information about its reproduction in freshwater habitats. However, these field studies were conducted over relatively short time intervals (<18 mo.) and were restricted to estuarine or freshwater sites. More recently, Bisazza et al. (2000) described the species' reproductive behaviour and mating system based on laboratory studies.

The main goal of the present study is to investigate the reproductive cycle and aspects of the life history of a wild population of *J. multidentata* over a steep salinity gradient along the Patos Lagoon system (extending over 200 km) and long time period (1996–2003). Abundance of *J. multidentata* in marine, estuarine, and lagoon habitats was examined in relation to physicochemical variables. Based on a standardized inter-annual survey, seasonal patterns of abundance, size dimorphism and sex ratio of the population in the estuarine zone of Patos Lagoon were documented.

Materials and methods

Study site

Patos Lagoon (32° S 49° W) is ca. 250 km long and 60 km wide, covering an area of 10 360 km² along the coastal plain of Rio Grande do Sul in southern Brazil (Figs. 1a, b). The estuarine zone is restricted to the southern portion of the lagoon (ca. 10% of total area) and is connected to the ocean via a channel bordered by jetties, 4 km long and 740 m wide, that were constructed to stabilize the mouth of the estuary and allow navigation along the entrance channel (Fig. 1c).

Tidal influence on hydrodynamic characteristics is minimal, with mean tidal amplitude of 0.47 m (Seeliger, 2001). Instead, northeasterly (mean 5 m s $^{-1}$) and southerly (mean 8 m s $^{-1}$) winds and seasonal pulses of freshwater inflow influence patterns of water circulation and salinity. The lagoon's drainage basin is large (201 626 km 2), and its freshwater discharge varies seasonally, with high discharge in late winter and early spring followed by moderate discharge through summer and fall. The mean annual discharge rate is ca. 2000 m 3 s $^{-1}$, although large year-to-year variation can occur (700 to 3000 m 3 s $^{-1}$) (Moller et al., 2001). During *El Niño* episodes, runoff greatly exceeds average

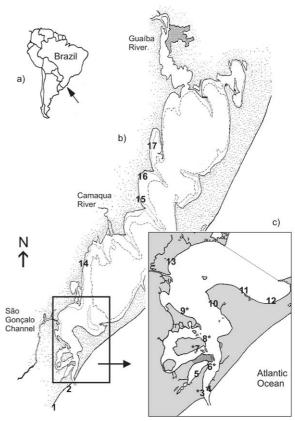


Figure 1. Patos Lagoon study area (b) in southern South Brazil (a) showing the 17 fixed beach seine stations located in the adjacent marine coastal area (sites 1 and 2), estuary (enlarged box, sites 3–13) and lagoon (sites 14–17). The main longitudinal axis of the lagoon is over 200 km. Sites 1–17 were sampled monthly from May 2000 to April 2001, and sites marked with asterisks (3, 6–9) were sampled monthly during a 6.5-yr survey (from August 1996 to March 2003).

values, and lagoon waters can remain fresh for several months (Moller et al., 2001). Additional information about the study site and its fish assemblage can be found in Garcia et al. (2001).

Field sampling

From May 2000 to April 2001, *J. multidentata* was collected from standardized monthly seine hauls (5 hauls/station/month) at 17 beach stations that included adjacent coastal marine (sites 1–2), estuarine (3–13), and lagoon habitats (14–17). All sites were located along the Patos Lagoon's main longitudinal axis extending over 200 km (Fig. 1b). The single year of sampling over this large area is referred to as the spatial survey. In order to obtain a more complete abundance data set of the species, monthly seine hauls (5 hauls/station/month) were conducted at 5 beach sta-

tions located at the estuarine zone of Patos Lagoon over 6.5 years (August 1996–March 2003). This estuarine sampling effort conducted over multiple years is referred as temporal survey. All stations were located in shallow (<2 m) areas that were representative of about 80% of Patos Lagoon (Moller et al., 2001).

Beach seine hauls were obtained using a 9×1.5 m seine (13 mm bar mesh in the wings and 5 mm in the center 3-m section) that was pulled to cover an area of ca. 60 m² per haul. Water temperature, transparency (Secchi depth), and salinity were measured at each station each month concomitantly with the biological sampling. Precipitation was recorded daily at the Rio Grande meteorological station located in the estuarine area. Specimens were preserved in 10% formalin and later identified, sexed, counted, and measured for total length $(L_{\rm T})$ to the nearest mm. Gender was determined based on the presence of the gonopodium (anal fin of males modified to serve as an intromittent organ). Maturing individuals ($< 20 \text{ mm } L_T$), in which the gonopodium was not completely formed, were classified as transitional.

Data analysis

Between-month variation in average number of individuals per haul $(\log_{10} x + 1)$ of each gender was analyzed by repeated measures ANOVA. The twenty seine hauls obtained at the 5 estuarine beach stations (sites 3 and 6-9, Fig. 1c) were averaged to create monthly means, using the 12 months as the repeated measure, and the 7 years as their replicates. The Huynh-Feldt (H-F) statistic test was used to test the assumption of sphericity (Zar, 1996; Kneib & Scheele, 2000). The associated probability provided by this statistic was concordant with the F-statistic in the repeated measures analyses, an indication of conformity to the required assumption of sphericity. Spearman rank correlation was performed to analyze relationships between seasonal variation in abundance of both genders and abiotic parameters (water temperature, Secchi depth, and salinity).

To examine annual recruitment patterns and size structure, average number of females, males, and maturing/transitional individuals per haul were plotted by 2 mm $L_{\rm T}$ intervals for each month (Garcia et al., 2001). The Chi-square statistic was used to test for differences between the observed sex ratio and a balanced (1:1) ratio. Between-month differences in the average sex ratio were tested by one-way ANOVA. Inter-annual variation in total abundance of $J.\ mul$

tidentata was tested by repeated measures ANOVA with a design similar to the one described earlier, but with years as the repeated measure, and 12 months as the replicates. The H–F statistic was used again to control for the assumption of sphericity. To achieve a balanced ANOVA design for this analysis without confounding months, only those years (1997–2002) with samples for all 12 months were used (data from August to December 1996, and January to March 2003 were excluded). The Newman–Keuls test was used for post-hoc comparisons after all ANOVA tests.

Based on the available abiotic parameters, multiple regression analysis was performed to assess the extent that independent variables predict spatiotemporal variation in total abundance of *J. multidentata*. The average number of individuals per month across the 17 beach stations (coastal marine, estuary, and lagoon) sampled during the May 2000–April 2001 survey was modeled using three independent variables (water temperature, Secchi depth, and salinity). The average number of individuals occurring in the estuary (obtained from 20 monthly seine hauls at 5 estuarine beach stations; sites 3 and 6–9, Fig. 1) was modeled using 4 independent variables (the previous 3 variables plus rainfall).

Results

Seasonal abundance, size distribution and sex ratio

Abundance of the one-sided livebearer J. multidentata revealed strong seasonal variation (Fig. 2b). Both genders were more abundant during warmer months (December to March) than cold months (June to August) (F = 5.43; d.f. = 11; p < 0.01). A relatively small increase in abundance also occurred from September to November. Total abundance of both genders was significantly positively correlated with water temperature (Female, F: n = 12; R = 0.87; p < 0.01, Male – M: n = 12; R = 0.87; p < 0.01), but not with salinity (F : n = 12; R = 0.51; p < 0.09,M: n = 12; R = 0.42; p < 0.17) and water transparency (F : n = 12; R = 0.55; p < 0.06, M :n = 12; R = 0.46; p < 0.13) (Figs. 2a, b). There was a significant size dimorphism (t = -3.07; d.f. = 116; p < 0.01), with females achieving higher average (49.1 mm $L_{\rm T}$) and maximum size (91 mm $L_{\rm T}$) than males (mean = 37.7 mm L_T ; max. = 66 mm $L_{\rm T}$). This sexual dimorphism was observed across all months (Fig. 2c).

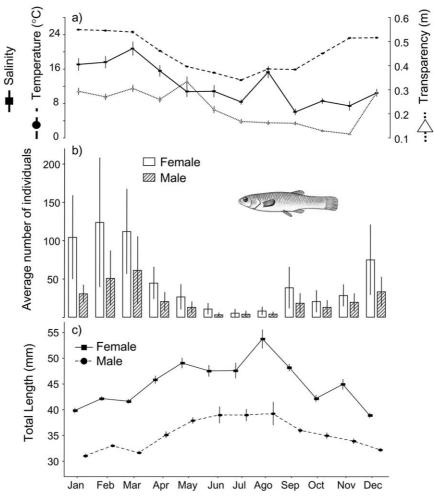


Figure 2. (a) Average monthly values (+S.E.) for water temperature (°C), salinity and water transparency (m), (b) average number of individuals (+S.E.) for female and male, and (c) average size (+S.E.) for female and male individuals of *Jenynsia multidentata* based on monthly sampling in 5 estuarine sites from August 1996 to March 2003.

Females, males and transitional individuals revealed a seasonal pattern of abundance by size class (Fig. 3). Transitional individuals occurred only from late spring (November–December) to early fall (April–May), being absent from samples collected during colder months. The size distribution of females showed a greater tendency towards bimodality (e.g., during January, December and September) than males. The size distribution for females was always broader than that of males, particularly during warmer months (January and February), with smaller differences during colder months (June and July).

Jenynsia multidentata had a significantly female-biased average sex ratio across all months (φ : σ : 3.2:1; $\chi^2 = 4214.83$; d.f. = 251; p < 0.01), and sex ratio also varied significantly between months (F = 1.96;

d.f. = 11; p > 0.03). Females strongly dominated the population during December and January. Sex ratio was closer to 1:1 with lower variance from July to November (Fig. 4).

Spatiotemporal trends in total abundance

During the spatial survey (May 2000–April 2001), the one-sided livebearer only occurred in the mixohaline waters of the estuary (sites 3–13), being absent from marine areas with high salinity (1–2) and freshwater areas of the upper lagoon (14–17) (Fig. 5). During the temporal survey at the estuarine area, the species was significantly more abundant during 1999 and 2000 (F = 11.35; d.f. = 5; P > 0.01) when rainfall was lower and salinity was higher than their historic aver-

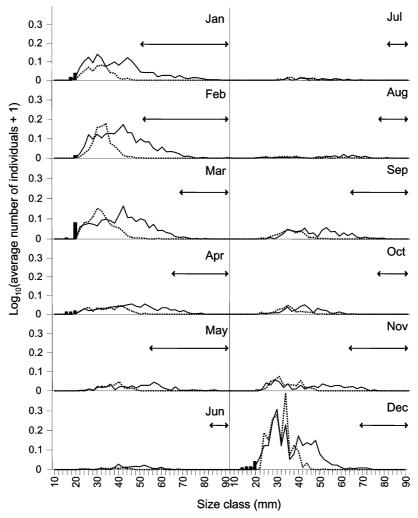


Figure 3. Monthly abundance (log [CPUE + 1]) by size class (mm $L_{\rm T}$) for transitional individuals (bars), females (solid line) and males (dashed line). Lines with arrows represent the difference in maximum sizes of males and females. CPUE was calculated as the average number of individuals per seine haul based on monthly sampling at 5 estuarine sites from August 1996 to March 2003.

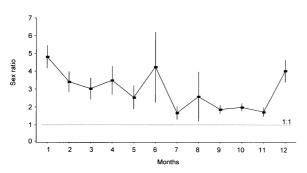


Figure 4. Average monthly values (+S.E.) of sex ratio (female/male) based on samples when both genders co-occurred collected at 5 estuarine sites from August 1996 to March 2003. A 1:1 ratio is represented by the dashed line; values above the line represent higher proportions of females.

ages. The opposite trend in abundance occurred during the period of above-average rainfall and lower average salinity observed during 1997–1998 and 2001–2002 (with the exception of the salinity in 1997; Fig. 6).

Multiple regression analysis indicated that abundance patterns can be predicted more reliably across years than across regions (Table 1). Multiple regression generated a 4-component model accounting for 49.9% of the variation in total abundance of *J. multidentata* across 6 years (1997 to 2002). In contrast, the 3-component model of the spatial analysis (based on the May 2000–April 2001 dataset) accounted for only 4.3% of the variation in abundance across 17 sampling sites (Table 1). This greater prediction strength on the temporal scale relative to the spa-

Table 1. Multiple regression model of number of individuals (N), water transparency (m), water temperature (C), salinity, and rainfall (mm) for *Jenynsia multidentata* relative to spatial and temporal dimensions. For the spatial analysis, N represents total number of individuals collected monthly in 5 beach seine hauls at 17 stations (encompassing adjacent marine coastal, estuarine and lagoon ecotones) from May 2000 to April 2001. For the temporal analysis, N represents total number of individuals collected monthly in 5 beach seine hauls at 5 estuarine stations from January 1997 to December 2002.

Spatial				
Dependent variables: N	$F_{3,199} = 2.30, P < 0.031, R = 0.208; R_2 = 0.043$			
Predictor variables	Coefficient	S.E.	t ₁₉₉	P
Intercept	-0.855	1.866	-0.458	0.647
Transparency	4.398	1.579	2.785	0.006
Temperature	0.056	0.078	0.717	0.474
Salinity	-0.031	0.047	-0.667	0.506
Temporal				
Dependent variables: N	$F_{4,67} = 16.66, P < 0.000, R = 0.706; R_2 = 0.499$			
Predictor variables	Coefficient	S.E.	t ₁₉₉	P
Intercept	-5.582	2.774	-2.012	0.048
Transparency	13.574	3.113	4.361	0.000
Temperature	0.241	0.134	1.791	0.078
Salinity	0.261	0.073	3.594	0.001
Rainfall	-0.016	0.008	-1.912	0.060

tial scale remained large even when both regression analyses were run with the same number of independent variables (i.e., when rainfall was eliminated from the temporal analysis). Low predictability in the spatial analysis also was observed when estuarine samples (sites 3–13) were analyzed separately. The 3-component model only accounted for 4.6% of the total variance in abundance of *J. multidentata* across the estuarine sites. Among the abiotic variables modeled, water transparency was the only variable that significantly contributed to the prediction of spatial patterns of abundance. In contrast, both water transparency and salinity significantly predicted inter-annual abundance of *J. multidentata* in the estuary (Table 1).

Discussion

Annual breeding cycle

A two-cohort model was proposed for the annual reproductive cycle of *J. multidentata* in the estuarine area of Patos Lagoon. This model is supported by the following evidence: (a) *J. multidentata* can achieve

maturity within short time intervals (2–5 mo.; Betito, 1984; Wischnath, 1993; Fontoura et al., 1994), (b) the annual abundance cycle is significantly correlated with water temperature, and (c) seasonal recruitment patterns observed in the CPUE by size plots (Fig. 3) for females, males and maturing/transitional individuals.

The first cohort contained individuals born during December–March. This cohort seemed to have a longer juvenile period (ca. 5 mo.), and probably higher mortality rates due to sub-optimum conditions associated with low temperatures during the late fall and winter. Individuals surviving the colder months started reproducing during late winter and spring (September–November).

The second cohort contained individuals born during September–November. The second cohort had a shorter interval to achieve maturation (ca. 2 mo.) and probably experienced lower mortality rates due to more optimal conditions associated with warmer temperatures during spring and summer. These individuals apparently reproduce for the first time during late summer and fall.

Betito (1984) was the first to observe that the onesided livebearer has a prolonged reproductive cycle in

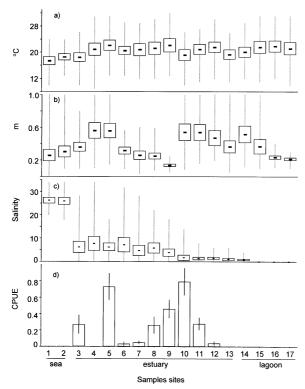


Figure 5. Average (dot), standard error (box) and max – min (dashed line) of (a) water temperature, (b) water transparency, (c) salinity, and (d) average CPUE (individuals per haul) across 17 sites that were sampled monthly from May 2000 to April 2001. Samples sites encompasses the coast outside the estuarine mouth (sites 1–2), estuary (3–13) and upper lagoon (14–17).

this estuary, but he recognized only an extended reproductive season from October to March. Fontoura et al. (1994) found that *J. multidentata* (Jenyns) has a similar two-cohort annual breeding cycle in the Fortaleza Lake (30° S; Rio Grande do Sul state). Aranha & Caramaschi (1999) observed a seasonal tendency in J. multidentata reproduction in the Ubatiba River (Rio de Janeiro state) located at 22° S. In a revision of the genus Jenynsia, Guedotti & Weitzman (1996) applied the name J. multidentata to a coastal taxon widely distributed from the Río de La Plata, Argentina to the city of Rio de Janeiro, Brazil and J. lineata to a species restricted to the Río Cebollatí drainage, Uruguay. However, some previous studies (Betito, 1984; Chao et al., 1985; Fontoura et al., 1994; Aranha & Caramaschi, 1999) used J. lineata for J. multidentata in areas beyond the restricted range proposed by Guedotti & Weitzman (1996).

Published information about breeding cycles in natural populations of anablepid fishes is scarce

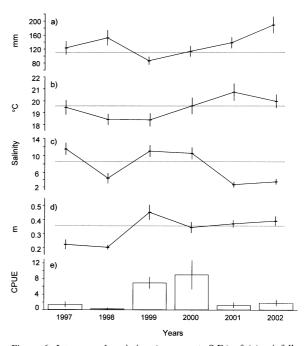


Figure 6. Inter-annual variation (average + S.E.) of (a) rainfall, (b) water temperature, (c) salinity, (d) water transparency, and (e) average CPUE (individuals per haul) of *J. multidentata* based on monthly sampling at 5 estuarine sites from January 1997 to December 2002. Rainfall data were obtained in the meteorological station of Rio Grande (located in the lower estuarine area). Dashed lines represent the historic averages (rainfall: 15 yr from 1988 to 2002; temperature, salinity and transparency: 15 yr from 1979–1984 and 1994–2002).

(Miller, 1979; Burns & Flores, 1981 for Anableps dowi Gill; and above cited references for Jenynsia). To put the current findings in a broader zoogeographic perspective, they were contrasted with results from studies on related livebearing poeciliid fishes. For instance, the mosquitofish Gambusia affinis (Baird & Girard) has an extended summer spawning season in temperate North America (Reznick & Braun, 1987). In contrast, livebearing poeciliids can have continuous annual reproduction in tropical habitats characterized by low environmental seasonality (e.g., Morris & Ryan, 1992). But, even in the tropics, these small viviparous fishes seem to regulate their reproductive effort in phase with major changes in their aquatic habitats. Winemiller (1993) showed that in a tropical rainforest region reproductive output of four poecillid species varied according to high and low rainfall periods. The two-cohort annual breeding cycle proposed for the *J. multidentata* population inhabiting the warm temperate Patos Lagoon estuary seems to be consistent with the opportunistic life-history strategy (early maturity, small clutches, and low survivorship) generally associated with small livebearing fishes that are proficient at colonizing unsaturated habitats (Winemiller, 1992).

Size dimorphism and sex ratio

Jenynsia multidentata reveals strong sexual size dimorphism, with females larger than males (so-called 'reversed' size dimorphism) throughout the year. Several hypotheses have been suggested to explain sexual size dimorphism based, for example, on energetic (e.g., Ghiselin-Reiss small-male model - Blanckenhorn et al., 1995) and ontogenetic considerations (the developmental constraints model - Fairbairn, 1990). More recently, it has been suggested that reversed size dimorphism in fishes can be an indirect consequence of the mating system (Magurran & Garcia, 2000). Bisazza & Pilastro (1997) proposed that reversed sexual size dimorphism in small livebearing fishes arises whenever the advantage of small males in a coercive mating system (i.e., when the male bypasses the female's consent – Clutton-Brock & Parker, 1995) exceeds the advantage of large size during female choice and male-male competition.

According to Bisazza et al. (2000), this hypothesis could explain the extreme size dimorphism observed in *J. multidentata*. In laboratory studies, he observed that males approached females from behind to thrust their copulatory organ (the anal fin modified into an intromittent organ, or gonopodium) at the female genital pore. Females counter mating attempts by either swimming away or attacking males. In coercive mating, small males may have advantages because they are less conspicuous and maneuver better when trying to copulate. Bisazza et al. (2000) demonstrated that small males of *J. multidentata* had significantly higher mating success than larger males.

Sex ratio of the one-sided livebearer was consistently female-biased, but values were generally greater from December to March. Female-biased sex ratios are observed in several livebearing fishes (Winemiller, 1993; Macías Garcia et al., 1998). It has been argued that female-biased sex ratio can result from sexual differences in foraging behaviour and male-biased predation. For instance, female guppies (*Poecilia reticulata* Peters) school more often, detect predators earlier, undertake more predator inspections, and show greater antipredator responses than males (Magurran & Nowak, 1991; Magurran & Seghers, 1994). A similar behaviour has been observed in the livebearer

Girardinichthys multiradiatus Meek (Macías Garcia et al., 1994). In both species, females suffer less predation mortality than males (Rodd & Reznick, 1997; Macías Garcia et al., 1998).

Piscivorous fishes are rare in the shallow waters of Patos Lagoon estuary (Vieira & Castello, 1996). Most piscivores are marine species that move into the estuary with saltwater intrusions during summer (Chao et al., 1985), or freshwater fishes that are carried into the estuary during periods of elevated rainfall and freshwater discharge (Garcia et al., 2003; Garcia et al., in press). In contrast, several species of piscivorous birds forage in the Patos Lagoon estuary, and usually form large flocks (up to 5000 individuals) on sand banks and inlets of the Patos Lagoon estuary (Vooren, 1996). Preliminary field observations in the estuary suggest that several of these birds could be potential predators of the one-sided livebearer (e.g., great kiskadee Pitangus sulphuratus, kingfishers Ceryle torquata and Chloroceryle americana, snowy egret Egretta thula, herons Butorides striatus and Nycticorax nycticorax, terns Sterna superciliaris, S. trudeaui, S. hirundo and Phaetusa simplex, and black skimmer Rhynchops nigra) (W. L. S. Ferreira, pers. commun.). Information currently is lacking to evaluate if sexual differences in behaviour or male-biased predation by piscivorous birds could explain the female-biased sex ratio observed for J. multidentata.

Spatiotemporal trends

Jenynsia multdentata has the broadest distribution among South American fishes of the genus Jenynsia, ranging from coastal drainages in the Rio Negro Province (Argentina) to the city of Rio de Janeiro (Brazil) (Ghedotti & Weitzman, 1996). This wide distribution can be attributed to its broad tolerance of physicochemical variation (Chao et al., 1985; Fontoura et al., 1994; Aranha & Caramaschi, 1999; Ortubay et al., 2002). Yet surprisingly, J. multidentata was captured only in the mixohaline waters of the estuary during the May 2000-April 2001 survey, and was absent from marine areas with high salinity as well as freshwater areas of the upper lagoon. The abiotic factors analyzed here (water temperature, Secchi depth, and salinity) could not explain the apparent preference of J. multidentata for the lower estuary's shallow waters. Other factors, such as presence of aquatic vegetation (e.g., low and mid-marshes and meadows of the widgeon sea grass Ruppia maritima L.), could be better predictors of *J. multidentata*'s distribution. Densely vegetated habitats are common in the estuary, but absent in the marine site, and restricted to low and mid-marshes in the upper lagoon (Seeliger et al., 1996). Additionally, Garcia & Vieira (1997) showed that *J. multidentata* occurs in significantly higher numbers inside widgeon meadows than in non-vegetated habitats of the Patos Lagoon estuary's shallow waters.

Abundance of *J. multidentata* in the estuary varied greatly between years, with higher abundance during dry periods (lower rainfall and higher salinity) than wet periods (higher rainfall and lower salinity). Probably the most parsimonious explanation for reduced abundance of *J. multidentata* in the estuary during periods of elevated rainfall is a dilution effect in association with flooding along the estuarine margin. During these high rainfall periods, the one-sided livebearer could have greater access to flooded vegetated habitats in low and mid-marshes, and therefore be less abundant at the stations used for standardized seine surveys.

Indirect evidence supports this hypothesis. Costa et al. (in press) showed that high rainfall periods are associated with more frequent flooding in the low and mid-marshes. A similar mechanism was observed in Costa Rica for livebearing poeciliids inhabiting tropical rainforest streams (Winemiller, 1993). In this region, the availability of shallow aquatic habitats increased many-fold during the rainy season floods at two study sites, which reduced the densities of these fishes on a per-area basis.

In conclusion, J. multidentata demonstrated a seasonal reproductive cycle that appears adaptive in response to seasonal variation typically found in the warm temperate region of coastal southern Brazil. This life history conforms to the opportunistic strategy associated with small livebearing poeciliids. Although current findings seem to corroborate Bisazza et al.'s (2000) hypothesis for size dimorphism, patterns of seasonal and ontogenetic (size class) variation suggest a more complex scenario than the one observed in laboratory studies. Strong spatial and inter-annual trends in abundance could not have been predicted from prior research. Although known for its broad physiological tolerance, J. multidentata was restricted to the estuary, and was absent from marine and lagoon sites. This pattern was not associated with temperature, Secchi depth or salinity. Other factors (e.g., aquatic vegetation) could determine this apparent preference for mixohaline waters. Moreover, abundance of J. multidentata was much higher during dry than wet periods, which could simply reflect a 'dilution effect' in the sampling due to the flooding conditions. Further investigations combining field experiments and laboratory studies could evaluate hypotheses explaining the spatial and inter-annual variation in abundance of J. multidentata. Future studies should analyze the influence of a coercive mating system and predation (particularly by piscivorous birds) on size dimorphism and sex ratios of natural populations of the one-sided livebearer.

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References

- Aranha, J. M. R. & E. P. Caramaschi, 1999. Estrutura populacional, aspectos da reprodução e alimentação dos Cyprinodontiformes (Osteichthyes) de um riacho do sudeste do Brasil. Revista Brasileira de Zoologia 16: 637–651.
- Betito, R., 1984. Dinâmica da população de *Jenynsia lineata* (Cyprinodontiformes, Anablepidae) na restinga de Rio Grande, estuário da Lagoa dos Patos (RS-Brasil), MSc Thesis, Rio Grande Federal University, Rio Grande, Brazil.
- Bisazza, A. & A. Pilastro, 1997. Small male mating advantage and reversed size dimorphism in poeciliid fishes. Journal of Fish Biology 50: 397–406.
- Bisazza, A., S. Manfredi & A. Pilastro, 2000. Sexual competition, coercive mating and mate assessment in the one-sided livebearer, *Jenynsia multidentata*: are they predictive of sexual dimorphism? Ethology 106: 961–978.
- Blanckenhorn, W. U., R. F. Preziosi & D. J. Fairbairn, 1995. Time and energy constraints and the evolution of sexual size dimorphism – to eat or to mate? Evolutionary Ecology 9: 360, 381
- Burns, J. R. & J. A. Flores, 1981. Reproductive biology of the cuatro ojos, *Anableps dowi* (Pisces: Anablepidae), from El Salvador and its seasonal variations. Copeia 1981: 25–32.

- Chao, L. H., L. E. Pereira & J. P. Vieira, 1985. Estuarine fish community of the dos Patos Lagoon, Brazil. A baseline study. In Yanez-Arancibia, A. (ed.), Fish Community Ecology in Estuaries and Coastal Lagoons: Towards an Ecoystem Integration. DR (R) UNAM Press, Mexico: 429–450.
- Clutton-Brock, T. H. & G. A. Parker, 1995. Sexual coercion in animal societies. Animal Behaviour 49: 1345–1365.
- Constantz, G. D. 1984. Sperm competition in poeciliid fishes. In Smith, R. L. (ed.), Sperm Competition and the Evolution of Animal Mating Systems. Academic Press, Orlando: 465–485.
- Costa, C. S. B., J. C. Marangoni & A. M. G. Azevedo, in press. Plant zonation in irregularly flooded salt marshes: relative importance of stress tolerance and biological interactions. Journal of Ecology 91
- Endler, J. A. 1995. Multiple-trait coevolution and environmental gradients in guppies. Tree 10: 22–29.
- Fairbairn, D. J., 1990. Factors influencing sexual size dimorphism in temperate waterstriders. The American Naturalist 136: 61–86.
- Farr, J. A. 1977. Male rarity or novelty, female choice behavior, and sexual selection in the guppy, *Poecilia reticulata* Peters (Pisces: Poeciliidae). Evolution 31: 162–168.
- Fontoura, N. F., A. S. Braun, D. S. Lewis & G. D. B. Souto, 1994. Dinâmica populacional da ictiofauna da Lagoa Fortaleza, Cidreira, Rio Grande do Sul II. *Jenynsia lineata* (Jenyns, 1842) (Teleostei, Anablepidae). Biociências, Porto Alegre 2: 75–78.
- Garcia, A. M. & J. P. Vieira, 1997. Abundância e diversidade da assembléia de peixes dentro e fora de uma pradaria de Ruppia maritima L., no estuário da Lagoa dos Patos (RS-Brasil). Atlântica, Rio Grande 19: 161–181.
- Garcia, A. M., J. P. Vieira & K. O. Winemiller, 2001. Dynamics of the shallow-water fish assemblage of the Patos Lagoon estuary (Brazil) during cold and warm ENSO episodes. Journal of Fish Biology 59: 1218–1238.
- Garcia, A. M., J. P. Vieira & K. O. Winemiller, 2003. Effects of 1997–1998 *El Niño* on the dynamics of the shallow-water fish assemblage of the Patos Lagoon estuary (Brazil). Estuarine, Coastal and Shelf Science 57 (3): 489–500.
- Garcia, A. M., M. B. Raseira, J. P. Vieira, K. O. Winemiller & A. M. Grimm, in press. Spatiotemporal variation in shallow-water freshwater fish distribution and abundance in a large subtropical coastal lagoon. Environmental Biology of Fishes.
- Ghedotti, M. J., 1998. Phylogeny and classification of the Anablepidae (Teleostei: Cyprinodontiformes). In Malabarba, L. R., R. E. Reis, R. P. Vari, Z. M. S. Lucena & C. A. S. Lucena (eds), Phylogeny and Classification of Neotropical fishes. EDIPUCRS, Porto Alegre (Brazil): 561–582.
- Ghedotti, M. J. & S. H. Weitzman, 1996. A New Species of *Jenynsia* (Cyprinodontiformes: Anablepidae) from Brazil with Comments on the Composition and Taxonomy of the Genus. Natural History Museum, The University of Kansas, Lawrence, Kansas: 1–25.
- Helfman, G. S., B. B. Collette & D. E. Facey, 1997. The Diversity of Fishes. Blackwell Science, Malden, Massachusetts.
- Kneib, R. T. & C. E. H. Scheele, 2000. Does tethering of mobile prey measure relative predation potential? An empirical test using mummichogs and grass shrimp. Marine Ecology Progress Series 198: 181–190.
- Macías Garcia, C., G. Jimenez & B. Contreras, 1994. Correlational evidence of a sexually-selected handicap. Behavioral Ecology and Sociobiology 35: 253–259.
- Macías Garcia, C., E. Saborío, & E. Berea, 1998. Does male-biased predation lead to male scarcity in viviparous fish? Journal of Fish Biology 53 (Suppl. A): 104–117.

- Magurran, A. E. & C. M. Garcia, 2000. Sex differences in behaviour as an indirect consequence of mating system. Journal of Fish Biology 57: 839–857.
- Magurran, A. E. & M. A. Nowak, 1991. Another battle of the sexes: the consequences of sexual asymmetry in mating costs and predation risk in the guppy, *Poecilia reticulata*. Proceedings of the Royal Society of London Series B-Biological Sciences 246: 31–38.
- Magurran, A. E. & B. H. Seghers, 1994. Sexual conflict as a consequence of ecology: evidence from guppy, *Poecilia reticulata*, populations in Trinidad. Proceedings of the Royal Society of London Series B-Biological Sciences 255: 31–36.
- Meffe, G. K. & F. F. J. Snelson, 1989. Ecology and Evolution of Livebearing Fishes (Poeciliidae). Prentice Hall, Englewood Cliffs, New Jersey.
- Meyer, A. & C. Lydeard, 1993. The evolution of copulatory organs, internal fertilization, placentae and viviparity in killifishes (Cyprinodontiformes) inferred from a DNA phylogeny of the tyrosine kinase gene x-src. Proceedings of the Royal Society of London Series B-Biological Sciences 254: 153–162.
- Miller, R. R., 1979. Ecology, habits and relationships of the Middle American cuatro ojos, *Anableps dowi* (Pisces: Anablepidae). Copeia 1979: 82–91.
- Moller, O. O. J., P. Casting, J.-C. Salomon & P. Lazure, 2001. The influence of local and non-local forcing effects on the subtidal circulation of Patos Lagoon. Estuaries 24: 297–311.
- Morris, M. R. & M. J. Ryan, 1992. Breeding cycles in natural populations of *Xiphophorus nigrensis*, *X. multilineatus*, and *X. pygmaeus*. Copeia 4: 1074–1077.
- Ortubay, S., M. Lozada, & V. Cussac, 2002. Aggressive bahaviour between *Gymnocharacinus bergi* (Pisces, Characidae) and other Neotropical fishes from a thermal stream in Patagonia. Environmental Biology of Fishes 63: 341–346.
- Reznick, D. 1983. The structure of guppy life histories: the tradeoff between growth and reproduction. Ecology 64: 862–873.
- Reznick, D. N. & B. Braun, 1987. Fat cycling in the mosquitofish (*Gambusia affinis*): fat storage as a reproductive adaptation. Oecologia 73: 401–413.
- Rodd, F. H. & D. N. Reznick, 1997. Variation in the demography of guppy populations: the importance of predation and life histories. Ecology 78: 405–418.
- Seeliger, U., C. Odebrecht & J. P. Castello, 1996. Subtropical Convergence Environments: the Coast and Sea in the Southwestern Atlantic. Springer-Verlag, New York.
- Seeliger, U., 2001. The Patos Lagoon Estuary, Brazil. In Seeliger, U. & B. Kjerfve (eds), Coastal Marine Ecosystems of Latin America. Springer-Verlag, Berlin: 167–182.
- Vieira, J. P. & J. P. Castello, 1996. Fish fauna. In Seeliger, U., C. Odebrecht & J. P. Castello (eds), Subtropical Convergence Marine Ecosystem: The Coast and the Sea in the Warm Temperate Southwestern Atlantic. Springer-Verlag, New York: 56–61.
- Vooren, C. M., 1996. Bird fauna. In Seeliger, U., C. Odebrecht & J. P. Castello (eds), Subtropical Convergence Marine Ecosystem: The Coast and the Sea in the Warm Temperate Southwestern Atlantic. Springer-Verlag, New York: 62–63.
- Winemiller, K. O., 1992. Life-history strategies and the effectiveness of sexual selection. Oikos 63: 318–327.
- Winemiller, K. O., 1993. Seasonality of reproduction by livebearing fishes in tropical rainforest streams. Oecologia 95: 266–276.
- Wischnath, L., 1993. Atlas of Livebearers of the World. T.F.H. Publications, Neptune City, New Jersey.
- Zar, J. H., 1996. Biostatistical Analysis. Prentice Hall, Upper Saddle River, New Jersey.