Environmental factors that define the spawning and nursery areas for Percophis brasiliensis *(Teleostei: Percophididae) in a multispecific reproductive coastal zone, El Rincón (39°–41°S), Argentina*

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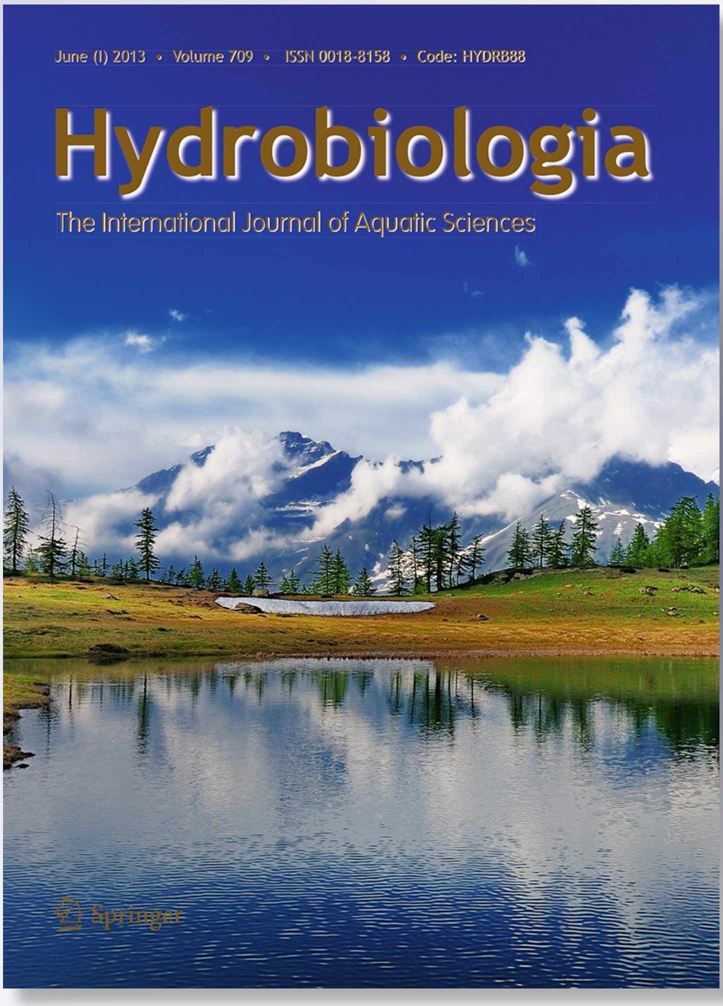

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PRIMARY RESEARCH PAPER

Environmental factors that define the spawning and nursery areas for *Percophis brasiliensis* (Teleostei: Percophididae) in a multispecific reproductive coastal zone, El Rincón (39°–41°S), Argentina

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Abstract The spatial distribution of *Percophis brasiliensis* at different maturity stages and its relationship to environmental factors was evaluated in the El Rincon area (39°–41°S) between 1994 and 2008 during eight cruises carried out in spring. For this, a canonical correspondence analysis was used. Results indicate that bottom temperature and bottom salinity horizontal gradient (BSHG) were the most important variables affecting the spatial distribution of *P. brasiliensis* maturity stages. Juveniles were mainly located in shallow waters with low salinity, high temperatures and vertical stratification. Conversely, gravid and running individuals were found in high BSHG and low temperatures. This link suggests that adults spawn in a well-defined area of hydrographic conditions that would tend to retain pelagic eggs and larvae, thus minimizing dispersal, and ensuring their transport from the spawning to nursery areas. On the coastal shelf of El Rincon, the water mass circulation shows an anti-cyclonic gyre whose recirculation cell during spring and summer is more constrained to inshore areas than during winter. Maximum reproductive activity of *P. brasiliensis* coincides with the highest retention period; therefore, dispersal of early-life stages (eggs) depends on the circulation pattern and transport pathway which would contribute importantly to its recruitment variability.

Keywords *Percophis brasiliensis* · Maturity stages · Environmental influence · Northern Argentine Sea · El Rincón

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Introduction

Fish population dynamics are generally found to be largely controlled by recruitment (i.e. net reproductive success), which corresponds to the integration over a season and shelf areas of processes affecting the survival of a population of larvae and juveniles along their drift trajectories. The survival of these individuals results from the interaction between spawning dynamics (which determines trajectories origin) and environmental variability (which determines transport and physical–biological interactions along the trajectories) (Allain et al., 2004). Many marine fish species utilize the same spawning location year after year, and this spawning site fidelity has probably "evolved" as an adaptive strategy to place progeny within environments that promote high rates of feeding, survival and growth during early life, and consequently a high probability of life cycle closure and recruitment success (e.g., Cushing, 1969; Ellertsen et al., 1989). Recruitment success is based primarily on the reliability of retention and physical attributes that define spawning areas and promote containment of eggs and larvae (Iles & Sinclair, 1982; Sinclair & Iles, 1985; Sinclair, 1988). This suggests that the optimal spawning location would coincide with persistent and predictable hydrodynamic regimes, and involve the interaction between larval behavior and oceanographic condition. Later studies have tended to incorporate several aspects of the interaction between larvae and the environment, and three major classes of physical processes that combine to yield favorable coastal fish reproductive habitat have been identified (Bakun, 1996, "ocean triad"): enrichment processes (upwelling, mixing, etc.); concentration processes (convergence, frontal formation, water column stability); and processes favoring retention within (or drift towards) appropriate habitat.

The Southwest Atlantic Coastal System (SACS; 34°–43°S) is a region characterized by two main multispecies spawning grounds, the Río de la Plata estuary and its maritime front (34°–39°S), and El Rincón coastal regimen (39°–41°S), where the reproductive activity (highest percentage of spawning females) has been related to the frontal system. Within the Río de la Plata, reproductive activity of some species, mainly estuarine (*Micropogonias furnieri*, *Brevoortia aurea*, *Ramnogaster arcuata* (Macchi et al., 1996; Macchi, 1997; Acha & Macchi, 2000; Rodrigues et al., 2008), occurs at the inner salinity front that separates freshwater and estuarine waters (Guerrero et al., 1997; Lucas et al., 2005). The high correlation of *M. furnieri* spawning females with the bottom salinity horizontal gradient (BSHG) supports the hypothesis that BSHG is dominant in determining reproductive grounds (Macchi, 1997; Jaureguizar et al., 2008) where high plankton concentration (Mianzan et al., 2001; Kogan, 2005; Bersategui et al., 2006) and prey abundance (Giberto, 2001; Bersategui et al., 2006; Schiariti et al., 2006) occur, and the wind pattern generates a retentive environment which could minimize advective losses of eggs and larvae to the adjacent ocean (Berasategui et al., 2004). Another species group, mainly marine species (*Cynoscion guatucupa*, *Percophis brasiliensis*, *Paralichthys patagonicus* and *Umbrina canosai*), show reproductive activity at the Río de la Plata outer salinity front (Macchi & Acha, 1998; Militelli & Macchi, 2006; Militelli, 2007) that separates estuarine waters and continental coastal waters (Guerrero et al., 1997; Lucas et al., 2005). This group of species also shows reproductive activity in the El Rincón coastal regime associated to the salinity front (Macchi & Acha, 1998). This front, parallel to the coast, separates diluted coastal water coming from the Río Negro and Río Colorado, and coastal shelf waters, and its location is determined by bathymetry and mean shelf circulation (Guerrero, 1998; Lucas et al., 2005).

Adults of some species have been proven to concentrate near the coast within SACS to spawn mainly between September and April (Cousseau et al., 1986; Macchi & Christiansen, 1996; Cousseau & Perrotta, 1998; Jaureguizar et al., 2003; Norbis & Verocai, 2005). The spawning areas and times are crucial to the reproductive success of these stocks. From the perspective of fishes, these spawning areas and periods are the most vital in their life history and also the most vulnerable to negative external impacts (Olsen et al., 2010). Although earlier studies have defined the spawning areas, taking into account the spatial distribution of gravid females, little is known about environmental influence on the spatial definition or the hydrographic processes affecting the distribution of reproductive stages in SACS that could affect the recruitment to the population.

Percophis brasiliensis (Brazilian flathead) is a marine species that shows high concentrations of mature individuals (Macchi & Acha, 1998; Militelli & Macchi, 2001a, b) and an intense fishery pressure in the El Rincón area (Fernandez Gimenez, 1995; Fernández Araoz et al., 2009). It is a multiple spawner with indeterminate annual fecundity that typically spawns small pelagic eggs from November to April (Austral spring–summer) (Militelli & Macchi, 2001a, b; Rodrigues, 2009). Recently, as a result of a drastic decrease in total biomass of traditional fishery resources (Argentine hake *Merluccius hubbsi*), fishing efforts have been directed to other fisheries based on coastal species (Aubone et al., 1998; Jaureguizar & Milessi, 2008) such as *P. brasiliensis*, whose landing has increased 100% over past years (from ~4,000 t in

2002 to 8,000 t in 2008), accounting for 7.8% of SACS total landing, and 40% of landing came from its main spawning ground (El Rincón) (Fernández Araoz et al., 2009).

Therefore, the aim of this article was to examine the relationship between maturity stages distribution patterns of *Percophis brasiliensis* and environmental conditions at El Rincón regime. The main environmental variables considered were bottom salinity gradient, water column stratification index, depth, temperature, and salinity.

Materials and methods

Specimens of *P. brasiliensis* and oceanographic data in El Rincón area were obtained during eight INIDEP fisheries evaluation cruises carried out in spring 1994–2008 (Fig. 1). Total fish caught ($n = 9{,}391$) were collected in 280 bottom trawl sets (Table 1) with an Engel trawl (200 mm mesh in wings and 120 mm mesh in cod ends, 4 m vertical opening and 15 m horizontal aperture) operating at 4 knots for 15 min per set. Individuals were sexed and reproductive development was macroscopically determined. To that end, a five-stage maturity key was employed following Macchi & Acha (1998): (1) immature; (2) developing or partially spent; (3) gravid (with hydrated oocytes) or running; (4) spent; and (5) resting. Table 2 shows the number of fish at each maturity stage. At each trawl station, Brazilian flathead abundance (thousands nm^{-2}) was estimated at every maturity stage for both sexes.

Oceanographic data (depth, temperature, and salinity) at each sampling station were obtained using a conductivity–temperature–depth (CTD) profiler. Data were calibrated for 1-m vertical resolution, with a final precision of ±0.03 °C for temperature and ±0.05 for salinity. Water stratification (SI) was estimated using the Simpson stratification index (φ) defined as the energy required to completely mix water column calculated from

$$\varphi = gh \int (\rho - \rho_0) z \, \mathrm{d}z,$$

where g is gravitational acceleration, h is total depth, ρ is in situ density, ρ_0 is water column mean density, and z is depth (Simpson, 1981).

To examine horizontal distribution of environmental variables in the study area, bottom salinity (BS), bottom temperature (BT), water stratification (SI), BSHG, and bottom temperature horizontal gradient (BTHG) were mapped. Parameters were interpolated onto a 0.3° latitude × 0.3° longitude grid using an inverse distance squared algorithm. The temperature and salinity horizontal gradients were calculated over a 0.05 × 0.05 grid resolution that has been spline smoothed from the 0.3 × 0.3 original grid. The horizontal gradients were reported as °C/100 km and psu/100 km for temperature and salinity, respectively.

The effects of environmental variables (depth, BS, BT, SI, BSHG, and BTHG) on *P. brasiliensis* stage-specific spatial distribution along the El Rincón gradient were analyzed using canonical correspondence analysis (CCA). The CCA is a direct analysis performed with computer program CANOCO (v.4.02) that selects linear combination of environmental variables and maximizes the dispersion of maturity stage scores along orthogonal axes; it was previously tested to determine whether or not the variables were collinear. Brazilian flathead stage scores are restricted to a linear combination of measured environmental variables; the correlation of environmental variables with the first two axes is called the intra-set correlation. The ordination output shows distribution patterns that are directly related to the environmental conditions being examined. The significance test was based on the Monte Carlo permutation test (103 permutations) for the sum of all eigenvalues. The significance of the relationship between gradients and individual environmental variables was evaluated using a t test (CANOCO, v.4.02). Maturity stages abundance data (1,000 $\mathrm{ind/nm}^2$) were log ($X + 1$) transformed before CCA to reduce the dominance effect of some maturity stages.

Results

Environmental conditions

Throughout the study, BS varied from 32.3 in the shallow area next to the river discharges to 34.41 in the offshore area (Fig. 2A). Maximum horizontal gradient (>2.7 psu/10 km) in the BS field occurred in the inner area of El Rincón, near the Colorado and Negro rivers, and weakened offshore towards higher salinity and

Fig. 1 Location and bathymetry of the study area

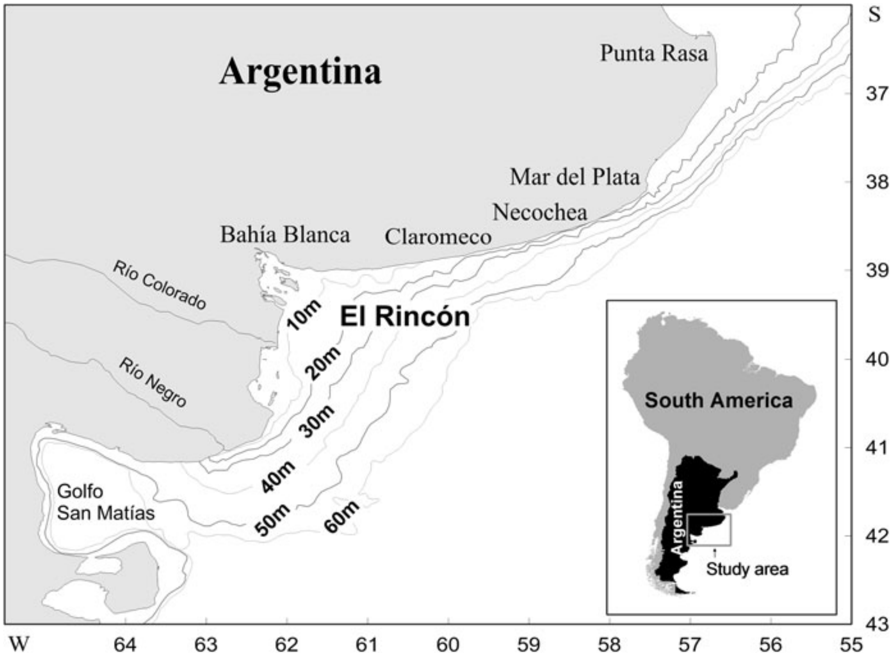

Table 1 Summary information of spring research surveys carried out between 1994 and 2008, indicating, for each year, the total bottom trawl sets with *Percophis brasiliensis*, and the number of fish per sex and total

Years	Trawls	Males	Females	Total fish
1994	19	628	459	1,087
1995	14	494	467	961
1998	23	872	832	1,704
1999	26	603	508	1,111
2000	30	548	524	1,072
2003	52	946	814	1,760
2005	62	738	587	1,325
2008	54	204	167	371

Table 2 Number of fish at each maturity stage per sex

Maturity stage	Males	Females
1	198	721
2	1,539	1,792
3	2,995	909
4	273	488
5	28	448

deeper waters (Fig. 2B). The BT field showed warm (15–18°C) shallow waters within the inner El Rincón and cold ones (11–15°C) along the deeper outer El Rincón area (Fig. 2C). The horizontal gradient in BT was, in general, weak (<5°C/10 km) and patchy with a relative maximum in the northern region near Claromecó (Fig. 2D). The BT field seemed to follow bathymetry while the BS minimum and BSHG maximum extended along the coast within the El Rincón area, near the river discharge. Vertical water stratification displayed its maximum (SI, Fig. 2E) in a cross-shelf direction at the 30–40 m isobaths south of 39°S (Fig. 2F). The highest SI value (>350 U) seemed to coincide with intermediate BT (14–15°C).

Environmental influence on *Percophis brasiliensis* spatial distribution

CCA included all variables because these were not collinear (correlation coefficient <0.55). The first two axes of the CCA ordination diagram explained 84.7% of the variance of *P. brasiliensis* maturity stages spatial distribution (Table 3; Fig. 3). The variance explained by the whole ordination, including the first axis, was significant ($P = 0.01$). The Monte Carlo permutation test was also significant ($n = 199$, $P = 0.01$ for both tests).

First canonical axis values showed that BT and BSHG were the factors with a major influence on the spatial distribution of Brazilian flathead maturity stages. The largest discontinuities along Axis 1 indicated that:

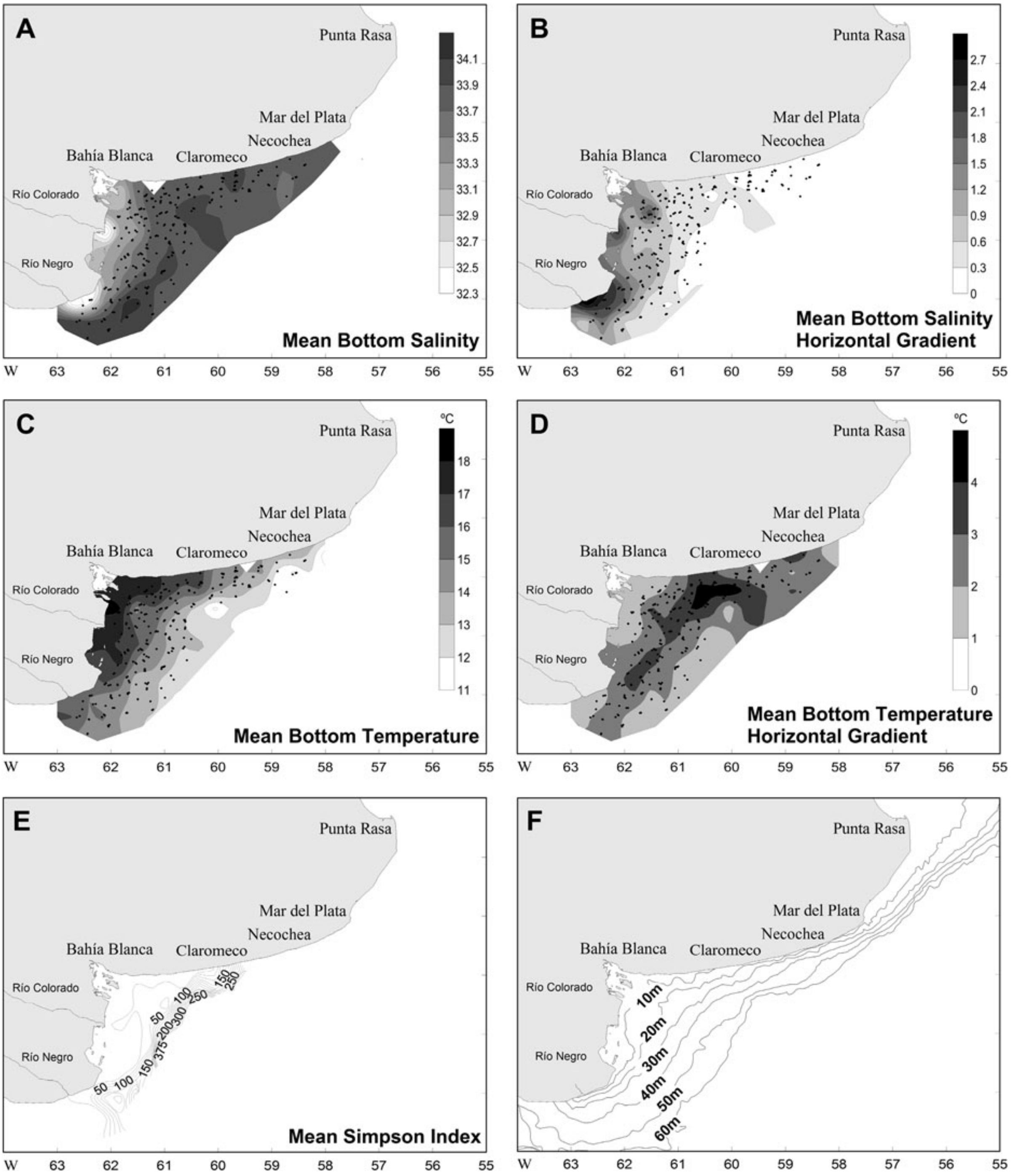

Fig. 2 Distribution of environmental parameters and spatial distribution of demersal trawl and CTD stations (*dots*)

immature specimens (M1, F1) and developing or partially spent (F2, M2) onces occurred in waters with high BT and the weakest BSHG, but these last were found in deeper waters; male and female in spent stages (M4, F4) and resting females (F5) were associated mainly with areas with intermediate BSHG and BT; and

Table 3 Canonical coefficients (100 × c) and intra-set correlation (100 × r) of environmental variables with the first two axes of canonical correspondence analysis

Name	Coefficients		Correlations	
	Axis 1	Axis 2	Axis 1	Axis 2
Z	−0.1622	0.2437	−0.2167	0.5308
BT	−0.5044	0.0469	−0.6737	0.1023
BSy	−0.1626	0.1912	−0.2172	0.4165
SI	−0.1399	−0.1795	−0.1868	−0.3909
BTHG	−0.1705	0.0316	−0.2278	0.0689
BSHG	0.4376	0.0295	0.5844	0.0643
Eigenvalues	0.208	0.046		
Species–environment correlations	0.749	0.459		
Cumulative percentage variance				
Of species data	15.7	19.1		
Of species-environment relationship	69.5	84.7		
Sum of all eigenvalues			1.329	
Sum of all canonical eigenvalues			0.300	
Total inertia			1.329	

Z Depth, *BT* bottom temperature, *BT* bottom temperature, *BS* bottom salinity, *SI* Simpson index, *BTHG* bottom temperature horizontal gradient, *BSHG* bottom salinity horizontal gradient

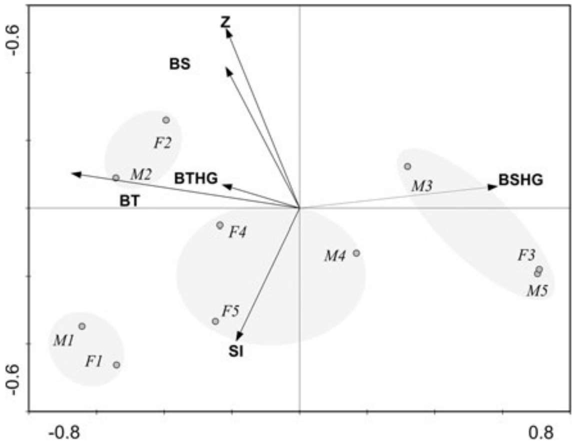

Fig. 3 Canonical correspondence analysis ordination diagram showing *P. brasiliensis* spatial distribution per sex (*M* male, *F* female); maturity stages (*1* immature, *2* developing and partially spent, *3* gravid or running, *4* spent, *5* resting); and environmental variables (*BT* bottom temperature, *BS* bottom salinity, *Z* depth, *SI* Simpson index, *BSHG* bottom salinity horizontal gradient, *BTHG* bottom temperature horizontal gradient)

gravid and running individuals (F3, M3) and resting males (M5) were associated with high BSHG and weakest BT.

Discontinuities along the second axis, driven by depth, BS and Simpson index indicated that immature specimens (M1, F1) and resting females (F5) were more abundant in areas with higher vertical water stratification (SI), shallow waters and low BS. Developing or partially spent (F2, M2) specimens occurred mainly in areas with high BS and depth and low SI. Spent and resting females (M4, F4) were found in areas with intermediate environmental conditions. Running males (M3) were associated with intermediate BS and depth, and the lowest SI, while the gravid females (F3) and resting males (M5) were found associated with low BS and depth and intermediate SI.

Discussion

During the spawning season, *Percophis brasiliensis* individuals, at different maturity stages, had a distribution pattern that indicates a preference for a particular habitat within the area of El Rincón, where environmental factors play an important role in this differentiation. Oceanographic data evaluated in this study were close to the mean condition observed for spring in other years (Guerrero, 1998; Lucas et al., 2005) and may be considered typical of the season for the El Rincón area. The highest values of BT extended along the coast, while the highest BSHG occurred both near river discharges, in agreement with mean position of salinity fronts reported by Guerrero (1998), and adjacent to anti-cyclonic circulation cells (Piola & Rivas, 1997; Palma et al., 2004, 2008; Lucas et al., 2005).

This pattern of habitat use observed agrees with maturity spatial distribution (Macchi & Acha, 1998; Militelli & Macchi, 2001b) and, partially, with the age-classes spatial distribution observed for only one spring (Barreto, 2007). As was reported in early studies, immature individuals (age-class 0 and 1) inhabit shallow areas associated with high temperature and low salinity (Barreto, 2007). The fact that juveniles have a preference for shallower waters, low salinity, and high temperatures is consistent with the spatial distribution generally observed in fishes (Macpherson & Duarte, 1991; Zeller & Pauly, 2001; Gillanders et al., 2003), and the theory of allocation of energy during the individuals' life cycle. The theory suggests that older demersal fish inhabit deeper and colder waters, where they may benefit from lower metabolic costs and greater longevity, while younger conspecifics occupy shallower and warmer waters, where food supply and growth rates may be greater (Macpherson & Duarte, 1991). Reduced metabolic cost implies that a greater fraction of resources consumed can be allocated to reproduction. The potential for relatively greater reproductive effort and greater longevity may significantly increase the total number of offspring produced by the fish and, consequently, total fish reproductive output (Macpherson & Duarte, 1991).

Although juveniles and spawning individuals were associated to similar BS and depth (Macchi & Acha, 1998), the results showed that the gravid stages were linked to habitats characterized by high BSHG, low temperature and vertical stratification of the water column (SI), while for juveniles it was low BSHG and high SI. The results obtained showed that reproductive activity of *Percophis brasiliensis* in El Rincón was more associated with the salinity front than with the thermal front suggested by Militelli & Macchi (2001b), and confirmed the hypothesis suggested by Macchi & Acha (1998) for multispecies spawning areas. The link between gravid stages and waters with high BSHG and low SI presumes that spawning aggregations correspond spatially and temporally with hydrographic features that will ensure the greatest survival rate of early history stages. Even though the circulation is not yet fully understood in the coastal shelf of El Rincon, the water mass circulation shows an anti-cyclonic gyre (Piola & Rivas, 1997; Palma et al., 2004, 2008; Lucas et al., 2005), whose recirculation cell during spring and summer is more constrained to the inshore area than during winter, and which is not affected by the NNE dominant drift in the mid-shelf (Palma et al., 2008), resulting in a more retentive mechanism. The maximum reproductive activity of *Percophis brasiliensis* (Rodrigues, 2009) coincides with the highest retention period; therefore, the dispersal of these early life stages (eggs) depends on the circulation pattern and transport pathway which would contribute importantly to its recruitment variability. As was observed, the efficacy of this process also depends on selection of the spawning location by adults and the behavior of early life stages (Houde, 2009). This retentive gyre serves as a mechanism of concentration, retention, and cross-coastal shelf transport to inshore nursery habitats of the product spawned, as has been observed in the Irish Sea (Dickey-Collas et al., 1997), Irminger Sea (Pedchenko, 2005), Bay of Biscay (Allain et al., 2007), Bay of Fundy (Caddy, 1979), Georges Bank (Houde, 2009) and the Santa Barbara Channel (Nishimoto & Washburn, 2002). The gyre in the El Rincon area presents three major classes of physical processes that combine to yield favorable coastal fish reproductive habitat (Bakun, 1996, "ocean triad"): (1) a concentration of nutrient-enriched coastal waters from the discharge rivers (Rio Negro and Rio Colorado), (2) a concentration of an abundant micro- and mesozooplankton food supply for the larvae, and (3) a retention process, which reduces the probability of advection to areas of low food availability, favoring the drift towards adjacent to inshore nursery habitats. Elevated densities of adequate larvae food (*Calanus australis*, *C. simillimus*, *Clausocalanus brevipes*, *Centropages brachiatus*, *Drepanopus forcipatus*, *Oithona atlantica* and *O. helgolandica*) (Perrota et al., 2003; Marrari et al., 2004; Cepeda, 2006) occur in the gyre area and in its adjacent shallow waters (10–20 m), particularly in the mouth of Bahia Blanca estuary, where the main nursery area of demersal species (*Cynoscion guatucupa*, *Umbrina canosai*, *Parona signata*) has been observed (López Cazorla, 2004; Hoffmeyer et al., 2009). Adult specimens of these species share the spawning area with *P. brasiliensis* (Macchi & Acha, 1998; Militelli, 2007).

These results, together with earlier studies, allow the determination that, in the main spawning areas (Río de la

Plata and El Rincón) within SACS (34°–43°S), the BSHG followed by BT (El Rincón) and depth (Río de la Plata) are the most important variables that force the spatial distribution of fish at different maturity stages (e.g., *Percophis brasiliensis, Micropogonias furnieri*). In the Río de la Plata, where the spawn of estuarine species is associated with the inner salinity frontal system (Macchi et al., 1996; Macchi, 1997; Acha & Macchi, 2000; Militelli, 2007; Rodrigues et al., 2008), the wind pattern generated a retentive environment (Berasategui et al., 2004; Jaureguizar et al., 2008; Simionato et al., 2008), while in El Rincón, the results obtained in this study allow the identification of the anti-cyclonic gyre circulation as the retentive process. The species *Cynoscion guatucupa*, *Percophis brasiliensis*, *Paralichthys patagonicus* and *Umbrina canosai* that share the spawning area in El Rincón also show reproductive activity in the outer surface salinity front of Rio de la Plata (Macchi & Acha, 1998; Militelli, 2007), which is associated with the confluence of estuarine waters and continental coastal waters (Guerrero et al., 1997; Lucas et al., 2005). Based on our results, we hypothesize that the anti-cyclonic gyre circulation in the outer area of Río de la Plata, shown by Palma et al. (2008), will also act as a retentive mechanism.

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