

Abstract.—Brazilian menhaden, *Brevoortia aurea*, is the only species of the genus *Brevoortia* in South American Atlantic waters and is abundant in the Río de la Plata estuary. We found that *B. aurea* in this area spawns almost exclusively in this estuary. We studied the temporal and spatial reproductive pattern of this menhaden and related the pattern to the major hydrographic features of the region. We based evidence of spawning activity on the presence of females with hydrated oocytes and on the occurrence of menhaden eggs in plankton samples. Our results show that *B. aurea* spawn during virtually every month of the year, but that they spawn mainly from September (late winter) to January (early summer). In the Río de la Plata estuary, spawned eggs occur in a thermohaline range of 13–23°C and 10–25 psu, mainly in stratified waters. *Brevoortia aurea* spawn very near the bottom salinity front, probably in a convergent flow between the riverine and estuarine waters that helps to retain eggs. In contrast to menhaden of the northern hemisphere (*B. tyrannus* and *B. patronus*), which spawn offshore and which drift during early life history stages, *Brevoortia aurea* in the Río de la Plata estuary are spawned and held in estuarine waters near spawning sites. The latter reproductive pattern is also shared by *Micropogonias furnieri* (whitemouth croaker), the most abundant fish species in the area.

Spawning of Brazilian menhaden, *Brevoortia aurea*, in the Río de la Plata estuary off Argentina and Uruguay*

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The Río de la Plata drains the second largest basin of South America. It flows into the Atlantic Ocean with an average discharge of 22,000 m³/s, generating a large estuary of about 35,000 km² and 5–15 m in depth, located at 36°S, 56°W (Framiñan and Brown, 1996). Brazilian menhaden, *Brevoortia aurea*, is abundant in this estuary (Cousseau, 1985; Boschi, 1988); it also inhabits coastal and estuarine environments from 13°S (Brazil) to 40°S (Argentina). Historically, two species of menhaden were thought to inhabit Brazilian–Argentine waters (de Ciechomski, 1968; Weiss et al., 1976; Weiss and Krugg, 1977; Whitehead, 1985; Lasta and de Ciechomski, 1988); however, Cousseau and Díaz de Astarloa (1993) concluded that *B. aurea* is the only species that inhabits South American Atlantic waters.

Little is known about the reproductive biology of *B. aurea*. De Ciechomski (1968) described eggs and early larval stages of *B. aurea* and reported a period of 86–88 hours from the time of spawning to hatching at 13–14°C. Spawning has been detected in the Río de la Plata estuary (Lasta

and de Ciechomski, 1988). Although their planktonic eggs also have been found in inshore waters along the Uruguayan and Argentine coasts (de Ciechomski, 1968; Hubold and Ehrlich, 1981; Cassia and Booman, 1985; Sánchez and de Ciechomski, 1995), Samborombón Bay (a shallow area inside the estuary) seems to be the locus of intensive spawning, where *B. aurea* eggs are exposed to low salinities (5–15 psu) (Lasta and de Ciechomski, 1988). Estuarine spawning by species producing pelagic eggs is uncommon (Dando, 1984; Haedrich, 1992; Potter et al., 1993); however no attempts have been made to describe the basic spawning habitat requirements of *B. aurea*. Furthermore, in the Río de la Plata, *Micropogonias furnieri*, the species with the largest biomass, releases pelagic eggs in the inner zone of the estuary (Macchi et al., 1996; Acha et al., 1999).

The life cycles of Northern Hemisphere menhaden, mainly *Brevoortia tyrannus* and *Brevoortia pat-*

ronus (the Atlantic and gulf menhaden, respectively) are well understood. Both species are typical representatives of estuarine dependent species that spawn in the marine environment (Lawler et al., 1988; Day et al., 1989) in contrast to the Brazilian menhaden, which spawns in an estuarine environment.

Since 1983 the coastal resources of the Argentine–Uruguayan Common Fishing Zone have been monitored by a number of cruises, and results pertaining to menhaden form the basis for this paper. Our objectives were to describe the timing and spatial occurrence of spawning in relation to the major hydrographic features of the region in order to gain insight into the spawning habitat requirements of the Brazilian menhaden. Whenever possible, comparative analyses with other species of the estuary and menhaden of the Northern Hemisphere were performed.

Materials and methods

Samples from 47 cruises from 1983 through 1998 were analyzed in our study. Twenty-two of these cruises were on research vessels of the National Institute for Fisheries Research and Development (INIDEP), covering the Río de la Plata estuary and adjacent coastal waters, throughout which stations were randomly distributed. Twenty-five cruises took place in Samborombón Bay, on small fishing boats using a systematic sampling design. Monthly distribution of the sampling effort is shown in the insert of Figure 1. During 1983 and 1987, nineteen cruises in Samborombón Bay were performed every 30–45 days during the entire year. The remaining six cruises in this bay correspond only to spring months (October, November, and December). Cruises were made with several objectives, hence covering different periods, but sampling effort was higher in spring (October–November) when cruises for stock assessment were performed. The high number of plankton samples in May was due mainly to one cruise, designed to study physical variables and plankton in the estuary. Cruises on the small boats and on the research vessels were not simultaneous. All data were employed as a composite representing mean conditions.

Plankton was collected at 980 sampling stations by oblique tows of 60-cm bongo nets, 20-cm bongo nets, or a Nackthai sampler (a modified Gulf V high-speed plankton net, see Nellen and Hempel, 1969). All nets were equipped with flowmeters. The volume filtered in each tow ranged from 10 to 400 m³. Sampling depth was estimated from measurements taken with an angle indicator (inclinometer) and a wheelout meter. All samples were preserved in 5% buffered formalin. Plankton samples were sorted and ana-

lyzed in the laboratory. *Brevoortia aurea* eggs were identified following the description of de Ciechomski (1968).

Estimates of egg density from the different samplers were not intercalibrated. They were arranged into four broad density classes (<10, 10 to 99, 100 to 999, ≥1000 eggs/m³), and marked on a map to delineate the geographic location of the spawning area. Monthly distribution of the average number of eggs per tow (catch per unit of effort, CPUE) and the percentage of positive stations for menhaden eggs were plotted to identify the spawning season. Stations with no catch were included in the CPUE estimates.

Data from the November 1995 cruise were useful for gaining insight into the vertical distribution of menhaden eggs. During that cruise, plankton was sampled at five stations in a small area near Montevideo, where schools of spawning *B. aurea* were previously detected. In each of those stations, two tows were conducted with the Nackthai net, one to sample the surface and the other to sample the bottom layers as defined by a strong halocline. The depth of the halocline was previously measured with a conductivity-temperature-depth (CTD) profiler.

On all cruises, menhaden were collected with bottom trawls, and the presence of females with hydrated oocytes (macroscopic examination) was considered evidence of imminent spawning. The percentage of females with hydrated oocytes for each tow was also indicated on the map to identify the location of the spawning area. In addition, the mean monthly percentage of females with hydrated oocytes was used to determine the spawning season.

Temperature and salinity information was taken from the oceanographic database created by Guerrero et al. (1997a), which included all the CTD stations sampled during the cruises that we performed. Bottom salinity and temperature data for spring–summer were used because they could be matched to the vertical distribution of the eggs and the main reproductive period. Salinity is expressed as psu (practical salinity units; Anonymous, 1981). Horizontal and vertical salinity contour lines were made to compare the spawning area with the salinity field. Egg density was plotted into a temperature-salinity diagram to show the environmental ranges of the spawning habitat of the Brazilian menhaden.

Results

Eggs in the plankton

Brazilian menhaden eggs were detected virtually all year round (Fig. 1). The highest CPUE occurred from

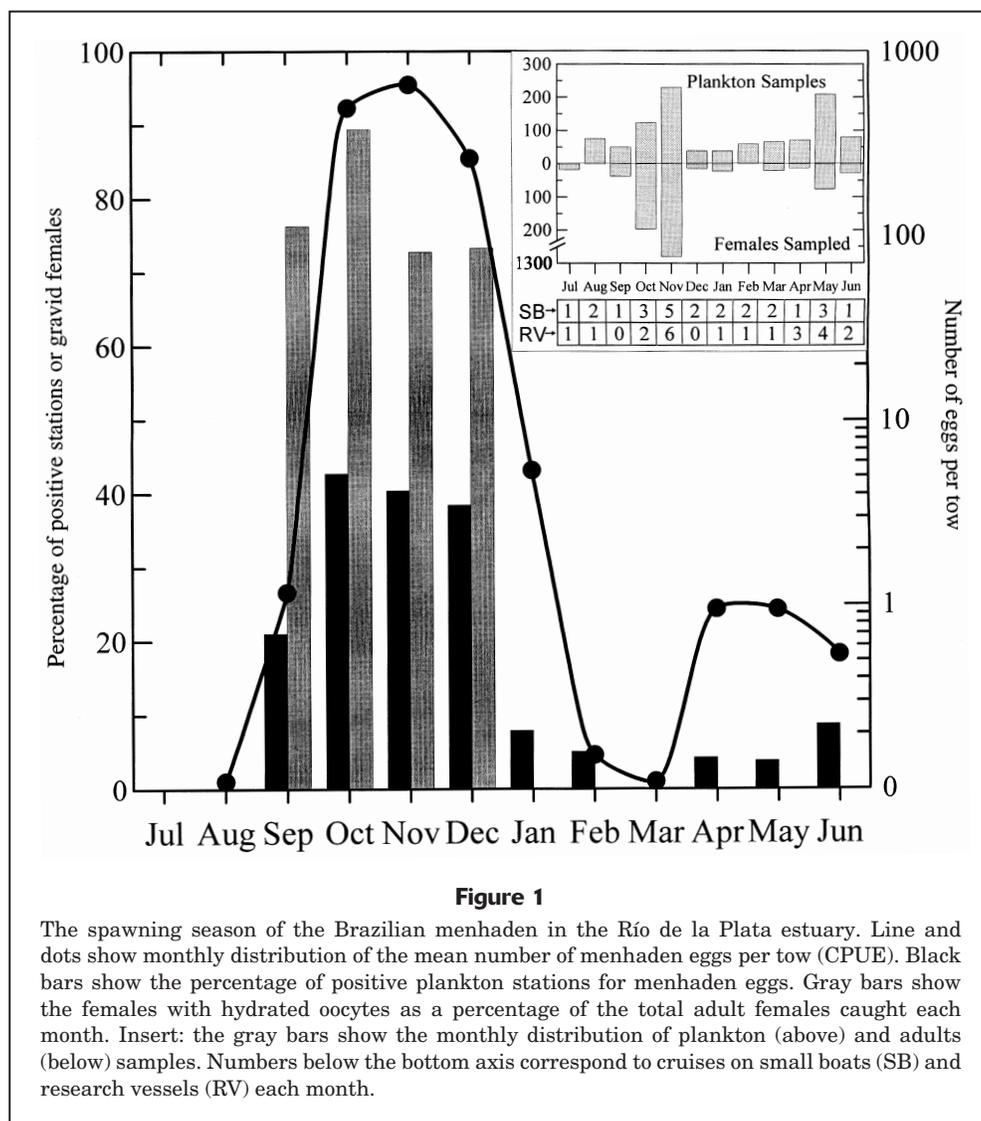


Figure 1

The spawning season of the Brazilian menhaden in the Río de la Plata estuary. Line and dots show monthly distribution of the mean number of menhaden eggs per tow (CPUE). Black bars show the percentage of positive plankton stations for menhaden eggs. Gray bars show the females with hydrated oocytes as a percentage of the total adult females caught each month. Inset: the gray bars show the monthly distribution of plankton (above) and adults (below) samples. Numbers below the bottom axis correspond to cruises on small boats (SB) and research vessels (RV) each month.

September through January and diminished during late summer, followed by a secondary peak during the fall (April–June). The percentage of positive stations for menhaden eggs had a similar pattern to that of the CPUE. There was no plankton sampling in July.

Menhaden eggs were identified in 220 samples that represented 22.5% of all samples analyzed. The eggs were found mainly in estuarine waters (Fig. 2A), especially at depths <10 m. Highest densities of eggs were found in Samborombón Bay and west of Montevideo in the innermost part of the estuary, where salinity values ranged between 10 and 20 psu. Medium egg densities were found along the Uruguayan coast between Montevideo and Atlántida (55°45'W) and in the middle area of the river between Montevideo and Punta Piedras. Lowest densities (<10 eggs/m³) were present in the rest of the estuary and adjacent coastal waters.

The study area (5 stations) of the vertical distribution of *B. aurea* eggs is shown by an arrow in Figure 2A. Total depth in this area was 6.5–7.5 m and halocline depth was 4.8–6.5 m. Menhaden eggs were present in the water layer below the halocline but were extremely scarce in the upper layer. In the bottom layer, egg density ranged from 50–2100 eggs/m³. Eggs were found within a thermohaline range of 9.7–27.3 psu and 18.5–20.2°C. The upper layer was less saline (0.7–10.8 psu) and warmer (19.7–21.7°C). Strong haloclines up to 21.5 psu/m were observed. Figure 3 shows the vertical distribution of salinity and *B. aurea* eggs along a transect in the estuary. This transect includes four of the five plankton stations sampled above and below the halocline. Menhaden eggs were detected in the region where the salt wedge intersects the bottom (the bottom salinity front). In this area of stratified

waters, depth of bottom layer (measured from the halocline to the bottom) was less than 3 m, and menhaden eggs were located below the halocline.

Menhaden eggs occurred in a wide environmental range (Fig. 4). Densities of >100 eggs/m³ were found

in a salinity range of 10 to 25 psu; minor densities were located in waters with salinities reaching 33 psu (continental shelf waters). The low salinity boundary for egg distribution seems more abrupt than the high salinity boundary; very few eggs were detected below 10 psu. Most eggs produced over the prolonged spawning season were found at temperatures between 13 and 23°C.

Gravid females

A total of 375 sampling stations were analyzed, in which 1084 gravid females were identified. All the gravid females were caught from September through December. In these months, the total percentage of females with hydrated oocytes ranged from 72.8% to 89.4% (Fig. 1).

Gravid females were detected across the river between Montevideo and Punta Piedras, and in Samborombón Bay (Fig. 2B). In that region, percentages of gravid females in each tow were $>50\%$. The highest percentages of females with hydrated oocytes appeared to be associated with the highest horizontal salinity gradient (the salinity front). No females with hydrated oocytes were detected in continental shelf waters.

Discussion

The distribution of eggs and gravid females reveals that *B. aurea* spawn in the estuary (Fig. 2). Gravid females were found in a more restricted area than that where eggs were found, thus providing a more accurate picture of the spawning spatial pattern, because currents may move eggs to more distant areas. An echo sounder showed Brazilian menhaden below the halocline on all cruises, including the occasions when spawning individuals were collected. The halocline was detected by

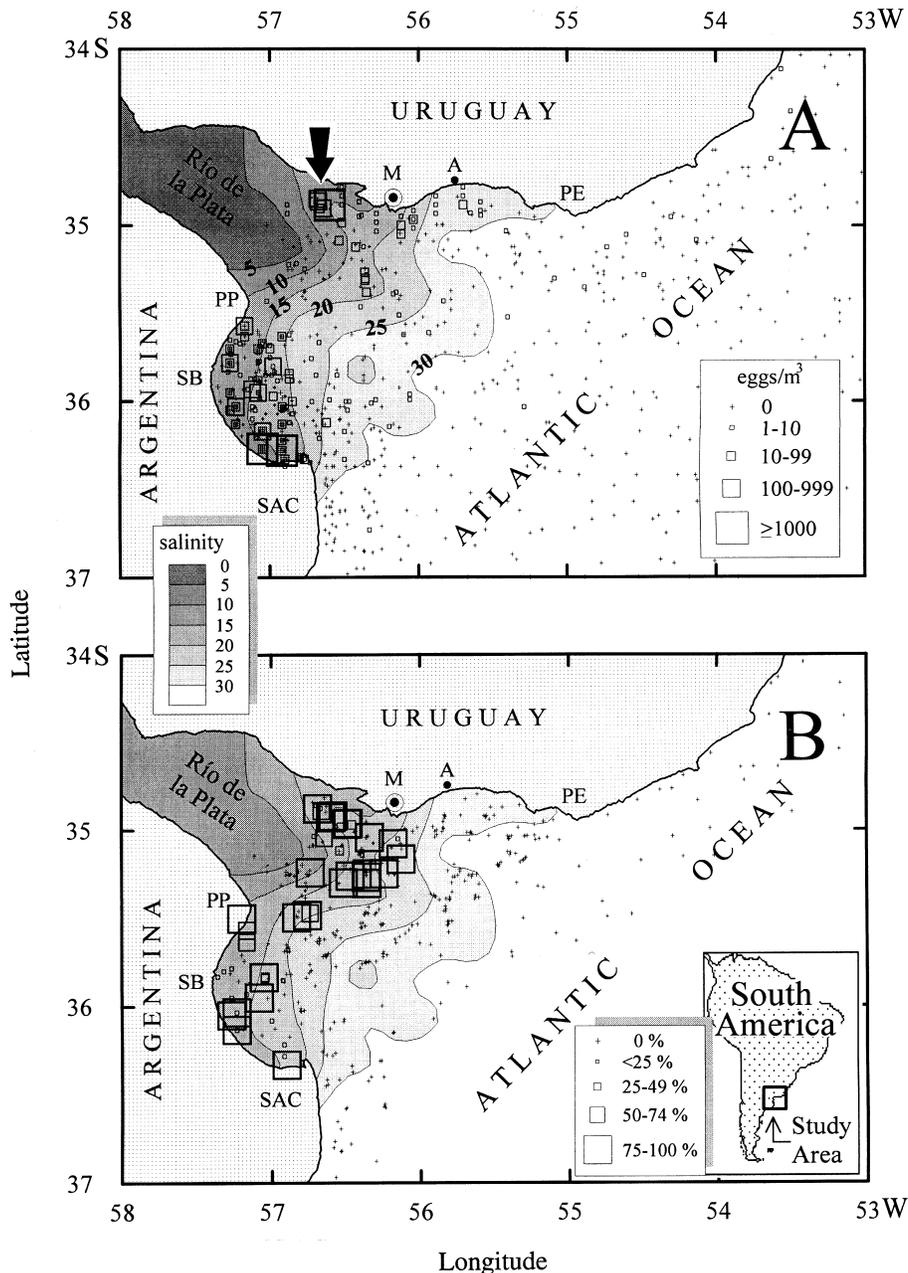
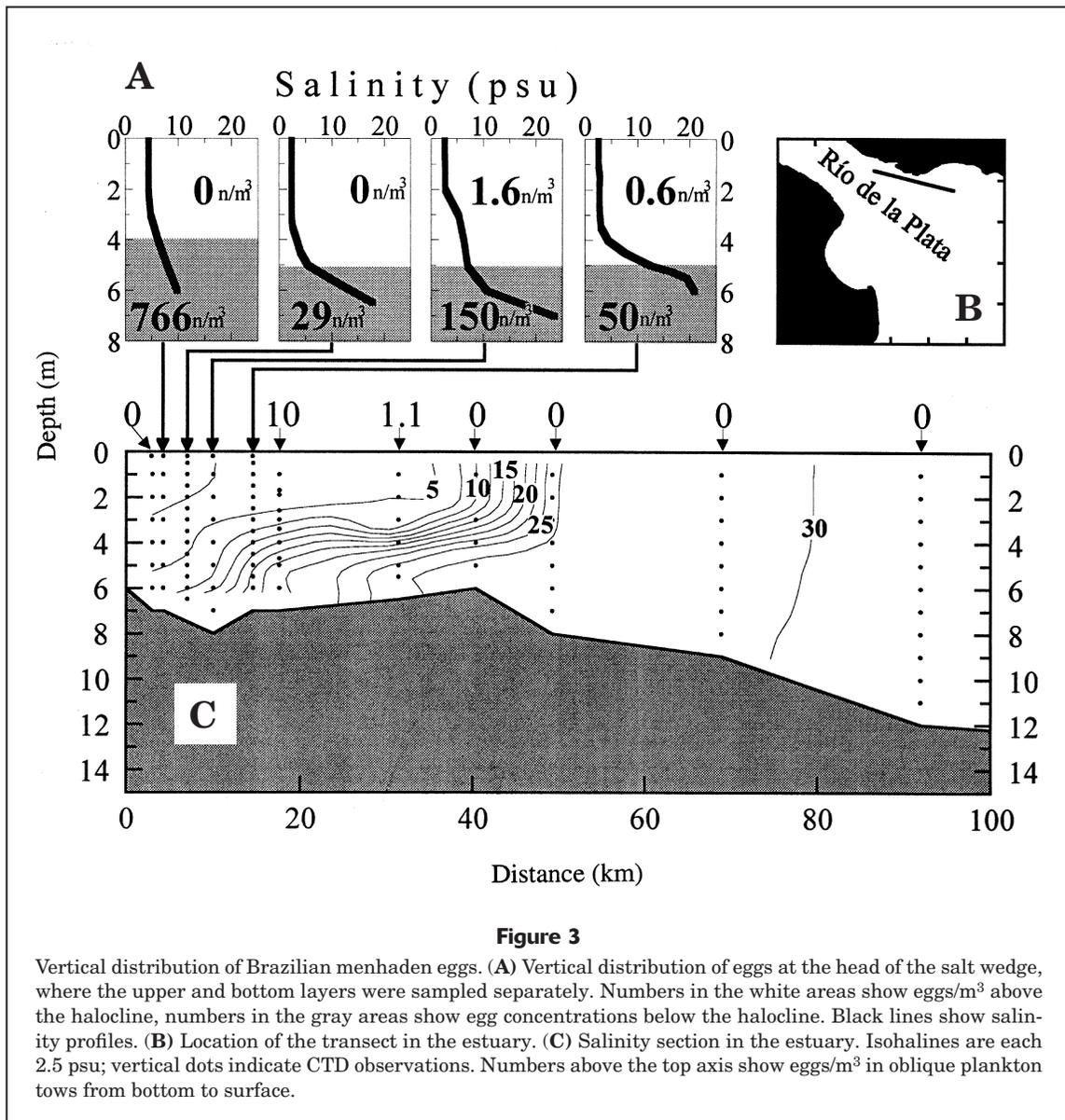


Figure 2

Location of the spawning area of the Brazilian menhaden. (A) The size of the symbols is proportional to the egg density from the plankton samples; the arrow shows the study site for examining the vertical distribution of eggs (see the text). (B) The size of the symbols is proportional to the percentage of females with hydrated oocytes. In both maps, the isohalines (expressed as psu) represent the bottom salinity field for spring-summer. PE = Punta del Este; A = Atlántida; M = Montevideo; PP = Punta Piedras; SB = Samborombón Bay; SAC = San Antonio Cape.



the echo sounder as a scattering layer, owing to the concentration of zooplankton (Madirolas et al., 1997). Brazilian menhaden appears to spawn close to the bottom, at the salinity front. The mean position of this front is strongly related to bottom topography (Guerrero et al., 1997a), having a relatively fixed location. This spawning area extends into the stratified waters of the estuary between Montevideo and Punta Piedras, and along Samborombón Bay. However, because waters of the inner zone of the bay are vertically homogeneous, or weakly stratified (Guerrero et al., 1997a), some high egg concentrations occur in nonstratified waters.

Menhaden eggs occurred in a wide range of salinities and temperatures. Because the bottom front is a

zone of major salinity changes, the eggs are exposed to a wide range of salinity values, and because the reproductive season extends over a long period, eggs are exposed further to a wide thermal range (Fig. 4). Low egg densities at low temperatures and high salinities represent samples taken in continental shelf waters, which were cooler than the estuarine waters during the warm season (Guerrero et al., 1997a, 1997b).

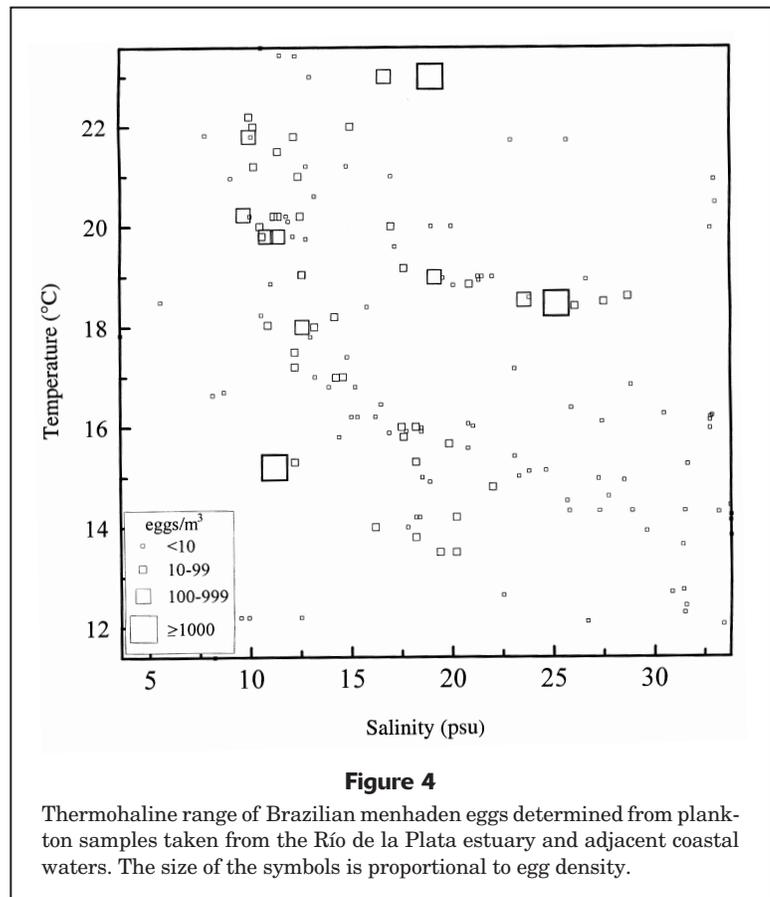
Presence of Brazilian menhaden eggs in the plankton year-round (Fig. 1) is strong evidence that they have a protracted reproductive season. Major spawning activity, based on incidence of eggs and hydrated ovaries (gravid females), occurs from September to January. Other reports of menhaden eggs, based on

partial temporal or spatial coverage, or both, fall within the temporal limits that we detected (de Ciechowski, 1968; Hubold and Ehrlich, 1981; Cassia and Booman, 1985; Lasta and de Ciechowski, 1988).

Brevoortia aurea eggs remain in the bottom layer of the water column, near where the halocline intersects the bottom (Fig. 3). At this frontal interface, a convergent flow near the bottom (Largier, 1993) would serve to retain eggs near the confluence of river and marine waters, minimizing their drift. Thus, specific gravity of the eggs seems to be an important feature of the reproductive strategy of *B. aurea*, allowing the eggs to stay in the saltier (and denser) bottom waters. Typically, bottom waters move landward in salt-wedge estuaries (Kjerfve, 1989; Mann and Lazier, 1991). Lower egg concentrations in the rest of the estuary probably indicate some dispersion of eggs or reduced spawning in these areas.

Disruptive events such as storms, which destroy the halocline (Guerrero et al., 1997a), intermittently occur in this region. These meteorological events are characterized by strong winds over 13 m/s from the southeast (Balay, 1961). The events have a characteristic duration of 1–3 (occasionally 5) days, occur throughout the year, and are usually the strongest from May to October (Anonymous, 1995). During these events, the estuarine circulation is modified, thus altering the egg retention properties of the system as well. The protracted reproductive season and multiple spawning of *B. aurea* (Macchi and Acha, 2000) may help to ensure that enough eggs survive in this unpredictable environment.

The four menhaden species in the Northern Hemisphere are the small-scaled menhaden *B. smithi* and *B. gunteri* and the large-scaled menhaden *B. tyrannus* and *B. patronus* (Ahrenholz, 1991). There is little information on the biology of *B. smithi* and *B. gunteri*. Conversely, *B. tyrannus* and *B. patronus* have been intensively studied, and the information on their life histories has been broadly reviewed (Ahrenholz, 1991; Powell, 1994). Both species have protracted reproductive seasons and a main spawning period in winter (Nelson et al., 1977; Shaw et al., 1985; Powell, 1994). Spawning of these menhaden takes place in marine waters. Larvae swim and drift with tides and currents toward estuaries where metamorphosis from larvae to juveniles takes place. In the case of *B. tyrannus*, larvae must be transported from the intensive spawning area south of Cape Hatteras, up to 100 km to



estuarine nursery areas (Warlen, 1992; Powell, 1994). *Brevoortia patronus* seems to spawn relatively close to estuarine nursery areas (Shaw et al., 1985).

Brevoortia aurea, *B. tyrannus*, and *B. patronus* all have protracted spawning periods. The southern species is a spring–summer spawner; the northern ones spawn during cooler months. In the case of *B. tyrannus*, however, adults search for temperatures $\geq 17^{\circ}\text{C}$ to spawn, and as larvae are transported nearer the coast, they enter cooler water (Warlen, 1992). Notwithstanding, the reproductive thermal range of the northern species ($12.9\text{--}21.2^{\circ}\text{C}$ for *B. patronus*, and $\geq 17^{\circ}\text{C}$ for *B. tyrannus* (Warlen, 1988; 1992) lies close to that of *B. aurea*. The proposed advantage of winter spawning refers to maximum onshore transport during that season, providing a mechanism for transporting larvae of both species into the vicinity of estuaries (Nelson et al., 1977; Warlen, 1988).

The main differences between *B. aurea* and those northern menhaden seem to be the population biomass and the spawning habitat. *Brevoortia tyrannus* and *B. patronus* exhibit large population sizes and are a significant component of United States fishery landings (Vaughan, 1991; Powell, 1994). Although there is no biomass assessment for *B. aurea*, it has

little importance as a fishery species (Argentine landings in 1997 were 893 t (Anonymous, 1998). Life history characteristics of *Brevoortia aurea* are probably more similar to those of *B. smithi* and *B. gunteri*, which tend to be more nearshore and estuarine-oriented species, form loose aggregations in coastal waters, and have protracted spawning periods during fall–winter months (Ahrenholz, 1991). Not enough information, however, on their reproductive biology exists to make further comparisons.

Drift of early life history stages is a major feature in the life cycle of *B. patronus*, and especially of *B. tyrannus*. On the contrary, egg retention seems to be a main property of the life cycle of the Brazilian menhaden in the Río de la Plata estuary. However, in southern Brazil, *B. aurea* does not seem to be an estuarine spawner (reported as *B. pectinata*, Weiss et al., 1976; Weiss and Krug, 1977; Weiss, 1981; Sinque and Muelbert, 1997). The greatest number of eggs occurred in nearshore waters, in a saline range of 33.04–35.50 psu. Several eggs were also found in the access channel to Lagoa dos Patos (a large coastal lagoon in southern Brazil, 32°S) during high salinity events, although its larvae and juveniles were distributed throughout the estuary in low salinity conditions (Weiss et al., 1976; Weiss, 1981; Sinque and Muelbert, 1997). The spawning area of *M. furnieri*, the most abundant fish species in the Río de la Plata, partially overlaps that of *B. aurea*, and the eggs of *M. furnieri* are retained in the estuary below the halocline (Acha et al., 1999). Like *B. aurea*, *M. furnieri* is an estuarine spawner in the Río de la Plata (Macchi et al., 1996) but seems to be a saltwater spawner in southern Brazil (Sinque and Muelbert, 1997). Both species have the potential for estuarine reproduction, but the eventual spawning site depends on the dynamic properties of the environment.

Major reviews of the role of estuaries for fishes state that spawning of pelagic eggs within estuaries is an unusual episode (e.g. Day et al., 1981; Day et al., 1989; Haedrich, 1992). Owing to 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).

In the Río de la Plata estuary, at least two fish species (*B. aurea* and *M. furnieri*) spawn pelagic eggs, taking advantage of the retention properties at the head of the salt wedge. These retention properties are not a feature unique to the Río de la Plata because estuaries with salt wedges are well known features (e.g. Mann and Lazier, 1991; Officer, 1992); however spawning of pelagic eggs at those locations is an uncommon event. Retention of eggs and larvae in the convergence zone may not be complete and

the net nontidal flows (residual currents) may drive them seaward. Given the large size of the Río de la Plata estuary, distance from the spawning area to the offshore limit of the salt wedge may reach 250 km (Guerrero et al., 1997a, 1997b). Therefore, larvae probably have enough time to develop to the stage where they become able to control their vertical position in the water column. The migratory behavior of larvae is manifested mostly in the vertical rather than horizontal plane (Norcross and Shaw, 1984). Thus, larval menhaden could take advantage of the two-layered circulation pattern and through vertical migrations compensate for the horizontal transport. This movement would be an important adaptation to maintain population (as the reproductive unit) coherency (Boucher, 1988; Sinclair and Iles, 1989).

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