Estuarine spawning of the whitemouth croaker Micropogonias furnieri (Pisces : Sciaenidae), in the Río de la Plata, Argentina

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Estuarine spawning of the whitemouth croaker *Micropogonias furnieri* (Pisces : Sciaenidae), in the Río de la Plata, Argentina

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Abstract. Most fishes that take advantage of the high productivity of estuaries exhibit offshore spawning, produce great numbers of small pelagic eggs and recruit to estuaries as larvae or juveniles. The reproductive pattern of *Micropogonias furnieri* (a planktonic egg spawner) in the Río de la Plata estuary (36°S,56°W) differs from this. Biological sampling and oceanographic data showed that the spawning area covers a narrow band across the river between Montevideo (34°50′S,56°10′W) and Punta Piedras (35°25′S,57°10′W) at depths ranging from 6 to 8 m. This area is characterized by strong haloclines, reaching 21.5 units m^{-1}. *M. furnieri* eggs were present only below the halocline, in salinities of 9.7–27.3, and at 18.5–20.2°C. Spawning occurred in the innermost part of the estuary, near the upstream edge of the salinity wedge and coinciding with the turbidity maximum (up to 150 mg L^{-1}). The regular spawning of pelagic eggs has been reported in estuaries of southern Africa and Australia characterized by intermittent landlocking. The present results show that a large estuary may also provide the opportunity for successful spawning of pelagic eggs.

Resumen. La mayoría de los peces que aprovechan la alta productividad de los estuarios efectúan sus desoves en el océano, producen gran cantidad de pequeños huevos pelágicos, y se reclutan a los estuarios como larvas o juveniles. El patrón reproductivo de *Micropogonias furnieri* (un desovante de huevos planctónicos) en el Río de la Plata (36°S,56°W), resulta diferente. Muestreos biológicos y datos oceanográficos demuestran que su área de desove cubre una estrecha franja a través del río, entre Montevideo (34°50′S,56°10′W) y Punta Piedras (35°25′S,57°10′W), en profundidades de 6 a 8 m. Esta área se caracteriza por fuertes haloclinas, de hasta 21.5 unidades m^{-1}. Los huevos de *M. furnieri* se encuentran sólo debajo de la haloclina, en salinidades de 9.7 a 27.3, y temperaturas de 18.5° a 20.2°C. El desove tiene lugar en la parte más interna del estuario, cerca del límite río arriba de la cuña salina, y en coincidencia con el máximo de turbidez (hasta 150 mg L^{-1}). En estuarios del sur de Africa y Australia, caracterizados por el cierre intermitente de su boca, ha sido reportado el desove regular de huevos planctónicos. Nuestros resultados demuestran que un gran estuario también puede proveer la oportunidad para el desove exitoso de huevos planctónicos.

Extra keywords: teleosts, reproduction, eggs, life-cycle closure, oceanographic structure

Introduction

Estuaries are one of the most productive ecosystems of the world, and several fish species have evolved life histories to take advantage of their high primary and secondary productivity (Day *et al.* 1989). Most fishes in estuarine communities are juveniles, and estuaries are often nursery grounds for fishes (Haedrich 1992). Their most common nekton life-history cycle involves offshore spawning with the production of a large number of small pelagic eggs, and recruitment to estuaries as larvae or juveniles (Lawler *et al.* 1988; Day *et al.* 1989).

The estuarine species, together with a few marine and freshwater species which enter estuaries to spawn, show various adaptations to spawning under estuarine conditions (Dando 1984). Because of the net seaward movement of estuarine waters, export of early life-history stages from the estuaries seems to be a major problem for estuarine spawners (Boehlert and Mundy 1988). Several species prevent export by producing large demersal eggs (Hempel 1979; Dando 1984), such as those spawned by atherinids and gobies. They are usually adhesive nonbuoyant eggs which cling to vegetation or rocks (Day *et al.* 1989; Haedrich 1992). Several species of external bearers like catfishes (mouth

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brooders) or pipefishes (pouch brooders), are also successful estuarine breeders, probably because this reproductive style prevents seaward drift. Excluding the resident species, there are not many fishes that actually spawn in estuaries, and most of them are small species (with relatively short life-spans). Their small size may reduce their physical ability to undertake migrations to and from the sea (Whitfield 1990; Haedrich 1992).

Estuarine fish faunas are dominated by relatively few forms, most of them having marine heritage (Haedrich 1992). Sciaenidae is an important Family in temperate and tropical American estuaries (Day *et al.* 1989; Haedrich 1992). Seven species belonging to this Family have been reported inhabiting the bottom waters of the Río de la Plata estuary (36°S,56°W) (Cousseau 1985): *Micropogonias furnieri*, *Cynoscion guatucupa*, *Macrodon ancylodon*, *Pogonias cromis*, *Menticirrhus americanus*, *Paralonchurus brasiliensis* and *Umbrina canosai*. The whitemouth croaker (*M. furnieri*) is the dominant species in terms of biomass, and it supports an important fishery in Uruguay and Argentina (Lasta and Acha 1996). This species is a multiple spawner (Vazzoler 1970, 1971; Macchi and Christiansen 1992) with small pelagic eggs (730–1053 μm, Weiss 1981) and a long life-span (39 years in Uruguayan and Argentine waters, Cotrina and Carozza 1997). Spawning takes place from November to April in the inner zone of the Río de la Plata estuary, in coincidence with the bottom salinity front (Macchi and Christiansen 1996). In the rest of the estuary, the individuals remain in the partially spent stage, moving afterwards to the inner sector where they complete maturation and spawn (Macchi *et al.* 1996). This reproductive pattern disagrees with the general observations and theoretical framework summarized above. However, it is similar to that in several south-western Australian and southern African estuaries, where many fishes breed within the estuaries, contrasting markedly with the temperate estuaries of the Northern Hemisphere (Potter *et al.* 1990) on which the main concepts of estuarine ecology are largely based.

The main objective of this study was to gain insight into the spawning site selection and spawning habitat requirements of the whitemouth croaker at the Río de la Plata estuary. Macchi *et al*. (1996) found a concentration of females with hydrated oocytes and new post-ovulatory follicles in the bottom salinity front, but no ichthyoplankton was sampled. Particular objectives of the present study were to locate and identify spawning aggregations by macroscopic examination of adult specimens, to verify spawning by collecting eggs, and to characterize spawning sites in terms of physical variables. The release of planktonic eggs into the estuary by a relatively large species with a long life-span is discussed in the light of the general theories on fish reproduction and estuarine ecology.

Materials and methods

Environmental information, biological data and specimens were obtained during a cruise performed in the Río de la Plata estuary from 13 to 24 November 1995.

Oceanographic sampling was performed with a Sea-Bird 19 CTD (conductivity–temperature–depth profiler), with a sampling rate of 2 scans per second and a lowering speed of 0.5 m s^{-1}. Data were processed to achieve a 1 m vertical resolution (precision of ± 0.03°C in temperature and ± 0.05 units in salinity). Salinity is reported as dimensionless values, following the Practical Salinity Scale (Anon. 1981).

Ichthyoplankton was collected in a Nackthai sampler (Nellen and Hempel 1969) having a single net with a 405 μm mesh aperture. It was equipped with a digital flowmeter and was operated with oblique tows, at 3–4 knots. Sampling depth was estimated from measurements taken with an angle indicator (inclinometer) and a wheelout meter. Volumes filtered during a tow varied from 7.0 to 35.8 m^3. The plankton samples were sorted and analysed immediately on board, in a search for whitemouth croaker eggs; these were identified on the basis of the descriptions by Weiss (1981). Collected materials were then preserved in 2% buffered formaldehyde.

Adult specimens were caught with a bottom trawl (200 mm mesh in the wings and 102 mm at the cod ends; vertical opening 4 m, horizontal aperture 15 m) operating at 4 knots and for 15 min at each station. The specimens were staged according to a macroscopic maturity scale of 5 levels adapted from Macchi and Díaz de Astarloa (1996).

A sample was taken at each of 40 stations covering the whole estuary to find females with hydrated oocytes and eggs in the plankton and relate them with the bottom salinity field. On the basis of the data from these stations, three high-resolution transects were sampled (20 samples) to ascertain the limits of the spawning area. To study vertical distribution of croaker eggs, two plankton tows were performed at each of five stations in the spawning area, separately sampling the surface and the bottom layers defined by the halocline.

The concentration of suspended sediment was estimated at 41 stations in order to detect the turbidity maximum. One litre of surface water was filtered through a previously weighed cellulose acetate filter of 0.45 μm pore size, then the matter retained after drying the filter at 105°C for 10 h was weighed. Data obtained were mapped as contour lines.

Results

Environmental conditions at the estuary during the cruise

Surface salinity varied from 0 upstream of Punta Tigre (Uruguay) and Punta Piedras (Argentina), to over 32 east of Montevideo and near Punta del Este (Fig. 1*A*). The isohalines show a north–south orientation, non-parallel to the river mouth. The salinity front is defined between the 5 and 27.5 isohalines. The Uruguayan coast is more saline and with a higher horizontal gradient than the Argentine coast. Diluted waters, with salinity values lower than 25, extend southward on the Argentine coast. At the bottom, salty waters show a greater upriver penetration than at the surface (Fig. 1*B*). A strong salinity front was detected between Punta Tigre and Punta Piedras, defined by the 0 and the 20 isohalines. As at the surface, the highest horizontal gradient is on the Uruguayan coast, and the diluted waters (<32.5) extend southwards along the Argentine coast.

Surface temperature ranged between 16° and 20°C, with the highest values at the innermost part of the estuary (Fig . 2*A*). Waters become cooler seaward, reaching 16°C near Punta del Este, showing penetration of shelf water at the surface level.

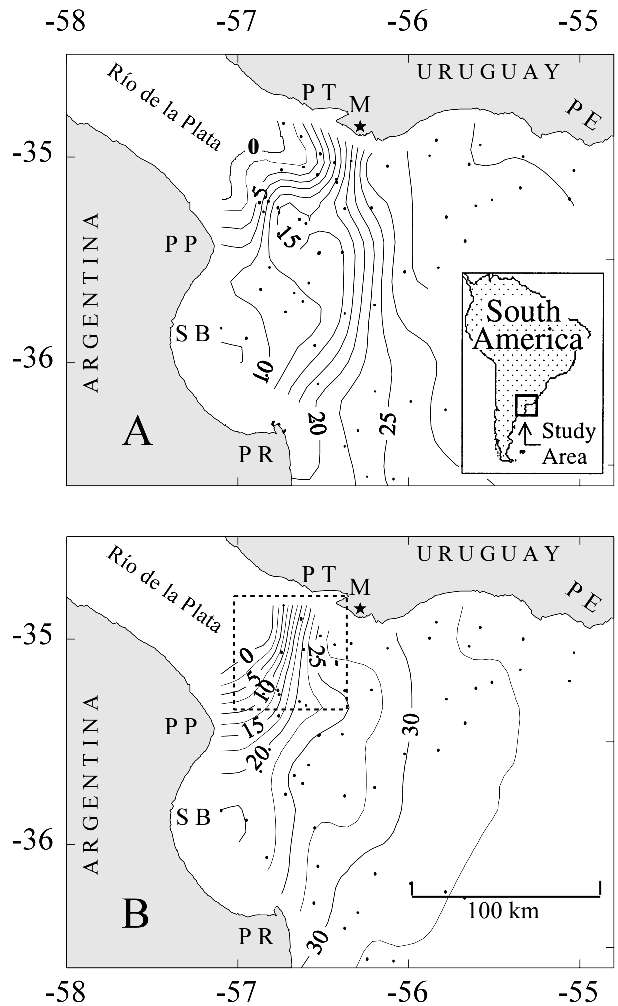

Fig. 1. Salinity distribution for *(A)* surface and *(B)* bottom layers during November 1995. Dots indicate stations. Insert in *(A)*: study area. Stations presented in Table 1 are within the square in *(B)*. M, Montevideo; PE, Punta del Este; PP, Punta Piedras; PR, Punta Rasa; PT, Punta Tigre; SB, Samborombón Bay.

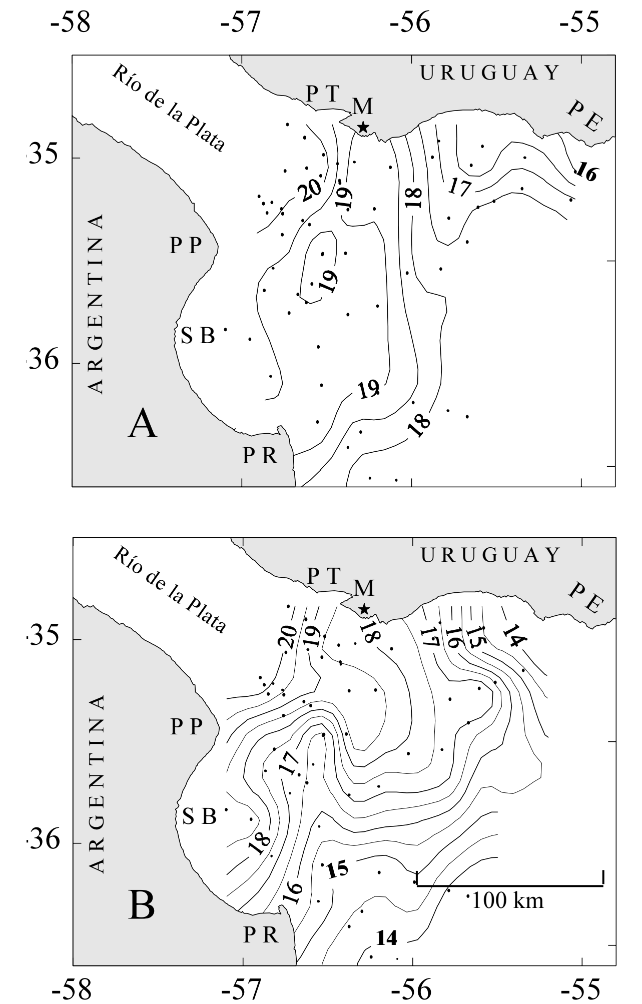

Fig. 2. Temperature distribution for *(A)* surface and *(B)* bottom layers during November 1995. Dots indicate stations. Abbreviations as in Fig. 1.

Bottom waters are cooler than surface waters (Fig. 2*B*), ranging between 14° and 20°C. Surface–bottom thermal differences increase towards the outer zone of the estuary.

An area of steep horizontal gradient of suspended sediment, bounded by the 20 and 60 mg L^{-1} isolines, lies between Punta Tigre and Punta Piedras in depths from 6 to 8 m (Fig. 3); this is assumed to be the turbidity front, although confirmation would require additional sampling further upstream. In the rest of the estuary the values are between 20 and 10 mg L^{-1}, and at the mouth of Samborombón Bay the values are <10 mg L^{-1}.

Location of the spawning area

The spatial distribution of croaker females with hydrated oocytes was somewhat upriver of the concentrations of eggs in the plankton (Fig. 4), and both clearly show the position of the spawning area; this covers a narrow band across the river, between Montevideo and Punta Piedras, at depths ranging from 6 to 8 m. This area is characterized by strong haloclines. Table 1 summarizes oceanographic and biological data for the stations where reproductive activity was detected.

The three high-resolution transects (one of them shown in Fig. 5*A*) were used to define the limits of the spawning area on the basis of the presence of croaker eggs and of females with hydrated oocytes. Figure 5*C* shows a typical picture of the salt wedge at the Río de la Plata estuary, with a fresher water layer overlying a saline bottom one. The presence of females with hydrated oocytes and of eggs in the plankton (Fig. 5*B*) shows that the spawning occurs near the place where the halocline intersects the bottom (the bottom salinity front), in the innermost part of the estuary. This small portion of the wedge ranged from 8 to 20 km for the three transects.

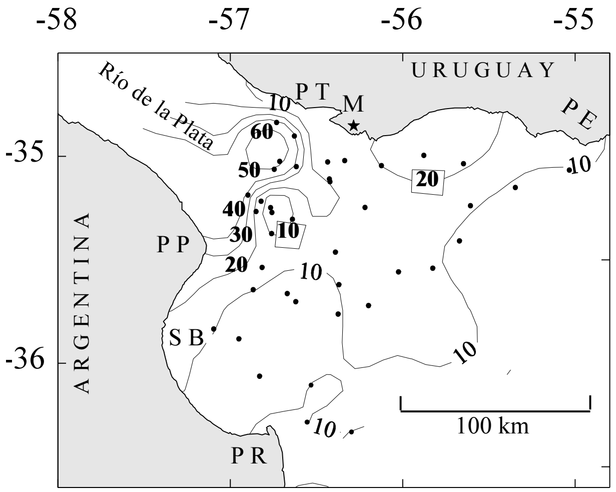

Fig. 3. Suspended sediment distribution for the surface layer during November 1995. Dots indicate stations. Abbreviations as in Fig. 1.

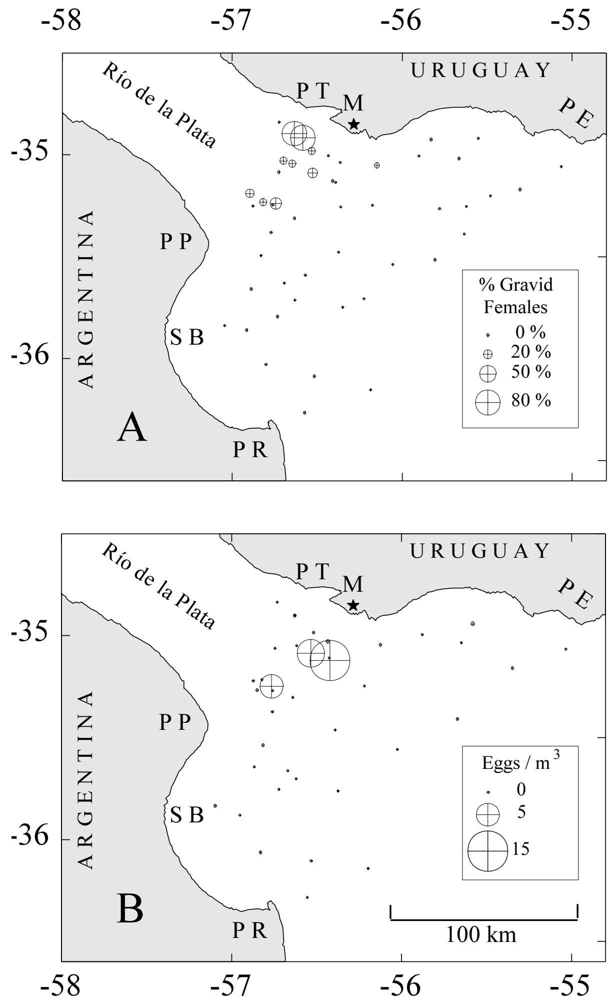

Fig. 4. Spatial distribution of females with hydrated oocytes, and eggs of whitemouth croaker during November 1995. Symbol size is proportional *(A)* to the percentage of gravid females and *(B)* to the eggs concentration. Abbreviations as in Fig. 1.

No *M. furnieri* eggs were detected in the fresher layer above the halocline; they were present only in the water layer below the halocline, in a salinity range from 9.7 to 27.3, and in a thermal range of 18.5° to 20.2°C (Table 1). The depth of this lower layer (measured from the halocline to the bottom) was equal to 3 m or less. No fish eggs were collected in the upper fresher layer, where the physical variables were in the range of 0.7–10.8 for salinity and 19.7–21.7°C for temperature. Strong haloclines of up to 21.5 units m^{-1} were recorded. Thermal stratification was weak and the vertical density field was controlled by salinity.

Discussion

Oceanographic conditions during the cruise were close to the recorded means for spring–summer (Guerrero *et al.* 1997*a*) and may be considered typical for the estuary. The presence of a salt wedge here is a quasi-permanent feature; it is formed between the halocline and the rising bottom, and its upstream reach (the bottom or basal front) is controlled by the topography. The mean position of this bottom salinity front coincides with a shallow area across the river, in the line Punta Piedras–Montevideo, named Barra del Indio.

The turbidity maximum is a region of locally elevated suspended matter concentrations, which over long-term time scales occur near the bottom salinity front in estuaries (Geyer 1993; Framiñan and Brown 1996). Location of the turbidity front during the cruise (Fig. 3) fits well with the mean spatial pattern based on a 4-year span of daily NOAA-AVHRR satellite images (Framiñan and Brown 1996).

Histological studies of adult females (Macchi *et al.* 1996) have shown that the whitemouth croaker spawns in coincidence with the bottom salinity front, and that in the rest of the estuary the individuals remain in the partially spent stage, moving afterwards to the inner sector where they mature and spawn. The addition of studies of egg distribution in the present study has confirmed that the spawning of the whitemouth croaker occurs in estuarine waters, in correspondence with the turbidity and bottom salinity fronts. This spawning area is also close to the main nursery grounds for this species, which are in Samborombón Bay (Argentine coast) (Lasta 1995), and between Punta Tigre and Montevideo (Uruguayan coast) (Puig and Fontenla 1993; Pin *et al.* 1997).

Along the wide latitudinal distribution of this species (20°N to 41°S, Isaac 1988), its larvae and juveniles have been reported in estuarine waters of several regions (Lowe-McConnell 1966; Sinque 1980; Weiss 1981; Lasta and Ciechomski 1988; Lasta 1995), but information on its spawning habitat is scarce. In the Patos Lagoon (32°S, Brazil), the eggs and larvae enter the estuary with salt water intrusions (Weiss 1981; Sinque and Muelbert 1997), and it is

Table 1. Oceanographic and biological data at the stations where reproductive activity of *Micropogonias furnieri* was detected
St, sampling station; MVSG, maximum vertical salinity gradient (units per meter); Zh, halocline depth; Zt, total depth; ST, surface temperature (ºC); BT, bottom temperature; SS, surface salinity; BS, bottom salinity; NtF, total no. adult females; %HF, percentage of hydrated females; nd, no data. Number of adults refers to 15 min tows. †Egg densities below the halocline, where plankton tows at different levels were performed. All stations were within the square inserted in Fig. 1*B*

St	MVSG	Zh	Zt	ST	BT	SS	BS	Eggs m^{-3}	NtF	%HF	Longitude	W Latitude S
868	4.66	5.5	6	19.84	18.97	4.66	13.21	0	19	31.58	56°46′	35°16′
906	8.96	5.5	6	19.74	19.14	8.55	17.96	0	36	80.56	56°38′	34°54′
910	21.47	3.5	6	21.72	18.82	0.74	23.31	0	34	17.65	56°37′	35°03′
911	17.52	4	6	20.31	18.52	6.45	27.27	5.1	27	25.93	56°32′	35°05′
912	8.19	4	6	20.10	18.59	10.82	28.56	14.8	28	0.00	56°25′	35°07′
914	0.09	6.5	6.5	20.92	20.93	3.24	3.28	n.d.	23	21.74	56°54′	35°11′
922	1.80	5.5	7	20.78	20.23	4.46	9.69	297.0	28	0.00	56°43′	34°51′
925	12.85	6.5	7	20.41	18.53	5.56	23.59	133.0†	n.d.	n.d.	56°40′	34°52′
927	9.44	5.25	7	20.24	19.17	2.38	17.63	17.9†	n.d.	n.d.	56°43′	34°52′
928	13.03	5.75	6	20.49	19.64	1.77	13.13	n.d.	27	40.74	56°41′	34°53′
929	13.70	4.75	6	20.29	18.85	2.62	20.87	24.1†	n.d.	n.d.	56°40′	34°54′
932	19.46	5.75	7	21.41	18.77	1.82	21.87	2.0†	10	100.00	56°40′	34°53′
935	14.83	5.75	7	21.20	18.46	2.99	25.22	10.9†	n.d.	n.d.	56°36′	34°53′
937	15.17	4	7	20.84	18.99	1.69	19.16	158.9	n.d.	n.d.	56°38′	34°54′

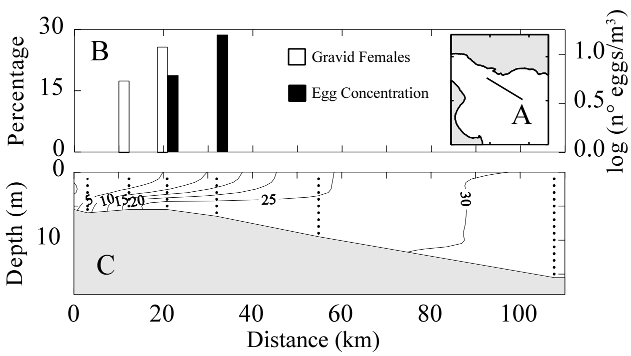

Fig. 5. Sections showing the location of the spawning area and the salt wedge during November 1995. *(A)* Location of the transect, *(B)* females with hydrated oocytes and planktonic eggs, and *(C)* distribution of salinity.

believed that adults spawn in adjacent waters, or in the mouth of the lagoon when salinity is high (Weiss 1981; Castello 1986; Vieira and Castello 1997). Direct evidence of spawning in estuarine waters has never been reported for the whitemouth croaker except in the Río de la Plata estuary. Moreover, the present results show that the spawning does not occur in the whole estuary, but in a specific region: the maximum upriver penetration of the salt wedge. This area is the ecotone between the estuary and the riverine fresh water.

There is no information on the temperature conditions for spawning of whitemouth croaker in other regions. The thermal range of the spawning area in the Río de la Plata estuary during November was 18.5° to 20.2°C, but taking into account that the reproductive season extends from November to April (Macchi and Christiansen 1996), spawning activity may take place in a broader thermal range of about 16° to 26.8°C (see Guerrero *et al.* 1997*b*). Although the distribution of *M. furnieri* reaches 41°S, reproductive activity has not been reported south of the Río de la Plata estuary. However, given the presence of juveniles in shallow waters along the coast, up to Bahía Blanca (López-Cazorla 1987) about 600 km south of the Río de la Plata estuary, some minor spawning grounds may exist, indicating that the species is able to spawn in areas with temperatures lower than those reported here.

Spawning of other Sciaenidae in the Northern Hemisphere seems to occur mainly outside the estuaries, e.g. *Cynoscion arenarius* (Shlossman and Chittenden 1981), *Leiostomus xanthurus* (Heitler and Powell 1981), *Micropogonias undulatus* (Heitler and Powell 1981; Warlen 1982), *Sciaenops ocellatus* (Holt *et al.* 1985; Peters and McMichael 1987), *Pogonias cromis* (Silverman 1979; Saucier and Baltz 1993) and *Menticirrhus* sp. (Holt *et al.* 1985). However, in some cases reproductive activities have been reported in estuarine environments, within bays and lagoons near passes to the sea (e.g. *Cynoscion nebulosus* (Holt *et al.* 1985; Saucier and Baltz 1993), *Cynoscion arenarius* (Copeland and Bechtel 1974), and *Pogonias cromis* (Thomas and Smith 1973)). Sciaenid fishes have in general high environmental tolerance, and probably some members of this Family have the potential for estuarine spawning. However, the eventual spawning site depends on the characteristics of the environment.

Some distinctive characteristics of the reproductive area of *M. furnieri* in the Río de la Plata estuary may be useful in understanding its selection of a spawning site. As a result of the confluence of the riverine and estuarine waters, a convergent flow on the bottom can be expected at the head of the salt

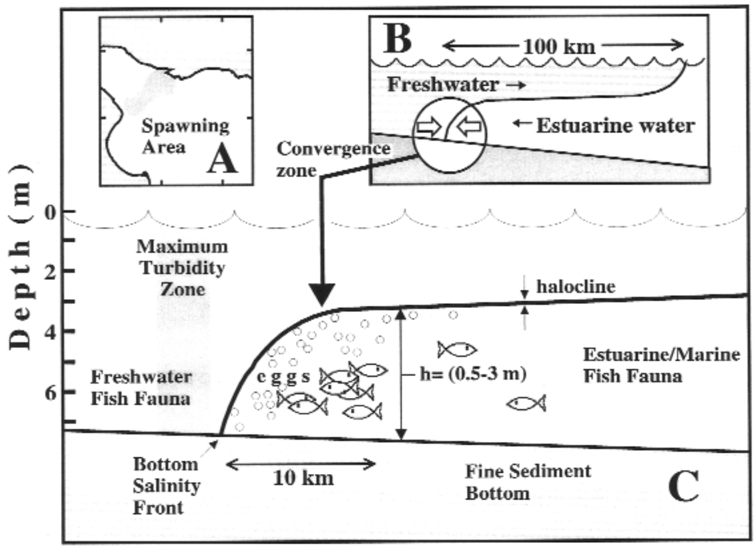

Fig. 6. Conceptual diagram of the spawning of the whitemouth croaker in the estuary of the Río de la Plata. *(A)* Horizontal view. *(B)* Section showing the presumed spawning place in the salt wedge of the estuary. *(C)* Magnified portion of the maximum upriver penetration of the salt wedge, showing the spawning site, the vertical location of the eggs and some important hydrographic and biological characteristics. In *(B)* and *(C)* the vertical scale is considerably exaggerated.

wedge intrusion (Largier 1993). The eggs spawned here would be retained near the frontal interface, minimizing their drift, thereby solving a major problem of estuarine spawners, namely the export of early life-history stages from the estuary.

Moreover, the existence of spatially stable larval retention areas may ensure coupling of mates in a particular geographical space, providing the opportunity for life-cycle closure (Sinclair and Iles 1989). The bottom salinity front in the Río de la Plata estuary is geographically stable for periods of months (Guerrero *et al.* 1997*a*). Consequently, the early life-history stages of *M. furnieri* would be retained in the estuary by an interaction between the behavioural characteristics of the species (homing to the head of the salt wedge to spawn), and the specific hydrodynamics of the salt wedge (upriver flow on the bottom and convergence at its maximum landward penetration).

Another important characteristic of the *M. furnieri* spawning area is the vertical structure of the water column. Strong haloclines have been reported by Guerrero *et al.* (1997*a*) in this estuary, reaching 15.8 units m^{-1}. In those stations where planktonic eggs and hydrated females were caught in the present study, the maximum vertical salinity gradients measured ranged between 0.09 and 21.5 units m^{-1}. Given that protein (the main substance in fish eggs) has a considerably higher specific gravity than fresh water (Hempel 1979), whitemouth croaker eggs would be too dense to float in the lighter freshwater layer above the halocline, thus restricting their vertical distribution to the bottom saline layer. As the fresh water flows to the sea, deeper salt water mixes with it and it becomes more saline. The more-saline water in the bottom layer moves landward (Day *et al.* 1989); the eggs are released at the head of the salt wedge, and they would thus be retained at the convergence zone.

Some ‘energetic’ processes (*sensu* Sinclair and Iles 1989) may also be related to the bottom salinity front as a spawning area. As a result of the convergence of the two water masses, a high concentration of food particles is expected, providing particularly favourable conditions for fish larvae. Moreover, high turbidity in the vicinity of the landward end of the seawater intrusion would probably diminish interspecific (but also intraspecific) predation on eggs and larvae, by reducing visibility to predators, such as has been proposed for juvenile fishes in South African estuaries (Cyrus and Blaber 1987). As fish larvae are predominantly visual feeders (Hunter 1981), high turbidity may also affect the catching capability of the larvae. However, it must be considered that the effects of turbidity on foraging ability may be a matter of scale of perception. The effect would be greatest for juvenile and adult fish which perceive and attack their prey at relatively large distances compared with larvae (Chesney 1989). Thus, high turbidity may reduce predation on fish larvae with few effects on their foraging ability.

Figure 6 presents a conceptual diagram of the whitemouth croaker spawning area in the Río de la Plata estuary. Spawning appears to take place close to the bottom, in a thin layer of saline water separated from the upper fresher layer by a strong halocline (pycnocline); an echosounder showed whitemouth croaker close to the bottom in all cruises, including the occasions when spawning individuals were caught. However, even though the salt wedge and the turbidity front are not features exclusive to the Río de la Plata estuary, spawning of pelagic fish eggs is rare in most estuaries. Moreover, *M. furnieri* has never been reported as an estuarine spawner in other estuaries, e.g. Patos Lagoon (Weiss 1981; Vieira and Castello 1997) or Cananéia Lagoon (Sinque 1980). The reasons for this reproductive pattern may be addressed only in general terms from our data. The distinctive feature of the Río de la Plata estuary is its large size. The distance from the spawning area to the offshore limit of the salt wedge may be up to 250 km (Guerrero *et al.* 1997*b*). Although retention of eggs and larvae in the convergence zone may not be complete and the net nontidal flows may drive them seaward, larvae have probably enough time to develop into the stage where they become able to control their vertical position in the water column. Then, behavioural traits would allow *M. furnieri* larvae to take advantage of the two-layered circulation pattern characteristic of stratified estuaries, as has been proposed for *Micropogonias undulatus* (Weinstein *et al.* 1980). If this is the case, the estuary as a whole could be considered as a retention area. Information on *M. furnieri* larvae is scarce for this region, and the early developmental stages of the species have solely been recorded within the estuary: at Samborombón Bay (Lasta and Ciechomski 1988) or near Montevideo and Punta Piedras (Acha, Mianzan, Lasta and Guerrero, unpublished). Larvae or early juveniles of *M. furnieri* have never been recorded in the coastal waters outside the estuary.

Our results suggest that the reproductive success of *M. furnieri* may be linked to the vertical structure of the water column. The salt wedge can be broken by wind-induced vertical mixing (Guerrero *et al.* 1997*a*). Synoptic winds stronger than 10 m s^{-1} and blowing longer than 12 h generate a homogeneous layer of average salinity. Restoration of the salt wedge is forced on by the strong horizontal pressure gradients due to the density differences between shelf waters, the wind-mixed estuarine waters, and the newly added fresh water (Guerrero *et al.* 1997*a*). Thus, during such unfavourable mixing events eggs and larvae are exposed to lower salinity and are probably advected from the estuary with mixed estuarine waters. There are indeed frequent meteorological events in this area, characterized by strong winds over 13 m s^{-1} from the south-east (Balay 1961). These events have a characteristic duration of 1–3 (occasionally 5) days and occur throughout the year, the strongest usually being from May to October (Anon. 1995). Thus, although some cohorts of eggs may be lost because of these disruptive events, the prolonged reproductive season of the whitemouth croaker, from November to April (Macchi and Christiansen 1996), may ensure survival of enough eggs to maintain the species in this unpredictable environment.

Major reviews of the role of estuaries for fishes (e.g. Day *et al.* 1989; Haedrich 1992) are largely based on teleosts in the Northern Hemisphere, stating that spawning of pelagic eggs within estuaries is an unusual episode. However, in estuaries of temperate Western Australia (Potter *et al.* 1990, 1994) and southern Africa (Potter *et al.* 1990; Connell 1996) spawning of pelagic eggs is a frequent event, which is perceived as an adaptation to the periodical landlocking of these estuaries (Potter *et al.* 1990, 1994). There, the small tidal range and low freshwater discharge during the spawning season minimizes the loss of eggs and larvae when the estuary is open (Potter *et al.* 1994). Our results show that a large-scale estuary, with high freshwater discharge and a broad and permanent connection to the sea, as in the Río de la Plata estuary, also provides the opportunity for successful spawning of pelagic eggs. Behavioural traits of adults (spawning at the bottom salinity front) and larvae (taking advantage of the two-layered circulation) appear to play a decisive role in the establishment of the reproductive grounds in estuarine waters. Consequently, the generally accepted statement that spawning of pelagic eggs is unusual in estuaries will need further revision.

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