Differences in reproductive strategies between two co-occurring mullets *Mugil curema* Valenciennes 1836 and *Mugil liza* Valenciennes 1836 (Mugilidae) in a tropical bay

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The female reproductive strategies of *Mugil curema* Valenciennes 1836 and Mugil liza Valenciennes 1836 occurring in a tropical bay in southeastern Brazil were found to differ. Gonadosomatic index values and macroscopic staging of gonads showed that *M. curema* spawning took place between August and January, while M. liza spawning occurred between May and August. M. curema spawning began just before the rainy season, whereas M. liza spawned during the dry season. Estimates of absolute fecundity (F) and relative fecundity (RF) were significantly greater (P < 0.01) for M. liza (mean F = $308 \times 10^4 \pm$ 104×10^3 ; mean RF = 1396.42 ± 67.02) than for *M. curema* (mean F $= 415 \times 10^3 \pm 32 \times 10^3$; mean RF = 750.54 ± 40.52). Oocyte diameters were slightly greater in *M. liza* (0.55 to 0.82 mm) than in *M. curema* (0.49 to 0.71 mm). Temporal segregation of the spawning season between M. curema and M. liza may avoid interspecific competition between offspring that recruit in inner bay areas. Additionally, greater fecundity and oocyte size in *M. liza* increase the chance of reproductive success during the dry season when there is less food resources for early juveniles.

KEY WORDS: fecundity, fish reproduction, interspecific competition, syntopic species, spawning.

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INTRODUCTION

Natural selection leads to maximization of the lifetime production of offspring, and more importantly, to maximization of the survivorship of offspring until adulthood. The main objective of a reproductive strategy is to maximize reproductively active offspring in relation to available energy and parental life expectancy (ROFF 1992, PIANKA 2000). Fishes follow different strategies and tactics to achieve this (POTTS & WOOTTON 1984). Presumably both the overall strategy and the tactical variations are adaptive (STEARNS 1992). Closely related species should develop strategies to avoid interspecific competition for limited resources and to overcome environmental constraints (WOOTTON 1992, AMARASEKARE 2003). For example, timing segregation in reproduction will enable offspring to maximize the use of the available resources, enhancing survival and reproductive success.

Mugilids are widely distributed in coastal and brackish waters of all tropical and temperate regions of the world. In many countries, mugilids are targeted by commercial fisheries (IBÁŃEZ-IBAŃEZ-AGUIRRE & GALLARDO-CABELLO 2004) and have also been widely cultured (Stvalingam 1975, Lee & Ostrowski 2001). They are also one of the most important forage fishes found in estuaries and represent a significant food source for upper-level piscivores (McDONOUGH & WENNER 2003). Consequently, the reproductive biology of a number of mugilids has been well studied.

Fishes of the family Mugilidae are iteroparous (BRUSLE 1981, FENDER DE ANDRADE-TALMELLI et al. 1994) and highly fecund (GREELEY et al. 1987, OKUMUŞ & BAŞÇNAR 1997). Mullets produce small pelagic eggs that typically develop in a group-synchronous pattern and they have two distinct size classes of oocytes present in mature ovaries. Mullets release the larger class of oocytes in one to a few spawning events (CHAN & CHUA 1980, RENDER et al. 1995, KENDALL & GRAY 2008) taking place in the lower reaches of estuaries and in near-shore coastal waters.

Mugil liza Valenciennes 1836 and *Mugil curema* Valenciennes 1836 are the most abundant species of Mugilidae in southeastern Brazil and are very important as a fishery resource. In Sepetiba Bay, Rio de Janeiro State, *M. liza* and *M. curema* accounted for 99.7% of the total number of mullets caught in experimental samplings between 1994 and 1997 (SILVA & ARAÚJO 2000). These species have similar feeding habits and offshore reproduction, and they use the inner bay areas to recruit (SILVA & ARAÚJO 2000, FROESE & PAULY 2008). Nevertheless, due to intraspecific and interspecific variation in spawning behavior (e.g., timing and duration), there is considerable variation in life-history characteristics of mugilids that inhabit similar environments (BRUSLE 1981). We hypothesize that there are differences in reproductive traits, such as reproductive timing, in order to avoid offspring competition. To test this hypothesis, we compared the gonadal cycle, fecundity and oocyte diameter between these two species.

MATERIAL AND METHODS

Study area

Sepetiba Bay is a sedimentary embayment in the southeastern region of Rio de Janeiro State (22°54'-23°04'S; 43°34'-44°10'W) with an area of ca 450 km² and open to the Atlantic Ocean on its western boundary. The bay has a mean depth of 8.6 m, a maximum depth of 30 m, and its drainage area is ca 2700 km² (ARAÚJO et al. 2002). The waters are predominantly polyhaline (salinity average = 30) and the mean temperature ranges from 21.5 °C in winter to 27 °C in summer (ARAÚJO et al. 2002). The annual rainfall is 1000-2100 mm (BARBIÉRI & KRONEMBERG 1994) but does not cause great changes in the salinity of the bay because the streams and channels that drain into the bay are small. The rainfall period in the bay region is mainly between October and February (summer), though it can sometimes extend into March (BARBIÉRI & KRONEMBERG 1994). The dry period extends from May to September (winter). Rainfall data were collected from Sepetiba Meteorological Base [(GEORIO FOUNDATION 2008), available at www.rio.rj.gov.br/georio].

Most of the bay has a substrate of silt and mud and a tidal range of approximately 1 m. Southwestern winds help move seawater into the bay and northeastern winds help take bay water out toward the continental shelf (SIGNORINI 1980). In the last few decades, the bay has undergone increasing degradation due to industrial outflows and municipal effluents brought into the bay by rivers and drainage channels on the outskirts of Rio de Janeiro city (PFEIFFER et al. 1985).

Data collection and analysis

We collected specimens from artisanal and commercial catches from July 2006 to June 2007 in the inner zone of Sepetiba Bay. The nets were 1500 m long, 3 m high and had three panels of different mesh sizes (35, 40 and 45 mm or 45, 50 and 55 mm stretched mesh sizes). This large mesh, designed to catch the larger fishes, mainly selects females, since females outnumber males in all size classes, with significant differences in the sex ratio for sizes larger than 500 mm LT for *M. liza* (ALBIERI & ARAÚJO 2010). Male mullets generally outnumber females of shorter lengths, while females outnumber males of greater lengths; this pattern has been reported for mullets elsewhere (NJOKU & EZEIBEKWE 1996, OKUMUŞ & BAŞÇNAR 1997, McDONOUGH et al. 2003).

We collected approximately 40 specimens of *M. liza* and of *M. curema* each month. Of these, 156 *M. liza* and 136 *M. curema* were examined to assess their reproductive biology. We measured total length (TL) to the nearest mm. Total (TW) and eviscerated (EW) weight were measured to the nearest gram, and gonad weight (GW) to 0.01 g. The gonadal macroscopic description followed ANDRADE-TALMELLI et al. (1996) and MARIN et al. (2003). Ripe ovaries were kept in Gilson solution to estimate fecundity and oocyte diameter.

The gonadosomatic index (GSI = $GW \times 100 \times EW^{-1}$) and frequency of gonad maturation stages were used to assess the gonadal cycle (VAZZOLER 1996). Eviscerated

weight was used in all index calculations to avoid the influence of the contents of the gonad and stomach on the weights. One-way analysis of variance (ANOVA) was used to compare GSI means among months (P < 0.05) and r-Spearman rank coefficient was used to assess the correlation between monthly rainfall and GSI. All data are expressed as means ± standard error.

Absolute fecundity (F) was estimated by the gravimetric method as described by VAZZOLER (1996). Relative fecundity (RF) was calculated as F per gram of eviscerated body mass (KENDALL & GRAY 2008). The diameter of 300 mature oocytes chosen from each ripe ovary was measured with an ocular micrometer to 0.01 mm. Fecundity and oocyte diameter were compared between the two species with Student's *t*-test.

RESULTS

Macroscopic morphology of gonads

Ovaries are paired, elongated, covered by a thin peritoneal layer and range from filiform to piriform depending on the developmental stage. Cranial regions are larger and the ovaries get thinner toward the caudal portion. Each gonad duct lies on the dorsal-medial region. These ducts have a small joint leading to a common orifice. Throughout the gonads, the arteries occupy a supra-visceral position

 Table 1.

 Macroscopic description of *M. liza* and *M. curema* ovaries (modified from ANDRADE-TALMELLI et al. 1996 and MARIN et al. 2003).

Stages	Characteristics
Immature	Ovaries small, filiform and adhered to the swim-bladder. They are translucent with no sign of blood irrigation.
Developing	Ovaries are fusiform and wider than at the previous stage, occupying almost 1/3 the abdominal cavity, and reddish in color. There is some sign of blood irrigation.
Maturing	Ovaries wider and almost piriform, filling approximately 2/3 of abdominal cavity. They are reddish-yellow with a granular appearance due to the oocytes and the arteries are easily visible.
Ripe/Running ripe	Ovaries are large, piriform, yellow, smooth in appearance, turgid and round and occupy almost the entire abdominal cavity. Oocytes are easily distinguished macroscopically (as granular) and blood irrigation is evident.
Spent	Ovaries are flaccid and wrinkled, occupying about $\frac{1}{2}$ of abdominal cavity. Purple in color.
Recovering/ Resting	The wall is thicker and rigid, and ovaries are fusiform, occupying less than 1/3 of the abdominal cavity. Cream in color and the ovarian mass is firm and reddish in color.

and spread through lateral ramifications that become evident during gonadal development. The right gonad is usually larger than the left. The maturation stages of ovaries are described in Table 1.

Spawning season

Mugil liza. The mean GSI showed seasonal differences during the study period (F = 4.34; P < 0.01; Fig. 1). The lowest GSI were recorded between October and March; these values then increased in April and May, peaked in June and then dropped sharply in July, August and September. There was a highly significant negative correlation (P < 0.01) between GSI and rainfall (r = -0.76). Ripe/running ripe ovaries were observed between May and August. Spent ovaries were recorded from May to September. Immature ovaries were observed between July and February; developing and recovering/resting ovaries were found throughout the study period. Maturing ovaries were observed from April to September (Fig. 2).



Fig. 1. — Monthly variation in rainfall (cm: --) and gonadosomatic index (GSI) of female *M. liza* (-) and *M. curema* (-).

Mugil curema. The mean GSI showed seasonal differences during the study period (F = 8.56; P < 0.01; Fig. 1). The lowest GSI were recorded between February and June; these values then increased in July and August, peaked in October and dropped sharply in November, December and January. No significant correlation (P > 0.05) was found between GSI and rainfall (r = 0.04). Ripe/running ripe ovaries were observed between August and January.

The only spent ovary was recorded in November. Immature and recovering/ resting ovaries were recorded from December to January and from November to June, respectively. Developing ovaries were found throughout the study period, with the highest percentages in April and May. Maturing ovaries were observed between July and January, with the highest percentages in September and October (Fig. 2).

Fecundity

Mugil liza mature after reaching about 55 mm TL, whereas *M. curema* mature by 25 mm TL (Table 2). The absolute fecundity for 20 *Mugil liza* adults ranged from 241×10^4 to 365×10^4 oocytes (mean: $308 \times 10^4 \pm 104 \times 10^3$ oocytes) for females measuring 590 to 680 mm TL. Relative fecundity ranged from 871.72 to 1940.42 oocytes g⁻¹ (mean: 1396.42 ± 67.02 oocytes g⁻¹) and the diameter of



Fig. 2. — Monthly changes in the percentage of maturity stages of female *M. liza* (A) and *M. curema* (B). Sample sizes are given above bars. Recovering (\Box); Spent (\blacksquare); Ripe/running ripe (\blacksquare); Maturing (\blacksquare); Developing (\blacksquare); Immature ($\mathbf{\Sigma}$).

Species	Size class	п	Total weight	GSI	$n_{\rm f}$	Absolute fecundity	Oocyte diameter
Mugil liza	30-35	1	365	0.02	0	_	_
	35-40	7	550.71 ± 28.83	0.15 ± 0.03	0	_	_
	40-45	38	845.02 ± 14.33	0.13 ± 0.02	0	_	—
	45-50	64	1050.84 ± 13.02	0.28 ± 0.03	0	_	—
	50-55	13	1382.30 ± 47.11	1.66 ± 1.39	0	_	_
	55-60	13	2051.53 ± 89.54	4.91 ± 1.78	5	$\begin{array}{c} 293 \times 10^4 \ \pm \\ 22 \times 10^4 \end{array}$	0.55-0.80
	60-65	14	2670 ± 86.28	8.33 ± 1.62	12	$328 \times 10^4 \pm 11 \times 10^4$	0.60-0.82
	65-70	3	3105 ± 125	10.45 ± 0.88	3	$342 \times 10^4 \pm 12 \times 10^4$	0.60-0.81
Mugil curema	20-25	7	165.71 ± 7.97	3.08 ± 1.92	1	124 × 10 ³	0.49-0.68
	25-30	52	242.53 ± 4.99	0.80 ± 0.28	1	151 × 10 ³	0.49-0.70
	30-35	27	366.88 ± 12.44	1.71 ± 0.48	2	$242 \times 10^{3} \pm 54 \times 10^{3}$	0.51-0.70
	35-40	43	627.74 ± 12.71	5.51 ± 0.68	16	$454 \times 10^{3} \pm 31 \times 10^{3}$	0.50-0.71
	40-45	7	773.52 ± 41.74	5.01 ± 1.07	2	$562 \times 10^{3} \pm 59 \times 10^{3}$	0.51-0.70

Size class distribution (TL in mm), total weight (g) and reproductive endpoints of *M. liza* and *M. curema* females.

(*n* = sample size; GSI = gonadosomatic index; n_f = number of ovaries used to assess absolute fecundity and oocyte diameter, in mm; mean ± SE).

mature oocytes measured 0.55 to 0.82 mm. The absolute fecundity of 22 *Mugil* curema adults ranged from 123×10^3 to 711×10^3 oocytes (mean: $415 \times 10^3 \pm 32 \times 10^3$ oocytes) for females measuring 245 to 445 mm TL. Relative fecundity ranged from 497.46 to 1255.46 oocytes g⁻¹ (mean: 750.54 ± 40.52 oocytes g⁻¹) and the diameter of mature oocytes measured 0.49 to 0.71 mm. Both F and RF differed significantly (P = 0.00, t = 25.21 for F; P = 0.00, t = -8.42 for RF) between the two species, with *M. liza* having higher values than *M. curema*. Oocyte diameter did not differ significantly (P > 0.05) between the two species. Absolute fecundity increased with body size and GSI while oocyte diameter did not change according to fish size, fecundity or GSI (Table 2).

DISCUSSION

Temporal segregation of the spawning seasons was found for *M. liza* and *M. curema*, with the former showing a shorter reproductive period of 4 months (May to August, peaking in July) and the latter a longer reproductive period of 6 months (August to January, peaking between August and October). SILVA & ARAÚJO (2000) reported peaks in recruitment of *M. liza* young-of-the-year in August. ARAÚJO et al. (1997) also found large numbers of *M. liza* juveniles in the inner bay zones during winter. These results match our findings, which indicate that the spawning of this species occurs in winter. Although no confirmatory information on the reproductive period of *M. curema* is available, our observations of GSI and frequency of gonadal stages indicate a reproductive period different from that of *M. liza*.

Different species may be limited by the same resource availability but differ in terms of when they exploit the resource (ARMSTRONG & MCGEHEE 1980, CHESSON 2000). Segregation of the reproductive periods is attributed to the reduction of competition between offspring for space and available food resources. According to several authors (e.g. YÁNEZ-ARACIBIA 1976, BLABER 2000, SILVA & ARAÚJO 2000, FROESE & PAULY 2008), mugilids have similar feeding habits, diets and recruitment habitats. Therefore, offspring competitive pressure could lead to the selection of different spawning periods of these two closely related species, a tactic used to enable coexistence since they use the same area to recruit.

Temporal separation of the spawning periods of mugilids has been reported elsewhere. COLLINS & STENDER (1989) collected mullet larvae of both species (*M. cephalus* Linnaeus 1758 and *M. curema*) in only 7.4% of neuston samples from February-May. IBÁŇEZ-AGUIRRE (1993) found that *M. cephalus* and *M. curema* coexist in Tamiahua Lagoon, with no difference in diet or digestive system but with a separation of 3 months in reproductive timing. DITTY & SHAW (1996) obtained *M. cephalus* larvae from the northern Gulf of Mexico between October and March, with peak abundance in November and December, and *M. curema* larvae between April and September, with peak abundance in April and May and a decrease from August to September. Differences in the reproductive period between congeneric and co-occurring mullets was also reported by IBAŇEZ-AGUIRRE & GALLARDO-CABELLO (2004) for *M. cephalus* and *M. curema* in Venezuelan waters, and by KENDALL & GRAY (2008) for *Liza argentea* (Quoy & Gaimard 1825) and *Myxus elongatus* Günther 1861 in southeastern Australia.

The periodicity of mullet reproduction may also be related to environmental variability in the signals for optimal early growth and survival. In the tropics, Mugilidae spawning encompasses the wet season (BLABER 2000). The spawning period of *M. curema* in Sepetiba Bay began just before the rainy season, suggesting that early juveniles could take advantage of the benefits of rainfall, such as food availability. MACGREGOR & HOUDE (1996) found that heavy rainfall seasons seem to increase plankton availability due to great amounts of nutrients carried by rivers, favoring the development of planktophagous fish. Early juvenile mullets (< 60 mm TL) are planktophagous (YAŃEZ-ARACIBIA 1976, BLABER 2000); hence, the adults could spawn before the rainfall season in order to increase larval and

juvenile survival, since suitable food in bays, coastal lagoons, river deltas and estuarine mangrove areas has been identified as an important factor influencing the reproduction and recruitment of juvenile Mugilidae (YAŃEZ-ARACIBIA 1976, BLABER & BLABER 1980).

On the other hand, *M. liza* spawn during the dry season in winter when the water column and environmental conditions are stable in Sepetiba Bay (ARAÚJO et al. 2002). Although the food availability is higher during the rainy season, *M. liza* may use two tactics to overcome this environmental constraint. First, *M. liza* increases fecundity (mean F: 3,080,000 ± 104 × 10³ oocytes, mean RF = 1396.42 ± 62.02 oocytes g⁻¹ for *M. liza*; mean F: 415,000 ± 32 × 10³ oocytes, mean RF 750.54 ± 40.52 oocytes g⁻¹ for *M. curema*) and has slightly larger oocytes (diameter: 0.55 to 0.88 mm for *M. liza*; 0.49 to 0.71 mm for *M. curema*). Oocyte diameter did not change with fish size, fecundity or GSI. Our finding that oocyte diameter for salmonid species. However, WARE (1975) and BENGTSON et al. (1987) pointed out that oocyte size is remarkably constant for a given marine fish species in a given geographical area.

Fecundity may vary due to different adaptations to environmental habitats (WITTHAMES et al. 1995) and is related to the feeding conditions in which the newly hatched larvae find themselves. Large larvae (large eggs) will be at an advantage when the plankton is sparse (WOOTTON 1992) but exceptions occur because some larger eggs have a larger perivitelline space and less nutritive yolk. Although *M. curema* has a longer reproductive period and better conditions for recruitment, *M. liza* developed high fecundity and slightly larger oocytes with a larger amount of yolk, enabling the larvae to survive and recruit even in a less favorable environment. Furthermore, the differentiation of spawning timing avoids competition between earlier juvenile recruitment, as mentioned before.

Mugil curema is a widespread mullet which coexists with *M. cephalus* mainly in the Gulf of Mexico (IBÁÑEZ-AGUIRRE & GALLARDO-CABELLO 2004), with *M. liza* in northeastern and southeastern Brazil (SILVA & ARAÚJO 2000), and with *Mugil platanus* Günther 1880 in southern Brazil (VIEIRA 1991). All those species (*M. cephalus, M. liza* and *M. platanus*) spawn in winter and have higher fecundity, larger eggs and reach larger sizes than *M. curema* which spawns mainly in spring. Therefore, it is reasonable to suppose that those three species developed a similar strategy to coexist with *M. curema*; the latter seems to use more favorable conditions to spawn whereas the former three species developed an alternative strategy to coexist.

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