Abstract–The reproductive biology of the whitemouth croaker (*Micropogonias furnieri*) inhabiting the estuarine waters of the Río de la Plata (Argentina-Uruguay) was studied by using histological analysis of the ovaries. Samples were collected during the spawning peak and the end of two breeding seasons (November 1995–February 1996 and November 1997–March 1998). *Micropogonias furnieri* is a multiple spawner with indeterminate annual fecundity. Spawning frequency, determined by using the percentage of females with postovulatory follicles, was about 31% in November 1995 and 25% in February 1996. At these frequencies, a female on average spawned a new batch of eggs every 3–4 days during the spawning season. Batch fecundity was fitted to a power function of length and a linear function of ovary-free female weight. The number of hydrated oocytes decreased at the end of the breeding season, coinciding with an increase of atresia. Annual egg production for a 40-cm-TL female was estimated to be between 3,300,000 and 7,300,000 eggs. In addition to the seasonal decrease in fecundity and spawning activity, a decline in egg size and weight toward the end of the breeding season was also observed.

Seasonal egg production of whitemouth croaker (*Micropogonias furnieri*) in the Río de la Plata estuary, Argentina-Uruguay

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The whitemouth croaker, *Micropogonias furnieri* (Sciaenidae)*,* is a demersal coastal species distributed along the eastern coast of Central and South America, from the Yucatán Peninsula to south of Buenos Aires Province (41°S), Argentina (Isaac-Nahum, 1988). It is an economically important resource in the Río de la Plata area and the most heavily exploited coastal species in the commercial fisheries of Argentina and Uruguay (Lasta and Acha, 1996).

The reproductive biology of *M. furnieri* has been extensively studied off Brazil, Uruguay, and Argentina (Vazzoler, 1970; Haimovici, 1977; Isaac-Nahum and Vazzoler, 1983; Castello, 1986; Macchi and Christiansen, 1992a; Acuña et al., 1992; Macchi et al., 1996; Lasta and Acha, 1996). Spawning in the Río de la Plata area extends over a protracted period, from early November to March, and peaks during November–December (Macchi and Christiansen, 1996). In this area, spawning takes place in the inner zone of the Río de la Plata estuary, where the river and the oceanic waters form a bottom salinity front (Macchi et al., 1996; Macchi, 1997; Acha et al., 1999).

Whitemouth croaker is a multiple spawner with an indeterminate annual fecundity; in other words, unyolked oocytes continuously mature and are spawned throughout the reproductive season (Macchi, 1997). Previously, fecundity estimates for *M. furnieri* were made by counting the number of yolked oocytes in ripe ovaries (Vazzoler, 1970; Macchi and Christiansen, 1992b; Pravia et al., 1995). This method does not account for the multiple spawning pattern of this species; therefore, estimates may be incorrect by as much as an order of magnitude (DeMartini and Fountain, 1981; Conover, 1985, Brown-Peterson et al., 1988, Lowerre-Barbieri et al., 1996). Spawning frequency and batch fecundity in the whitemouth croaker of the Río de la Plata area has been estimated only during the spawning peak (November) and is, therefore, considered to be a preliminary estimate for this species (Macchi et al., 1996).

In this paper, we examine ovaries histologically and analyze planktonic eggs of *M. furnieri* from the Río de la Plata estuary, collected during the spawning peak and near the end of the breeding season. We also determine the time of day when this species spawns and compare the spawning frequency, batch fecundity, and egg sizes obtained during the spawning peak and the end of the reproductive season.
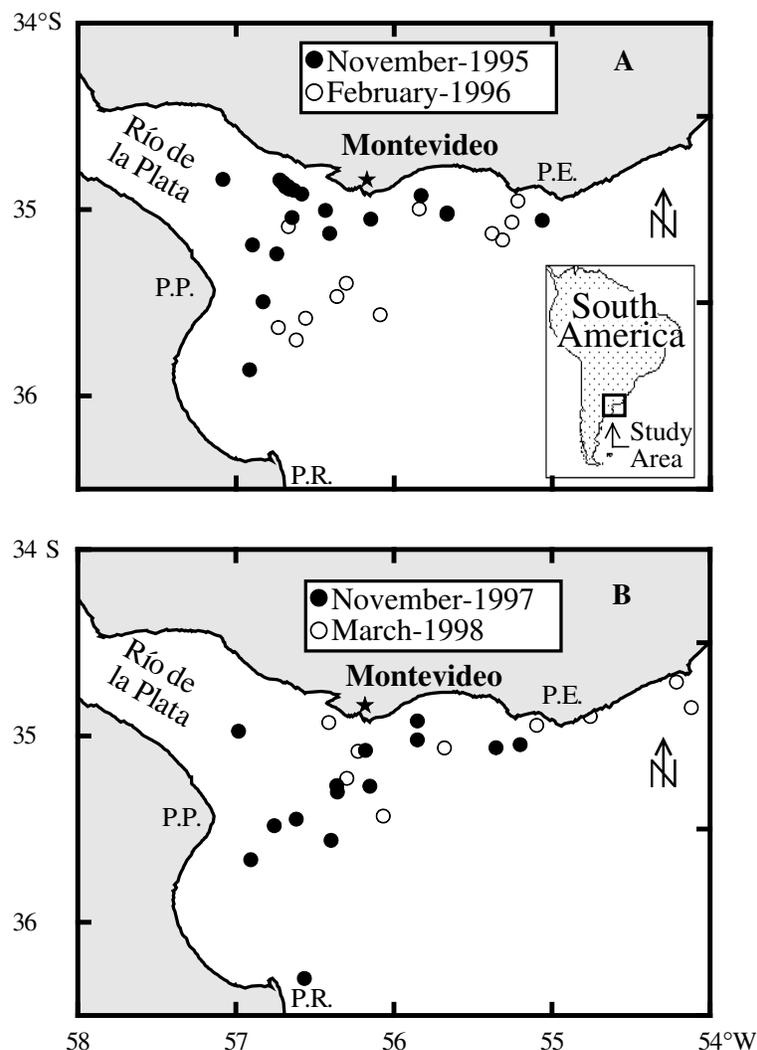
Figure 1

Study area and samples location for the 1995–96 (**A**) and 1997–98 (**B**) spawning seasons. November samples correspond to the main spawning peak and February–March to the end of the breeding season of *M furnieri*. PE = Punta del Este, Uruguay; PP = Punta Piedras; and PR = Punta Rasa, Argentina.

Material and methods

Sampling

Whitemouth croaker females were collected in the Río de la Plata estuary during four research surveys (Fig. 1), namely during the peak of spawning and at the end of the breeding season for the two spawning seasons (November 1995–February 1996 and November 1997–March 1998). Fish were collected with bottom trawls by using a net with a mouth width of about 20 m, a height of about 4 m, and with a 20-mm mesh at the inner cover of the codend. Total length (TL, cm) and total wet weight (TW, g) were recorded for each fish sampled. Only adult females larger than 30 cm

TL were analyzed (Table 1) because *M. furnieri* mature at approximately 33 cm TL (Macchi and Acha, 1998).

During the 1995–96 spawning season, oceanographic sampling was performed with a Sea-Bird 19 CTD (conductivity–temperature–depth profiler), with a lowering speed of 0.5 m/s. Data were processed to achieve a 1-m vertical resolution (precision of ±0.03°C in temperature and ±0.05 units in salinity).

Whitemouth croaker eggs were taken from the plankton samples during the spawning peak and late reproductive season only in the 1995–1996 breeding period. Ichthyoplankton were collected with a Nackthai sampler (Nellen and Hempel, 1969) equipped with a single net with a 20-cm diameter mouth opening and 405-µm mesh (Acha et al.,

Table 1

Statistic data from the seasonal samples of *M. furnieri* females collected in the Río de la Plata estuary. TL = total length; SD = standard deviation.

Date	*n*	Length range (cm)	Average TL (cm)	SD
November 1995	359	31–72	44.6	7.8
February 1996	206	32–67	41.9	6.4
November 1997	159	33–62	44.3	3.9
March 1998	154	32–58	42.6	4.2

1999). Eggs of *M. furnieri* were identified on the basis of the descriptions reported by Weiss (1981).

Laboratory processing

Ovaries were removed immediately after capture of the fish and fixed in 10% buffered formalin for two weeks. The ovaries were weighed (GW) to the nearest 0.1 g and a sample of about 2.0 g was removed from each ovary, dehydrated in methanol, cleared in benzol, and embedded in paraffin. Sections were cut at 4 μm and stained with Harris' hematoxylin and eosin Y. Ovaries were classified histologically into seven categories: developing early (1), developing late (2), fully developed (3), gravid (4), partially spent (5), spent (6) and resting (7). This classification is a modification of that given by Mayer et al. (1988) and has previously been employed to describe the ovarian development in *Cynoscion guatucupa* (Macchi, 1998). The criteria for identifying the different atresia stages and the atretic condition of the ovary were adopted from Hunter and Macewicz (1985).

One hundred planktonic eggs collected during the main spawning peak and during the end of the breeding season were measured (±0.01 mm) by using a microscope equipped with a calibrated eyepiece. Two diameters at right angles to each other were measured per egg and an average was taken. Egg weights were estimated for each portion of the spawning period from two samples of 100 eggs each. The eggs were rinsed in distilled water, dried for 20 hours at 60°C, and weighed (±0.1 mg). The diameter and weight of the eggs collected during the spawning peak and the end of the breeding season were compared by analysis of variance (Draper and Smith, 1981).

Estimation of spawning frequency

Spawning frequency was estimated by the incidence of females with postovulatory follicles (POF), following the method described by Hunter and Goldberg (1980). The description of the stages of POF degeneration was based on six females that spawned in captivity during the research cruise carried out in March 1998. Two fish were sampled at the time of spawning and the others were sacrificed 6, 12, 24, and 36 hours after spawning. The ovaries of these

fish were preserved in 10% buffered formalin and used to establish histological criteria for the aging of POFs of the sea-caught females.

Postovulatory follicle degradation in *M. furnieri* was faster than that reported by Hunter and Goldberg (1980) for northern anchovy (*Engraulis mordax*). A 24-h-old POF showed advanced signs of degeneration similar to those observed in *E. mordax* 48 h after spawning. Therefore, daily percentage of spawning females (spawning frequency) was estimated by taking the total of females with POFs less than 24 h old (Hunter et al., 1986). Mean and variance of this parameter were calculated according to the equation developed by Picquelle and Stauffer (1985), which allows weighing of each station according to the subsample size.
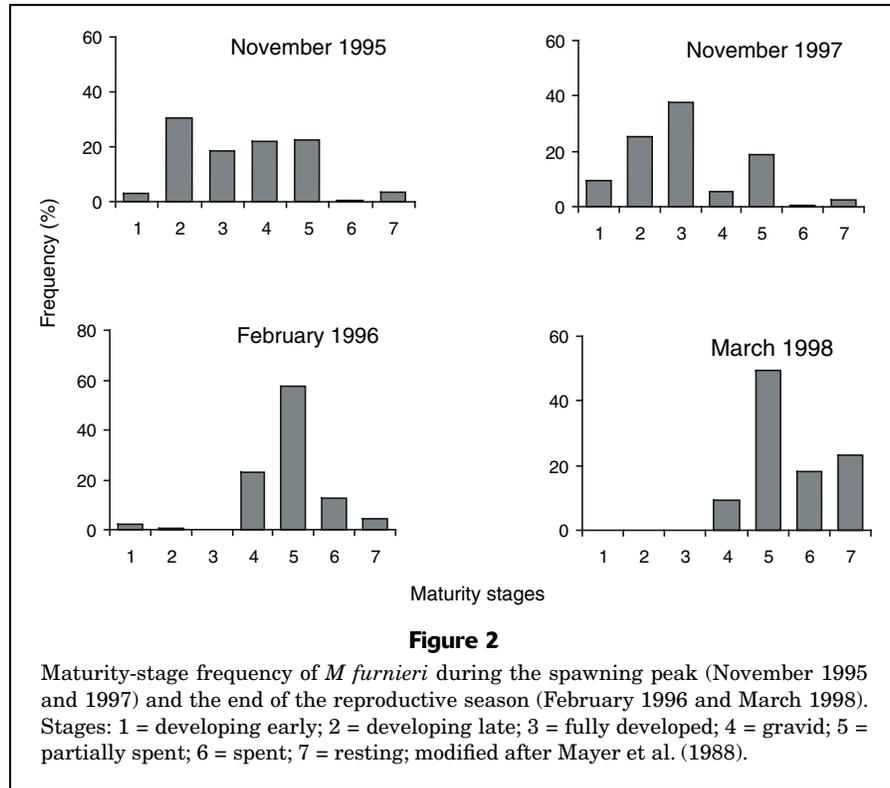
Fecundity estimation

Batch fecundity (BF; number of oocytes released per spawning) was estimated gravimetrically with the hydrated oocyte method on fixed ovarian samples (Hunter et al., 1985). Ovaries used showed no evidence of recent spawning (i.e. no new POFs). Batch fecundity was determined for 87 females (57 from November 1995, 16 from February 1996, three from November 1997, and 11 from March 1998). Three pieces, approximately 0.1 g each, were removed from the anterior, middle, and posterior part of each ovary, weighed (±0.1 mg), and the number of hydrated oocytes were counted. Batch fecundity for each female was the product of the mean number of hydrated oocytes per unit of ovarian weight and the total ovarian weight. Relative fecundity (RF) was defined as the number of hydrated oocytes per gram of ovary-free body weight. Fecundity values obtained for the different months within the spawning season were compared with a test of equality of means (Draper and Smith, 1981). The relationships of batch fecundity to total length and to total weight (ovary free) were described with standard linear regressions. Comparisons between the different months were based on overlapping length ranges of the samples, and an analysis of covariance with log-transformed data was applied (Draper and Smith, 1981).

Results

Spawning season

During November 1995, in the Río de la Plata estuary, 93% of the sampled females were found to be in a reproductive state, with ovaries being either in a developing phase or partially spent (maturity stages 2 to 5). Gravid females (with hydrated oocytes) accounted for about 20% and spent ovaries were scarce (Fig. 2). Near the end of this spawning season (February 1996), 98% of the females had apparently spawned at least once and the proportion of spent ovaries was about 15%. During November 1997, females were mainly undergoing ovarian development and only a few individuals with hydrated oocytes were observed (Fig. 2). In March 1998, the proportion of spent ovaries was about 20% and the proportion of those in the resting stage was

Figure 2

Maturity-stage frequency of *M. furnieri* during the spawning peak (November 1995 and 1997) and the end of the reproductive season (February 1996 and March 1998). Stages: 1 = developing early; 2 = developing late; 3 = fully developed; 4 = gravid; 5 = partially spent; 6 = spent; 7 = resting; modified after Mayer et al. (1988).
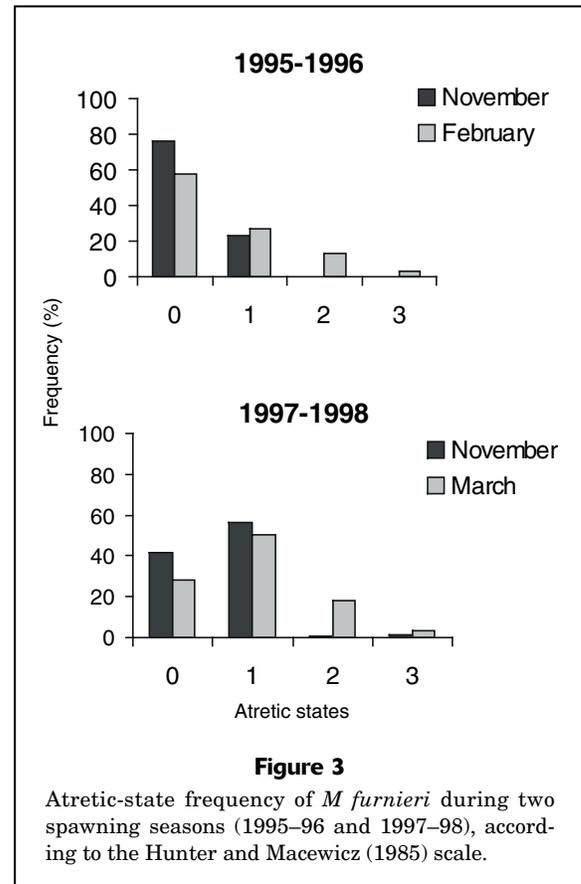
higher than in February 1996 (3% vs. 25%, respectively). In general, we noted an increase in the presence of atretic oocytes as the spawning season progressed (Fig. 3). Furthermore, the incidence of atresia was higher in 1997–98 than in 1995–96 (Fig. 3); during the last season about 60% of females were classified as in atretic state 1, whereas in 1995–96 about 20% of females were in this state.

Spawning site and oceanographic variables

Bottom salinity at the estuary ranged between 0 and 30 psu. Maximum upriver penetration of salt water during November 1995 and February 1996 was similar, reaching a line between Montevideo and Punta Piedras (Fig. 4). The Argentine coast of the estuary showed a similar salinity pattern during both months, whereas the salt water intrusion along the Uruguayan coast showed more upriver penetration during November 1995, which generated a stronger horizontal salinity gradient (Fig. 4A). In contrast, the salinity pattern along the Uruguayan coast during February 1996 showed a weaker horizontal salinity gradient (Fig. 4B).

Bottom temperature in the estuary ranged from 13.8 to 20.2°C during November 1995, and from 20.1° to 25.0°C during February 1996. In the spawning area, bottom temperatures ranged from 20.0°C to 20.2°C during the main reproductive period and from 21.5°C to 25.0°C at the end of the breeding season.

Whitemouth croaker of the Río de la Plata estuary spawn in the region of high salinity gradients. During November 1995, spawning took place near Montevideo, coinciding with the bottom salinity front (Fig. 4A). During February
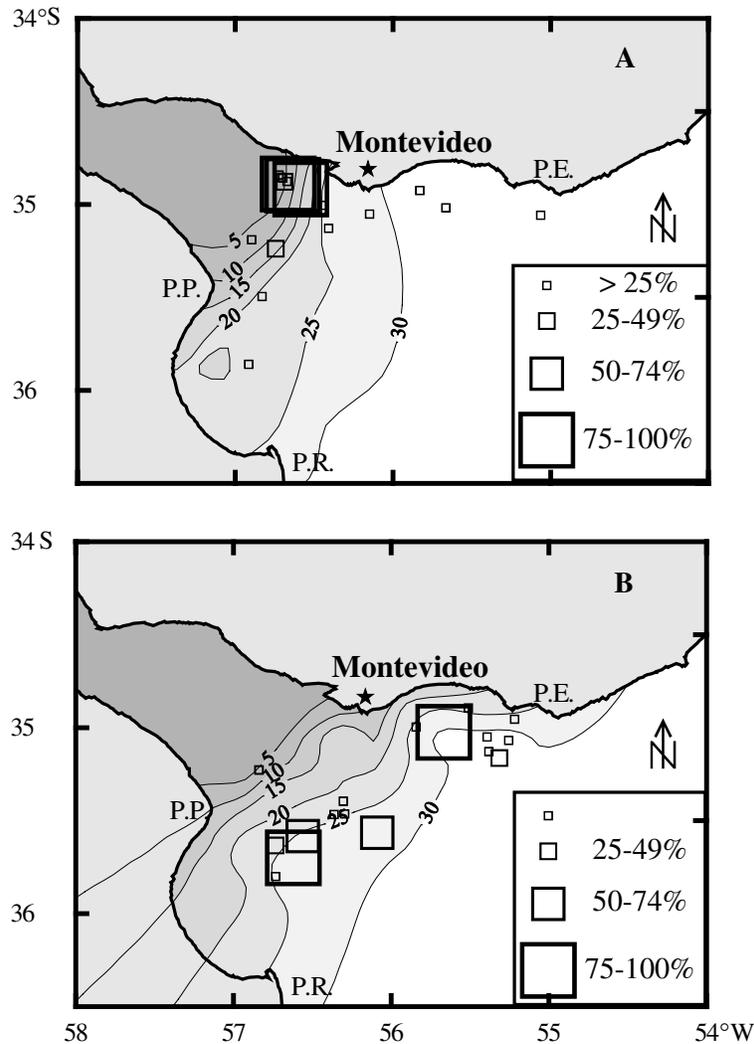

Figure 3

Atretic-state frequency of *M. furnieri* during two spawning seasons (1995–96 and 1997–98), according to the Hunter and Macewicz (1985) scale.

Figure 4

Spatial location of the *M furnieri* spawning area during November 1995 (**A)** and February 1996 (**B**). The size of the squares is proportional to the percentage of gravid females (with hydrated oocytes). In both maps, the isohalines expressed as psu) represent the bottom salinity field. PE = Punta del Este, Uruguay; PP = Punta Piedras; and PR = Punta Rasa, Argentina.
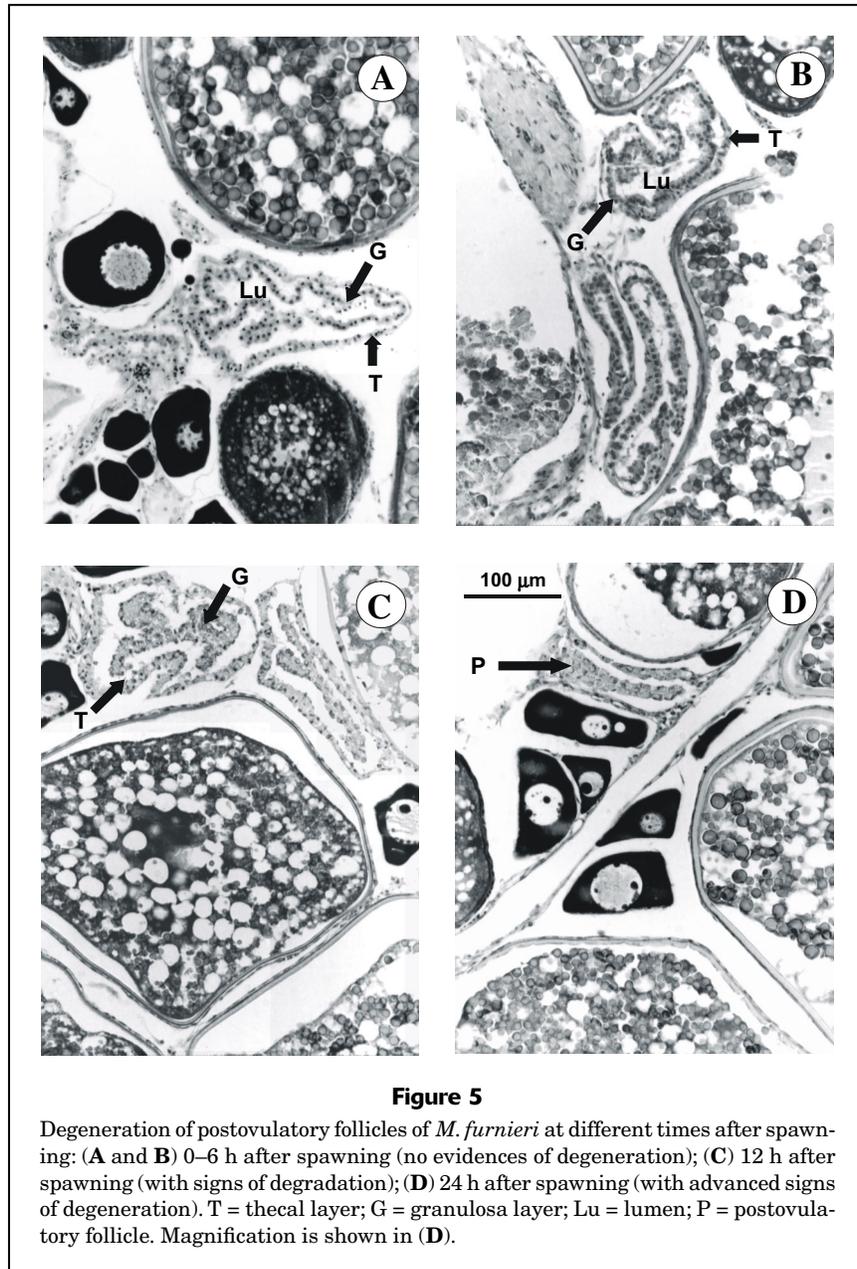
1996, spawning occurred in the outer part of the estuary, and gravid females were more scattered compared to November 1995 (Fig. 4B).

Postovulatory follicles and spawning frequency

The new POFs (between 0 and 6 h after spawning) have an irregular shape with many folds; the granulosa cells are aligned with a prominent nucleus, and the lumen is clearly visible (Fig. 5, A–B). A 12-h-old POF shows degenerative processes with fewer convolutions, the walls of the granulosa cells are not well defined, and the lumen becomes reduced (Fig. 5C). A 24-h-old POF shows pronounced signs of degeneration and forms a compact structure much smaller than that at age-12-h. The granulosa layer is still evident but consists of a few cells (Fig. 5D). Postovulatory follicles older than 24 h are difficult to distinguish and may be confused with atresia stages.

Only females collected during the season 1995–96 were used to estimate spawning frequency of *M. furnieri* because during 1997–98 spawning females (with POF or hydrated oocytes) were scarce. For the samples taken in November 1995 (Table 2), the mean percentage of mature females with postovulatory follicles was 31.51% (CV=0.18), equivalent to a spawning interval of about 3 days. During February 1996, the percentage of mature females with postovulatory follicles was 25.35% (CV=0.27), which would indicate that each female spawned about every 4 days (Table 3).

Figure 5

Degeneration of postovulatory follicles of *M. furnieri* at different times after spawning: (**A** and **B**) 0–6 h after spawning (no evidences of degeneration); (**C**) 12 h after spawning (with signs of degradation); (**D**) 24 h after spawning (with advanced signs of degeneration). T = thecal layer; G = granulosa layer; Lu = lumen; P = postovulatory follicle. Magnification is shown in (**D**).

Daily cycle of spawning

Percentages of females with hydrated oocytes and with POFs collected at different times during the spawning peak in November 1995 can be observed in Figure 6. Hydrated ovaries were observed mainly in the morning and in the afternoon. At dusk, females with hydrated oocytes were not observed, and ovaries showing age-0-h POFs increased sharply to about 40%, declining to about 5% at midnight. Postovulatory follicles older than 6 hours (POF stages 1 and 2) were observed at different times during the day and night. These observations indicate that some spawning of whitemouth croaker apparently took place early in the afternoon, when many females had hydrated oocytes. How-ever, the vast majority of spawning occurred at dusk (near 20:00 h), when the frequency of hydrated oocytes decreased to 0% and the incidence of females with new postovulatory follicles reached a maximum.

Fecundity

Batch fecundity estimates for females sampled during 1995–96 revealed significant differences (*P*<0.01) between the spawning peak and the end of the reproductive season, being significantly greater in November (216,700 ±151,700 oocytes) than in February (96,900 ±52,000 oocytes). During 1997–98, females with hydrated eggs were scarce, but fecundity values obtained in March were

Table 2

Number of reproductively active females of *M. furnieri* sampled during November 1995 in the Río de la Plata estuary. H = hydrated oocytes without POF; POF-0 = elapsed time from spawning $\leq$ 6 h; POF-1 = elapsed time from spawning $\cong$ 12 h; . POF-2 = elapsed time from spawning $\cong$ 24 h.

Day of month	H	POF-0	POF-1	POF-2	Total mature females
16	0	0	0	0	5
16	0	7	2	5	37
17	0	0	0	0	16
18	0	0	1	0	20
18	1	1	2	0	6
18	0	0	1	0	10
19	0	0	0	0	10
19	0	0	0	0	7
19	0	0	0	0	10
21	1	0	2	0	9
21	17	0	10	5	36
21	1	1	4	3	29
21	0	1	1	2	20
22	7	0	2	3	25
22	0	11	5	5	26
22	1	1	5	3	13
23	0	0	2	4	9
23	9	0	3	9	30
23	2	7	2	2	13
23	0	4	0	2	11
Total	39	33	42	43	342

Table 3

Number of reproductively active females of *M. furnieri* sampled during February 1996 in the Río de la Plata estuary. H = hydrated oocytes without POF; POF-0 = elapsed time from spawning $\leq$ 6 h; POF-1 = elapsed time from spawning $\cong$ 12 h; . POF-2 = elapsed time from spawning $\cong$ 24 h.

Day of month	H	POF-0	POF-1	POF-2	Total mature females
10	0	1	0	3	5
11	0	0	0	0	6
11	0	0	0	1	26
11	0	5	4	4	21
12	0	0	0	1	13
14	2	1	2	2	26
14	6	4	2	1	14
15	6	5	1	1	21
15	0	2	0	0	28
17	3	0	0	0	6
17	0	0	1	0	9
18	5	0	1	2	10
Total	22	18	11	15	185

lower than in November, similar to that observed in the 1995–96 season. The relationship between batch fecundity and total length, for females taken during the spawning peak (combining November 1995 and 1997 data) and near the end of the season (combining February 1996 and March 1998 data), was curvilinear in both cases (Fig. 7A) and described by the equations

$$BF = 0.676TL^{3.282}$$

$(r^2=0.82, n=60)$
(spawning peak)

$$BF = 0.028TL^{4.009}$$
$(r^2=0.69, n=27)$
(end of reproductive season).

Analysis of covariance indicated that the regression slopes did not differ between months ($P>0.05$), but the intercepts were significantly different ($P<0.01$).

The relationship between batch fecundity and ovary-free body weight was linear (Fig. 7B):

$$BF = 223.15TW - 23{,}693$$
$(r^2=0.81, n=60)$
(spawning peak)

$$BF = 231.82TW - 82{,}325$$
$(r^2=0.81, n=27)$
(end of reproductive season).

Relative fecundity ranged from 52 to 305 hydrated oocytes per gram of female (ovary-free). Mean values obtained from the spawning peak (196 ±55 oocytes) and the end of the reproductive season (139 ±50 oocytes) for females of the same average length (45 cm TL) were significantly different ($P<0.01$).

Egg production

The spawning season of *M. furnieri* lasted about six months. Taking into account the above estimations, a female would spawn between 60 and 45 times during this period, assuming a spawning interval of three or four days. On the other hand, batch fecundity appears to vary within the reproductive season, declining toward the end of the spawning period. With the minimum and maximum values of batch fecundity and spawning frequency, it is possible to obtain an approximate range of the annual oocyte production. We estimated that a 40-cm-TL female could produce annually between 3,300,000 and 7,300,000 eggs, depending on whether batch fecundity and spawning frequency were estimated during the end of reproductive season or the spawning peak, respectively.

Because batch fecundity is proportional to female body size, larger females (>50 cm TL) showed relatively high egg production than the most abundant size classes (35–45 cm TL) at least during the spawning peak (Fig. 8).

Egg size

Egg size in plankton samples declined as the spawning season progressed. Mean egg diameter for November 1995 was 970.4 μm (SD=34.1 μm) and 865.6 m (SD=35.0 μm) for February 1996. Mean dry weight of 100 eggs was 2.60 mg (SD=0.1 10^{-4} mg) for the first period and 1.92 mg (SD=1.16 10^{-4} mg) for the second. Analysis of variance indicated significant differences ($P<0.01$) in egg diameters and in egg dry weights ($P<0.05$) from samples collected during early and late spawning season.

Discussion

In the Río de la Plata estuary, reproductive investment of *Micropogonias furnieri* varied both within the spawn-
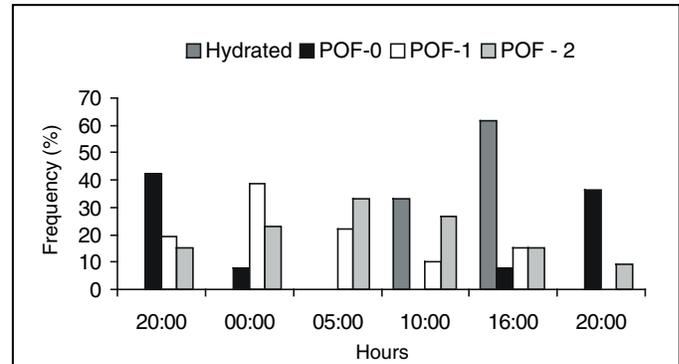

Figure 6

Hourly incidence of ovaries with hydrated oocytes (hydrated) and with postovulatory follicles in POF-0 (elapsed time from spawning ≤6 h), POF-1 (elapsed time from spawning ≅12 h) and POF-2 (elapsed time from spawning ≅24 h) stages, sampled within the spawning area during November 1995.
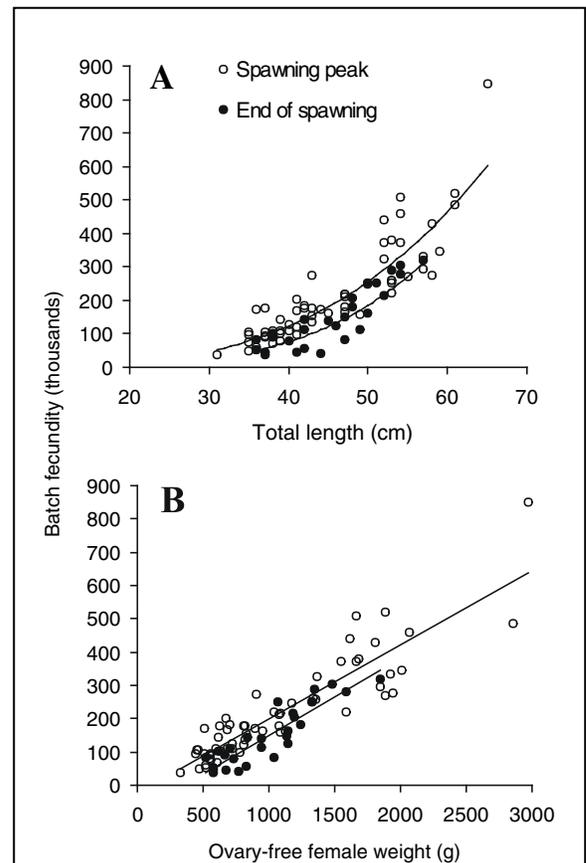

Figure 7

Batch fecundity as a function of total length (**A**) and ovary-free female wet weight (**B**) for data obtained during the spawning peak (November 1995 and 1997) and the end of the reproductive season (February 1996 and March 1998).

ing season and between years. In the 1995–96 season, a higher percentage of gravid females (with hydrated oocytes) was observed than in 1997–98. In both cases, we found that near the end of the season (February–March) the number of reproductively active females decreased when compared to the main spawning peak (November), and at the same time increased rates of atresia were observed. High levels of atresia have been used to identify regressing ovaries and to establish the cessation of spawning in other species (Hunter and Macewicz, 1985; Hunter et al., 1986; Dickerson et al., 1992; Barbieri et al., 1994).

Whitemouth croaker spawn in the estuarine waters of the Río de la Plata. During November, spawning occurs in the innermost part of the estuary, coinciding with the bottom salinity front (Macchi et al., 1996; Macchi, 1997; Acha et al., 1999). In the outer sector of the estuary, the females remain in recovering stage, eventually returning to the inner part where they complete maturation and spawn (Macchi et al., 1996). During February 1996, at the end of the reproductive season, the salinity front shows a more seaward position and a weaker horizontal salinity gradient than during November 1995, especially on the Uruguayan coast. Thus gravid females show a more scattered distribution, and the spawning area seems to be located in more coastal waters (25–30 psu). This may indicate that oceanographic conditions take priority over salinity in spawning-site selection, as had been suggested by Acha et al. (1999).

We observed a diel spawning periodicity in whitemouth croaker at Río de la Plata estuary, which may allow fish in spawning condition to concentrate at the same time and maximize fertilization (Holt et al., 1985). The estimated time of spawning peak for *M. furnieri* was near dusk, based on the incidence of females with new postovulatory follicles (less than 6 h after spawning). Spawning at dusk is a general reproductive pattern for different sciaenids, which are not dependent on light for courtship behavior because they use sound to locate mates (Holt et al., 1985). Maximum sound production for different sciaenids occurs during spawning, generally between 17:00 and 22:00 h (Saucier and Baltz, 1993). Spawning in darkness may reduce predation on eggs by visual feeders and may minimize the deleterious effects of sunlight on eggs (Saucier and Baltz, 1993). In the highly turbid waters of the Río de la Plata estuary, however, these advantages may not be as important.

Postovulatory follicle degradation in *M. furnieri* of the Río de la Plata was faster than that observed for *E. mordax* (Hunter and Goldberg, 1980). This more rapid degeneration may be a reflection of water temperature in the spawning area of whitemouth croaker, which is higher (20–25°C) than that recorded for the northern anchovy (Hunter et al., 1985). This result is coincident with that reported by Fitzhugh and Hettler (1995), who analyzed the effect of temperature on POF degeneration in Atlantic menhaden (*Brevoortia tyrannus*).

Spawning frequency estimated during the main reproductive peak in November 1995 (31.51%) was slightly high-
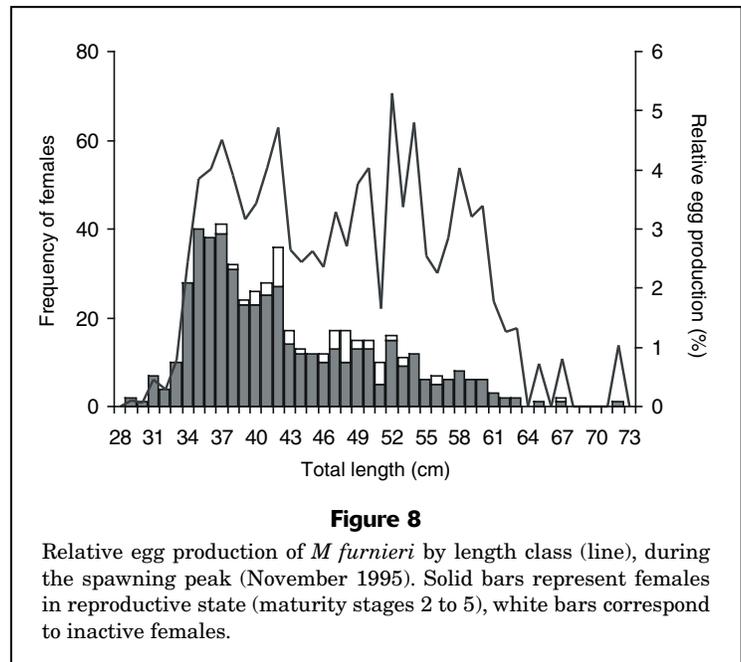

Figure 8

Relative egg production of *M furnieri* by length class (line), during the spawning peak (November 1995). Solid bars represent females in reproductive state (maturity stages 2 to 5), white bars correspond to inactive females.

er than that estimated at the end of the spawning season in February 1996 (25.3%). These percentages indicate that the spawning interval of *M. furnieri* in the Río de la Plata estuary, ranged between three and four days during the season 1995–96. Daily spawning fraction estimated for this species was similar to that reported for *Pogonias cromis* from the Gulf of Mexico (Fitzhugh et al., 1993), but higher than those estimated for other sciaenids, such as *Seriphus politus* (DeMartini and Fountain, 1981), *Genyonemus lineatus* (Love et al., 1984), *Cynoscion nebulosus* (Brown-Peterson et al., 1988) and *Cynoscion guatucupa* (Macchi, 1998). There is only one previous report of spawning frequency for *M. furnieri* of the Río de la Plata area (Macchi et al., 1996). However, this estimate is not definitive because at that time the duration of the POF was unknown, and the authors used only a fraction of the females with postovulatory follicles to estimate this parameter.

Analysis of covariance applied to the batch fecundity and length data from November (1995–97) and February 1996–March 1998 showed similar slopes. However, the regression intercept for November was significantly greater than the intercept estimate for February–March. This result indicates that batch fecundity of *M. furnieri* decreases at the end of the breeding season, coinciding with an increase of atresia. The number of oocytes per female weight showed the same pattern, decreasing in February–March. The mean relative fecundity for whitemouth croaker during the reproductive peak (196 ±55 oocytes) was less than that obtained for other sciaenids, such as *Cynoscion nebulosus* (451 ±43 oocytes); (Brown-Peterson et al., 1988), *Cynoscion regalis* (200–750 oocytes); (Lowerre-Barbieri et al., 1996) and *Cynoscion guatucupa* (210 ±53 oocytes); (Macchi, 1998). Nevertheless, this variable varies among years, depending on environmental or nutritional factors (Nieland and Wilson, 1993).

From the duration of the breeding season, batch fecundity, batch fecundity, and spawning frequency, it is possible to get a rough estimate of the annual egg production for whitemouth croaker of the Río de la Plata. Therefore, assuming a spawning season of about six months, we estimated that a 40-cm-TL female could produce between 3,300,000 and 7,300,000 eggs, depending on whether batch fecundity and spawning frequency were estimated near the end of the season or during the spawning peak, respectively. This annual egg production is within the range of that estimated for *M. furnieri* from the West Indies (from 2.4 to 13.5 million eggs); (Manickchand-Heileman and Ehrhardt, 1996).

During February–March, the percentage of whitemouth croaker females with active ovaries decreased significantly and oocyte production was half of that estimated for the spawning peak. Furthermore, the plankton data showed that *M. furnieri* egg diameters and dry weights decreased at the end of the breeding season. The seasonal decrease in egg size has been reported for other species (Ware, 1975; DeMartini and Fountain, 1981; Kjesbu et al., 1996). Explanations for this change in marine batch spawners include variations in temperature or nutritional state of the female (Hinckley, 1990; McEvoy and McEvoy, 1991). Some authors have suggested that larger eggs are advantageous because they result in larger hatchlings that are able to avoid predators more effectively (Hinckley, 1990; Wootton, 1994). In this case, in addition to the decrease in fecundity and spawning activity observed during the end of breeding season, the quality of the eggs produced for the last batches could be lower than in the spawning peak. These results suggest that the annual recruitment of *M. furnieri* in the Río de la Plata area depends to a great extent on females spawning during November.

Acknowledgments

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