Ocean–estuarine connection for ichthyoplankton through the inlet channel of a temperate choked coastal lagoon (Argentina)

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Abstract. We examined the fish larvae colonising pattern of the Mar Chiquita lagoon (Argentina). We hypothesised that in this microtidal lagoon, winds could regulate fish larvae dynamics. Ichthyoplankton samples were taken in marine waters, the surf zone and the estuary. Previous studies showed no reproduction by fishes with planktonic eggs inside the lagoon. However high abundance of eggs and larvae of *Brevoortia aurea* collected within the estuary also suggest possible spawning activity. Throughout the study period, the cumulated richness of fish larvae was slightly higher in the estuary. However, univariate analysis revealed a higher number of species per tow in marine waters than in the estuary. The lowest average values of fish density, number of species and diversity recorded in the surf zone suggest that this area is only used as a transient corridor between the sea and the lagoon. The canonical correspondence analysis (CCA) indicated that wind direction, tidal stage, temperature and rainfall contributed significantly to the fish larvae distribution patterns observed; being 'onshore wind' the most important variable affecting fishes. Our results show how winds, in addition to pushing seawater into the lagoon, contribute to larvae recruitment into this estuary. Finally, we discuss the role of small lagoons in the life-history of coastal fishes.

Additional keywords: choked coastal lagoon, fish larvae, ocean–estuarine gradient, recruitment patterns, surf zone, wind effect.

Introduction

Estuarine ecosystems (e.g. estuaries and coastal lagoons) are physiologically demanding, relatively impracticable and, in many ways, inhospitable environments. However, small larval and juvenile forms of fish and crustaceans are specially abundant in these environments, despite their aparent seeming fragility and complex life cycles (Cowan *et al.* 2013). Estuarine ecosystems provide rich food supply, refuge against predators, and optimal temperature conditions for larvae and juveniles which use them as nursery grounds (Blaber 1985; Yáñez-Arancibia *et al.* 1985; Able 2005). Therefore, physiological and behavioural costs that the nekton pays for living in these

ecosystems appear to be compensated for by the higher survivability of juveniles (Cowan *et al.* 2013).

The most common nekton life history cycle of fishes inhabiting estuaries involves offshore spawning with the production of a large number of small pelagic eggs, and recruitment to estuaries as larvae or early juveniles (Lawler *et al.* 1988; Day *et al.* 1989; Acha *et al.* 1999). Therefore, the exchange between the ocean and estuaries is a key issue to coastal scientists because many species of fish move between the continental shelf and estuaries during their early life history (Boehlert and Mundy 1988; Epifanio and Garvine 2001). Moreover, this movement is, indeed, crucial for successful

completion of the life cycle of several species sustaining commercial coastal fisheries (Muelbert and Weiss 1991; Islam et al. 2007).

Several authors have debated about the principal factors involved in the shoreward transport of the offshore-spawned fish larvae. Most studies have emphasised that the influence of fresh water flow rates and the resultant physico-chemical cues (turbidity and/or salinity gradients) are significant in aiding fish larval recruitment into estuaries (e.g. Beckley 1985; Whitfield 1989a; Harris et al. 2001). These findings also explain why fish larvae do congregate in the surf zone adjacent to estuaries (Whitfield 1989b; Harris et al. 2001; Watt-Pringle and Strydom 2003). In stratified estuaries, where net current directions vary vertically, fish larvae can exploit currents to maintain their position in the estuary by altering their vertical position (Melville-Smith et al. 1981), or be assisted by the different currents in either upstream or downstream movement. Conversely, in unstratified estuarine channels, where flow velocities vary little vertically (Beckley 1985; Whitfield 1989a), fish larvae are strongly influenced by the tidal flux regardless of their vertical position in the water column (Roper 1986; Trnski 2001). Unlike most estuaries, choked coastal lagoons are largely influenced by local winds because the inlet channel acts as a dynamic filter which significantly reduce tidal fluctuations or tidal currents (Kjerfve and Magill 1989; Kjerfve 1994). In this scenario, recruitment models for fish larvae based on tidal cycles (Weinstein et al. 1980; Boehlert and Mundy 1988; Forward et al. 1999) could assumed not to be suitable.

Despite the extensive literature related to the movement of fish larvae from offshore spawning grounds to coastal estuarine nursery grounds, only few studies have dealt with the wind-mediated transport of fish larvae in choked coastal lagoons (e.g. Martins et al. 2007).

Mar Chiquita lagoon (37°32′S, 57°19′W, Argentina), is a small (46 km^2) and very shallow (0.80 – 3 m) choked coastal lagoon affected by semidiurnal low amplitude (<1 m) tides (Reta et al. 2001). An inlet channel 6 km long and 200 m in width links this lagoon to the ocean (Reta et al. 2001). The largest inflows have been recorded to occur under the influence of strong south-easterly winds (Olivier et al. 1972). Mar Chiquita fish fauna has been decribed from adults and juveniles stages (e.g. Cousseau et al. 2001; González-Castro et al. 2009) and is similar structurally to the ichthyofauna of other temperate lagoons or estuaries around the world (González-Castro et al. 2009). Although it is well established the role of the lagoon as nursery ground for juvenile fishes (Cousseau et al. 2001; Martinetto et al. 2007; Valiñas et al. 2010), there are no works about the use of this coastal lagoon by the earlier life stages, where wind is the main physical forcing driving the water levels (Reta et al. 2001).

The main goal of this study was to investigate the fish larvae recruitment patterns from the sea to a very shallow temperate wind-dominated choked lagoon. In order to do so, we explore patterns in fish larvae abundance and distribution in Mar Chiquita lagoon inlet channel and adjacent coastal area. We hypothesise that in this context of low tidal influence, other factors such as wind force may be regulating fish larvae dynamics. Particularly, we hypothesised that onshore winds are strongly related to fish larvae recruitment into Mar Chiquita inlet channel.

Material and methods

Study area

Mar Chiquita coastal lagoon (Fig. 1), a UNESCO Man and the Biosphere Reserve (UNESCO, 1996), has an elongated shape with a general direction NNW-SSE and receives the discharges of several freshwater streams and canals (Reta et al. 2001). The mouth of this lagoon has been partially fixed in 1971 by a jetty construction (Isla 1997). Mudflats and surrounding marshes dominated by the cordgrass *Spartina densiflora* (e.g. Isacch et al. 2006) and the burrowing crab *Neohelice granulata* (e.g. Iribarne et al. 1997) characterise this very shallow lagoon. Temperature and salinity are extremely variable. Variations of surface temperature range between 3°C (in winter) to 21°C (in summer). Salinity fluctuates over a wide range from freshwater to more than 30 PSU (González-Castro et al. 2009; Cousseau et al. 2011).

Intrusion of the saline wedge varies according to the tidal stage and the wind direction. Strong winds from the NE direction prevent the entrance of marine waters into the lagoon. Winds from N and NW directions aid the fast discharge of the lagoon water into the sea. On the other hand, strong winds from the sea (E – SE) force the marine waters to enter into the lagoon several kilometers from the inlet. Neap and spring tides reinforce winds effects promoting the lagoon discharge or the marine waters entrance, respectively (Reta et al. 2001). Wind directions show a seasonal pattern, with a dominance of winds from the north and north-east during spring and summer; and many calms and a weak dominance of winds from the south-west and north-west during autumn and winter (Lucas et al. 2005).

A bridge was constructed at the head of the mouth that induced a large shoaling of the inlet channel. Tidal effect is perceived up to the bridge (~5 km); upstream this point tidal effects are negligible (Reta et al. 2001). The inlet channel is the portion of the lagoon that has distinctly estuarine features, and jointly to the offshore zone adjacent to the lagoon's mouth, constitutes the study region (Fig. 1).

Biological and environmental sampling

Fifteen sampling stations were spaced over 5 km within the Mar Chiquita coastal lagoon system and extended ~1.6 km out to the inner continental shelf, including the surf zone in between (Fig. 1). Sampling was conducted during December 2009 and February 2010 for the Ocean zone stations and every two weeks from December 2009 to March 2010 for the Surf zone and the Estuary zone stations. This sampling period was appropriate to cover the reproductive season of most fish species cited for the area (Cousseau and Perrotta 2004). A conical net with 0.15 m^2 mouth area and 300 μm mesh span net was towed by means of a 60 HP boat against the prevailing current at 2 kn for 10 min at the Ocean stations. The volume filtered was ~37.99 m^3 and depth ranged from 5–6 m (~0.6 km offshore; O3, O4, O5) to 9 m (~1.6 km offshore; O1, O2) (Fig. 1). For the Surf zone and the Estuary zone stations, a conical net with 0.07 m^2 mouth area and 300 μm mesh span net was pulled against the prevailing current for 50 m parallel to shoreline at ~1 m depth, filtering a volume of ~3.53 m^3. Sampling was performed in duplicate (each duplicate was averaged for statistical analysis) during daytime and in the case of the Surf zone and the Estuary zone stations, one ebb and one flood tide condition for each month was
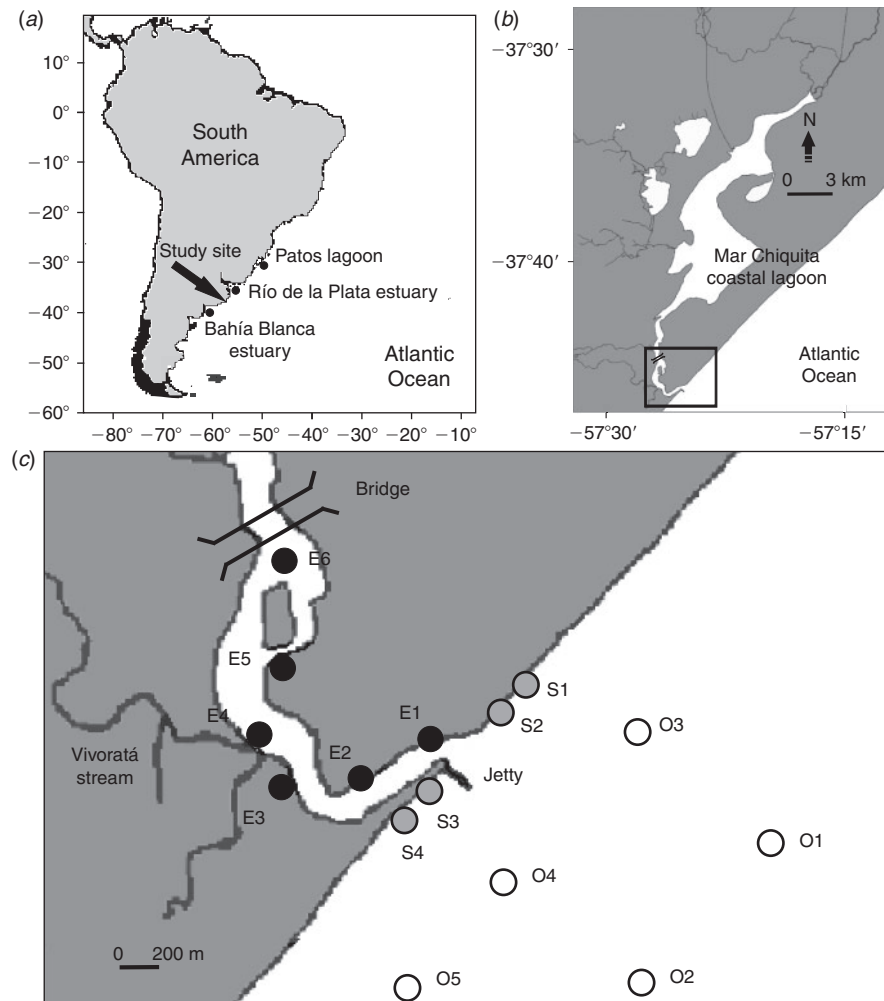
Fig. 1. Map of the study site. (*a*) Location of Mar Chiquita coastal lagoon (Argentina) in South America and the main nearby estuarine systems, (*b*) the seccion of Mar Chiquita coastal lagoon under study and (*c*) location of the sampling stations in the offshore, surf zone and estuarine environments along the ocean–estuarine gradient in Mar Chiquita coastal lagoon.

possible to achieve. After the completion of each tow/pull, nets were washed and the samples fixed and preserved in 4% buffered formaldehyde–seawater solution.

Fish larvae (and eggs whenever possible) were sorted and identified under a stereoscopic microscope to the lowest possible taxon, using field guides or diagnostic keys (Weiss 1981; Fahay 1983; Richards 2006). Larvae were then counted and measured to the nearest 0.01 mm using an ocular micrometer. Notochord lenght (NL) was measured for all preflexion and flexion larvae and total lenght (TL) for all postflexion larvae (Fuiman 2002). These were termed as 'body length' (BL) for all species caught.

Water temperature (°C), salinity (based on PSS 78) and transparency (cm) were recorded with a hand thermometer, a Hydrobios refractometer and Secchi disc, respectively. Transparency was not possible to be meassured at the Ocean zone stations. Average wind speed, mode wind direction and total amount rainfall, during the sampling day plus the 5 previous days, were calculated for statistical analysis. Data were provided by the national weather service (Servicio Meteorológico Nacional, Argentina).

Environmental data analysis

To test the null hypothesis of no differences in temperature, salinity and transparency (only for the Surf zone and the Estuary zone) among sampling stations, a Kruskal–Wallis rank sum test was used. If significant differences were observed, a pair-wise Mann–Whitney U-test was employed.

Fish composition analysis

In order to explore fish larvae distribution patterns, mean fish abundance (ind. $100\,m^{-3}$), species richness (as average number of species), and Shannon-Weiner diversity index (H') (Magurran 1988) per tow/pull were calculated. To test the null hypothesis of no differences in each parameter calculated among sampling stations, a Kruskal–Wallis rank sum test and *a posteriori* pairwise Mann–Whitney U-test (when necessary) were used.

For evaluating spatial and temporal variations, sampling stations were grouped and considered replicates of each zone (i.e. Ocean, Surf and Estuary) and months were grouped into seasons as follow: Early summer (December and January) and

Late summer (February and March). Since Ocean stations were not possible to be sampled in January and March for this zone, Early summer and Late summer were represented by December and February, respectively. Therefore, a two-way non-parametric permutation multivariate analysis of variance (PERMANOVA) using Bray–Curtis distances with 10000 permutations of matrix data (Anderson 2001) on the density (ind. $100\,m^{-3}$) of fish larvae was used to test de null hypothesis of no differences in species composition among zones, seasons and their interactions. This test is designed on the basis of a distance measure between each pair of observation units to obtain a distance matrix. The permutation test is used to create a distribution of PseudoF and obtain a p(perm)-value (Anderson 2001). If significant differences were observed, *a posteriori* one-way PERMANOVA was used. Similarity percentages (SIMPER) were used to determine which species were most responsible for the Bray–Curtis dissimilarity between each pair of groups.

In order to assess the differences on the fish larvae length among zones by seasons, a Kruskal–Wallis rank sum test was used. If significant differences were observed, a pair-wise Mann–Whitney U-test was employed.

Fish composition related to physical environment analysis

Canonical correspondence analysis (CCA) was used to assess the relationship between species composition and environmental variables (ter Braak and Verdonschot 1995). This sorting method relates two data matrices, one of species abundances of several samples and other of environmental characteristics from the samples. This results in an arrangement in which the axis of species is restricted to a pattern that maximises the correlation with environmental variables (ter Braak and Schaffers 2004). The biological variables were log-transformed densities [i.e. log (ind. $100\,m^{-3} + 1$)] of species abundances. To reduce the effects of rare species in the analysis, those species with less than 5% average occurrence frequency were omitted. The environmental matrix included only the environmental variables that were available for all stations. The environmental variables employed were temperature (°C), salinity, rainfall amount (mm), wind speed ($m\,s^{-1}$), wind direction, and tidal stage (flood $= +1$ and ebb $= -1$). Since wind direction is a circular variable, it was transformed into a linear variable by using the cosine of the angle that the wind made on two orthogonal axes aligned perpendicular and parallel to the shoreline (Clark *et al.* 1996; Beyst *et al.* 2001). Onshore winds (SW, S, SE, E) were considered positive $(+1)$ while offshore winds (NE, N, NW, W) were considered negative (-1). Monte Carlo permutation analysis simulation was used to evaluate the significance ($P < 0.05$) of each variable's contribution.

All multivariate analyses were performed under R software (R Development Core Team 2012).

Results

Physical environment

Temperature was not significantly different among sampling stations (Fig. 2*a*), as revealed by the Kruskal–Wallis rank sum test ($\chi^2 = 7.366$, d.f. $= 14$, $P = 0.9197$). However, Ocean stations
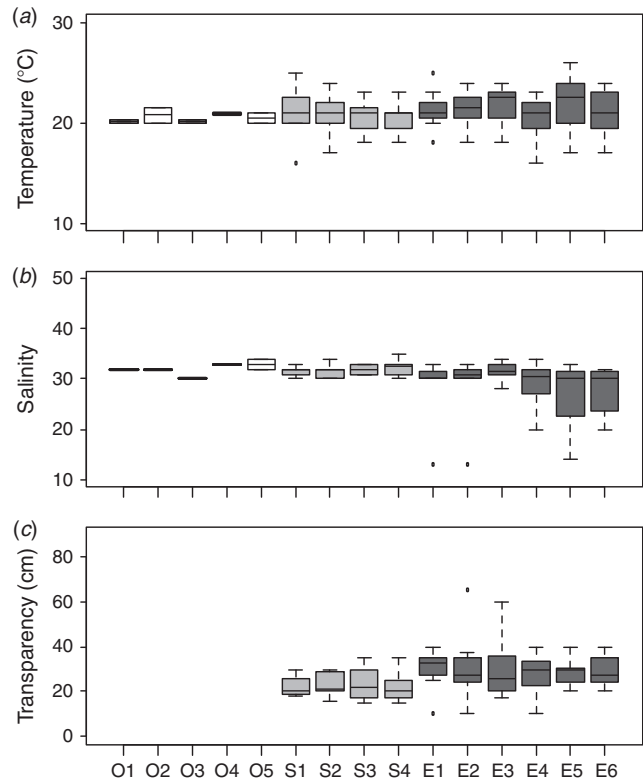

Fig. 2. Spatial variation in (*a*) water temperature, (*b*) water salinity and (*c*) water transparency (as Secchi depth) along the ocean–estuarine gradient in Mar Chiquita coastal lagoon (line: median; box: 25th to 75th percentiles; whiskers: minimum to maximum value range).

showed the narrower range of values (20 – 21.5°C) compared with the Surf zone (16 – 25°C) and the Estuary stations (16 – 26°C). Neither significant differences in salinity ($\chi^2 = 23.677$, d.f. $= 14$, $P = 0.051$) nor transparency ($\chi^2 = 12.519$, d.f. $= 9$, $P = 0.1856$) among stations were found (Fig. 2*b*, *c*). Nevertheless, when considering sampling stations as replicates of the corresponding zone (i.e. Ocean, Surf and Estuary zone), significant differences among zones were observed (Table 1). Salinity values for Ocean zone (mean $= 32$, median $= 32$) and Surf zone (mean $= 31.8$, median $= 32$) were similar from each other and higher than those for the Estuary zone (mean $= 28.8$, median $= 30.5$) (Table 1). Water transparency indicated spatial variations with significant differences between the Surf zone and the Estuary zone ($W = 397.5$, $P = 0.0009$). Significant lower averages values were recorded in the Surf zone (mean $= 22.8$ cm, median $= 20$ cm) compared with those from the Estuary zone (mean $= 29.5$ cm, median $= 30$ cm).

Rainfall was more abundant during March (145.6 mm), while less values were obtained during January (108.9 mm) and reached up a total of 510.1 mm during the study period (Fig. 3*a*). Easterly winds were dominant in December (frequency $= 32.26$%) (Fig. 3*b*), January ($F = 32.26$%) (Fig. 3*c*), and February ($F = 35.71$%) (Fig. 3*d*), with average maximum speeds of 10.53, 10.86 and $10.45\,m\,s^{-1}$, respectively. During March, northerly winds were dominant ($F = 29.03$%) with average maximum speeds of $10.52\,m\,s^{-1}$ (Fig. 3*e*).

Table 1. Kruskal-Wallis rank sum test results and posteriori Mann–Whitney U-test comparisons for water parameters and fish larvae composition collected in each sampled zone (i.e. Oc: Ocean, Surf: Surf zone and Est: Estuary) in Mar Chiquita lagoon and surrounding coastal area, during the study period
Esum: early summer, Lsum: late summer

| Source	Kruskal–Wallis rank sum test			Mann–Whitney U-test
	χ^2	df	P-value	
Temperature	4.044	2	0.1324	–
Salinity	11.397	2	0.0033	Oc = Surf > Est
Transparency	–	–	–	Est > Surf
Fish larvae density	10.612	2	0.0049	Oc = Est > Surf
Number of species	16.67	2	0.0003	Oc > Est > Surf
Diversity (H')	12.03	2	0.0024	Oc = Est > Surf
Fish length (Esum)	10.38	2	0.0056	Oc = Surf, Oc > Est, Surf < Est
Fish length (Lsum)	14.55	2	0.0007	Oc = Surf, Oc < Est, Surf = Est
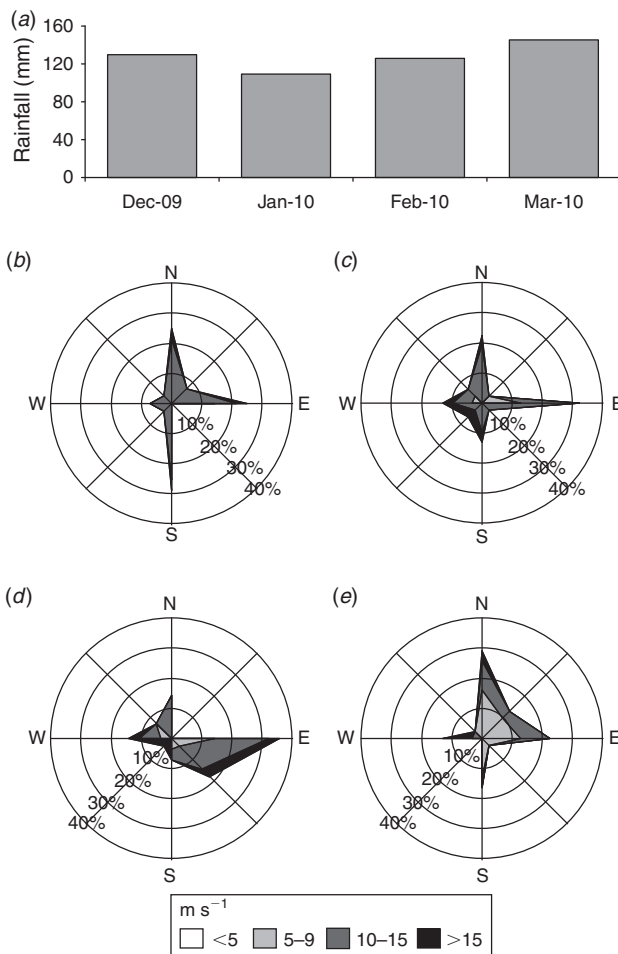
Fig. 3. Temporal variation of (*a*) rainfall amount, and of wind direction and speed for (*b*) December 2009, (*c*) January 2010, (*d*) February 2010 and (*e*) March 2010.

Fish composition

Planktonic eggs occurred in all three zones during the study period. Egg abundances were lower in the Surf zone and the Ocean zone but higher in the Estuary zone (Table 2). Almost all egg taxa collected were present at Ocean stations. Type 1 and Type 2 eggs, were different from each other and include individuals of presumably several species.

Fish larvae of at least 19 taxa occurred during the study period in all three zones (Table 3). *Engraulis anchoita* (1.18 ± 3.75 ind. $100\,\mathrm{m}^{-3}$), *Peprilus paru* (0.13 ± 0.42 ind. $100\,\mathrm{m}^{-3}$), *Porichthys porossisimus* (0.53 ± 1.66 ind. $100\,\mathrm{m}^{-3}$), *Stromateus brasiliensis* (0.26 ± 0.55 ind. $100\,\mathrm{m}^{-3}$) and *Umbrina canosai* (5.66 ± 10.67 ind. $100\,\mathrm{m}^{-3}$) were present only in the Ocean zone. Conversely, *Menticirrhus americanus* (0.29 ± 2.04 ind. $100\,\mathrm{m}^{-3}$) and three unidentified species were present only in the Estuary zone (Table 3).

Gobiosoma parri was the most abundant species in the Ocean zone followed by the Engraulidae family, which includes unidentifed individuals of likely *Anchoa marinii*, *E. anchoita* and/or *Lycengraulis grossidens* (Table 3). The Engraulid species were, however, more abundant in O1 (13.16 ± 18.61 ind. $100\,\mathrm{m}^{-3}$), O2 (249.38 ± 352.68 ind. $100\,\mathrm{m}^{-3}$), O3 (168.45 ± 238.22 ind. $100\,\mathrm{m}^{-3}$), and O4 (567.19 ± 802.14 ind. $100\,\mathrm{m}^{-3}$) stations, while *G. parri* was more abundant (1135.71 ± 1606.13 ind. $100\,\mathrm{m}^{-3}$) in O5 station. Few species were present in the Surf zone, being *Brevoortia aurea* the most abundant (Table 3). This species presented the highest abundance in S3 (45.14 ± 111.72 ind. $100\,\mathrm{m}^{-3}$) station, while in S1 and S2, *Paralichthys orbignyanus* was the most abundant species with 0.64 (± 1.70) ind. $100\,\mathrm{m}^{-3}$ and 1.07 (± 2.83) ind. $100\,\mathrm{m}^{-3}$, respectively. Also *B. aurea* was the most abundant species in the Estuary zone (Table 3). The highest abundance of this species was collected in E1 (61.0 ± 150.6 ind. $100\,\mathrm{m}^{-3}$), E2 (14.71 ± 32.31 ind. $100\,\mathrm{m}^{-3}$), E5 (2.50 ± 5.02 ind. $100\,\mathrm{m}^{-3}$) and E6 (0.15 ± 0.89 ind. $100\,\mathrm{m}^{-3}$) stations. Conversely, the Engraulidae group was more abundant in E3 (1.43 ± 3.54 ind. $100\,\mathrm{m}^{-3}$) and E4 (0.14 ± 0.35 ind. $100\,\mathrm{m}^{-3}$) stations.

No significant differences in fish density ($\chi^2 = 12.14$, d.f. = 14, $P = 0.5951$) (Fig. 4*a*), species richness ($\chi^2 = 18.73$, d.f. = 14, $P = 0.1755$) (Fig. 4*b*), and diversity (H') ($\chi^2 = 18.31$, d.f. = 14, $P = 0.1931$) (Fig. 4*c*) were observed among sampling stations, as revealed by the Kruskal–Wallis rank sum test. However, when considering sampling stations as replicates of the corresponding zone, some spatial trends were observed (Table 1). Fish density was significantly lower on the Surf zone (mean = 314.2 ind. $100\,\mathrm{m}^{-3}$, median = 0 ind. $100\,\mathrm{m}^{-3}$) than the Ocean zone (mean = 889.6 ind. $100\,\mathrm{m}^{-3}$, median = 25.66 ind. $100\,\mathrm{m}^{-3}$) and the Estuary zone (mean = 357.4 ind. $100\,\mathrm{m}^{-3}$, median = 14.15 ind. $100\,\mathrm{m}^{-3}$) ($W = 234$, $P = 0.0049$; and $W = 498.5$, $P = 0.0115$, respectively). Species richness also differed among zones, with the highest number of species collected at the Ocean zone (mean = 3.4, median = 2.5) compared with the Estuary zone (mean = 0.94, median = 1) ($W = 350$, $P = 0.0174$) and the Surf zone (mean = 0.27, median = 0) ($W = 251$, $P = 0.0003$) (Table 1). Diversity was lower at the Surf zone (mean = 0.01, median = 0) compared with the Estuary zone (mean = 0.16, median = 0) ($W = 575.5$, $P = 0.0185$) and the Ocean zone (mean = 0.44, median = 0.39) ($W = 222.5$, $P = 0.0003$).

Table 2.   Eggs composition recorded from Mar Chiquita lagoon inlet channel and its surrounding coastal area between December 2009 and March 2010

Abbreviations are as follow: MD, mean density (ind. $100\,m^{-3}$); (EWE) percentage of eggs without embryo. Standard deviation in brackets

Species	Ocean		Surf zone		Estuary	
	MD	EWE	MD	EWE	MD	EWE
Brevoortia aurea	0.88 (2.71)	0	–	–	4.13 (20.84)	57.14
Engraulis anchoita	0.44 (1.86)	0	–	–	–	–
Type 1 egg	0.44 (1.86)	100	–	–	–	–
Type 2 egg	–	–	1.42 (4.32)	66.67	25.66 (102.76)	59.32
Trichiurus lepturus	1.32 (3.29)	100	–	–	12.68 (42.24)	25.58

A two-way PERMANOVA revealed significant differences (p(perm) < 0.001) in fish larvae composition among zones (Table 4), but not between seasons (p(perm) = 0.0513). However, zone × season interaction was significant (p(perm) = 0.0013). During Early summer, fish larvae composition from the Ocean zone was significantly different from that of the Estuary zone (PERMANOVA pairwise comparison: Mean Sq. = 0.566, d.f. = 1, PseudoF = 3.65, p(perm) = 0.0144), but there was no significant differences between the Surf zone and the Ocean zone (PERMANOVA pairwise comparison: Mean Sq. = 0.094, d.f. = 1, PseudoF = 6.43, p(perm) = 0.2502) nor between the Surf zone and the Estuary zone (PERMANOVA pairwise comparison: Mean Sq. = 0.230, d.f. = 1, PseudoF = 1.26, p(perm) = 0.337) (Fig. 5a, b). During Late summer, fish larvae composition from the Ocean zone was significantly different from that of the Surf zone (PERMANOVA pairwise comparison: Mean Sq. = 1.559, d.f. = 1, PseudoF = 8.06, p(perm) = 0.0075), and from that of the Estuary zone (PERMANOVA pairwise comparison: Mean Sq. = 2.275, d.f. = 1, PseudoF = 12.11, p(perm) < 0.001) (Fig. 5a, b). Fish larvae composition also differed between the Surf zone and the Estuary zone (PERMANOVA pairwise comparison: Mean Sq. = 0.889, d.f. = 1, PseudoF = 3.55, p(perm) = 0.0163) (Fig. 5a, b).

Brevoortia aurea and *Hypleurochilus fissicornis* were the most contributing species to the differences between the Ocean zone and the Estuary zone during Early summer (SIMPER contribution = 92.77%; Table 5), being both species more abundant in the Estuary zone. During Late summer, Engraulidae family and *G. parri* contributed most to the differences observed between the Ocean zone and the Surf zone (SIMPER contribution = 96.28%, Table 5) and to the differences between the Ocean zone and the Estuary zone (SIMPER contribution = 92.82%, Table 5). Higher densities of both species were collected at the Ocean zone. In the case of the differences found between the Surf zone and the Estuary zone, *B. aurea* and *P. orbignyanus* were the most cointributing species (SIMPER contribution = 78.75%, Table 5). The former was more abundant in the Estuary zone whilst the latter was more abundant in the Surf zone.

Overall, postflexion stage larvae were more abundant and frequent over the other stages in all three zones (Table 3). However, lengths of fish larvae caught in the study area differed significantly among zones during both, Early and Late summer (Table 1). For the former period, postflexion stage larval fishes

were dominant at the Ocean zone (mean = 25.86 mm BL, median = 25.86 mm BL), yolk sac stages were dominant at the Surf zone (mean = 1.94 mm BL, median = 1.94 mm BL) and preflexion stage larval fishes were dominant at the Estuary zone (mean = 13.13 mm BL, median = 14.95 mm BL) (Fig. 6a). However, only significant differences between the Ocean zone and the Estuary zone (W = 293, P = 0.029) and between the Surf zone and the Estuary zone (W = 2.5, P = 0.0173) were found, as revealed by *a posteriori* Mann–Whitney U-test (Table 1). During Late summer, postflexion stage larval fishes were dominant at the three zones (Fig. 6b). *A posteriori* Mann–Whitney U-test (Table 1) revealed only significant differences between the Ocean zone and the Estuary zone (W = 32 274, P = 0.0001). Larger fish larvae were collected at the Estuary zone (mean = 17.21 mm BL, median = 20.5 mm BL) compared with those collected at the Ocean zone (mean = 14.91 mm BL, median = 13.69 mm BL).

Fish composition related to physical environment

The CCA explained 33.3% of the total variability found in the relationship between environmental variables and species composition. Axes 1 and 2 accounted for 60.96% and 30.81% of the explained variability, respectively. Wind speed and salinity were removed from the CCA since they were not of significant contribution (P = 0.650 and P = 0.261, respectively). According to vector length, wind direction (−0.788) and tidal stage (0.546) were best correlated with axis 1, and distinguished Ocean zone sampling stations with ebb tide and onshore winds conditions on the left (Fig. 7). Whereas temperature (0.807) and rainfall (−0.554) were best correlated with axis 2, and distinguished Surf zone and Estuary zone sampling stations (with warmer and less rainfall amount conditions) on the top, and Ocean zone sampling stations (with cooler and higher rainfall amount conditions) on the bottom.

Associations between environmental parameters and the most abundant species were also observed (Fig. 7). *Micropogonias furnieri*, *P. orbignyanus* and the Engraulidae family were associated to onshore winds, ebb tide, high temperature and low rainfall amount conditions on the top-left of the ordination diagram. *Cynoscion guatucupa*, *U. canosai*, *G. parri* and *A. marinii* were also associated to onshore winds and ebb tide, but low temperature and rainy conditions on the bottom-left of the ordination diagram. *Brevoortia aurea* and *H. fissicornis* were the only species associated to flood and offshore winds

Table 3. Species, total density (ind. 100 m^{-3}) by developmental stage and body length (BL, mm) range of fish larvae collected between December 2009 and March 2010 in Mar Chiquita lagoon inlet channel and its surrounding coastal area

Ys: yolk sac, Pr: preflexion, Fl: flexion, Po: postflexion, Ej: early juvenil. Average fish larvae density collected by zones and the corresponding number of sampling stations are also given. Standard deviation in brackets

|	Ocean						Surf				Estuary					
	Ys	Pr	F	Po	Ej	BL (mm)	Ys	Po	Ej	BL (mm)	Ys	Pr	F	Po	Ej	BL (mm)
Anchoa marinii	–	–	–	130.3	–	11.19–29.1	–	2208.1	6808.2	17.87–24	–	–	–	–	14.2	24.55
Brevoortia aurea	–	–	–	–	–	–	–	14.2	–	4.51	169.9	254.8	254.8	10615.7	4699.2	3.03–51
Cynoscion guatucupa	–	–	–	481.6	289.5	5.34–41	–	–	–	–	–	–	–	14.2	–	19.78
Engraulidae	–	–	–	3732.2	15.8	8.52–34	–	–	–	–	283.1	–	35.4	35.4	70.8	2.01–26
Engraulis anchoita	–	–	42.1	11.8	–	15.2–20.4	–	–	–	–	–	–	–	–	–	–
Gobiosoma parri	–	21.1	–	3790.1	–	3.84–14.9	–	–	–	–	–	–	–	14.2	–	6.51
Hypleurochilus fissicornis	3.9	–	–	–	–	1.32–1.68	28.3	–	–	1.92–1.95	325.5	56.6	–	–	–	1.89–2.67
Macrodon ancylodon	–	–	–	6.6	–	21–23	–	–	–	–	–	–	–	14.2	–	15.53
Menticirrhus americanus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14.2	20.04
Micropogonias furnieri	–	–	–	307.9	–	5.34–26.1	–	353.9	–	–	–	–	–	127.4	–	5.01–21.71
Paralichthys orbignyanus	–	–	–	–	–	–	–	–	–	5.18–8.02	–	–	–	84.9	–	7.68–9.35
Peprilus paru	–	–	–	1.3	–	23	–	–	–	–	–	–	–	–	–	–
Porichthys porosissimus	–	–	–	1.3	3.9	19.54–45	–	–	–	–	–	–	–	–	–	–
Stromateus brasiliensis	–	–	–	1.3	1.3	19.21–32.5	–	–	–	–	–	–	–	–	–	–
Umbrina canosai	–	–	–	56.6	–	6.35–16.7	14.2	–	–	2.07	–	–	–	–	–	–
Type A larvae	–	–	–	–	–	–	–	–	–	–	14.2	–	–	–	–	1.95
Type C larvae	–	–	–	–	–	–	–	–	–	–	14.2	–	–	–	–	1.62
Type F larvae	–	–	–	–	–	–	–	–	–	–	28.3	–	–	–	–	1.59–1.65
Type G larvae	–	–	–	–	–	–	–	–	–	–	14.2	–	–	–	–	2.19
Total	3.9	21.1	42.1	8521	310.5		42.5	2576.2	6808.2		906.1	254.8	290.2	10906	4798.4	
Average density				889.6 (1500.72)				314.2 (1630.86)					357.4 (1773.17)			
Total sampling stations				10				30					48			
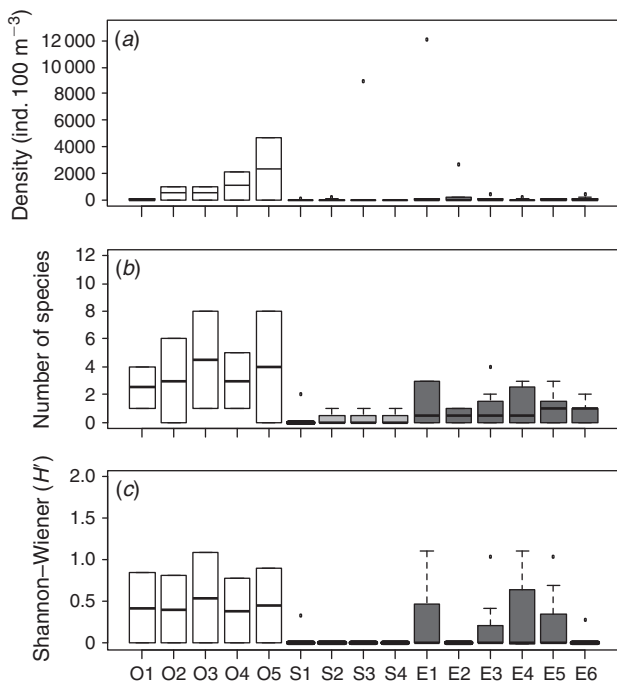
Fig. 4. Spatial variation in (*a*) fish larvae density, (*b*) number of species and (*c*) Shannon–Wiener diversity along the ocean–estuarine gradient in Mar Chiquita coastal lagoon (line: median; box: 25th to 75th percentiles; whiskers: minimum to maximum value range).

Table 4. Summary results from two-way PERMANOVA testing differences for zones, seasons and their interaction on fish larvae species density (ind. 100 m^{-3})

Mean Sq.: mean square, d.f.: degrees of freedom

Source	df	Mean Sq.	PseudoF	p(perm)
Zones (A)	1	0.608	2.32	0.0513
Seasons (B)	2	1.317	5.14	<0.0001
A × B	2	0.794	3.03	0.0013
Residuals	33	0.262		
Total	38			

conditions on the right of the ordination diagram. The former was also associated to high temperature and low rainfall amount on the top of the diagram whilst the latter was associated to the opposite conditions on the bottom of the diagram (Fig. 7).

Discussion

Mar Chiquita as nursery ground for early life history stages of coastal fishes

Our results revealed that fishes use the Mar Chiquita lagoon inlet and adjacent coastal area as nursery ground for early life stages. According to the presence of planktonic eggs in early developmental stages throughout the study area (Table 2), it can be thought that, at least part of them could be spawned inside the
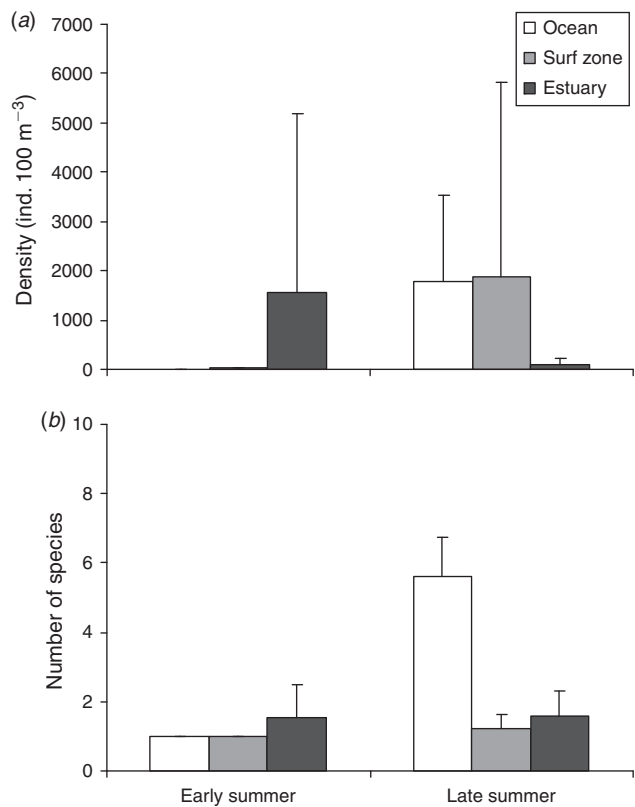

Fig. 5. Temporal variation of fish larvae density and number of species along the ocean–estuarine gradient in Mar Chiquita coastal lagoon.

lagoon. However, reports on reproductive stages of adult fishes inside Mar Chiquita lagoon show a lack of gravid females for those species having planktonic eggs (Cousseau *et al.* 2011; González-Castro *et al.* 2011); therefore most of the eggs and larvae occurring in the lagoon should be spawned at sea. However, Cousseau *et al.* (2011) speculated that although most individuals of *B. aurea* were at incipient maturation or spent stages, the presence of few individuals in advanced maturation could indicate that some spawning may also occur inside the lagoon. The high abundances of *B. aurea* eggs and larvae (in almost all developmental stages) collected within the Estuary zone during our study supports such hypothesis, and consequently the larvae of *B. aurea* found in our study could be spawned either, inside and/or outside Mar Chiquita. Nevertheless, as postflexion larvae were dominant in both the Surf zone and the Estuary zone (Table 3), the bulk of the spawning should be at sea. Moreover, eggs of *Trichiurus lepturus* (a marine spawner; Weiss 1981) and unidentified yolk sac larvae (with very low densities) collected inside the lagoon (Table 3) would have been dragged by the currents from the sea.

The presence of gravid females within the lagoon have been only reported for the benthic-eggs spawner (*sensu* Balon 1975) *Odontesthes argentinensis* (González-Castro *et al.* 2009), but during the present study, no larvae of this species were collected. The blenny *H. fissicornis* is another benthic-eggs spawner whose yolk sac larvae have been abundant in the Estuary zone during this study. Spawning of this species have been reported in caves over rocky intertidal bottoms 5 km south of Mar

Table 5.   Discriminating species (% contribution) of the dissimilarity between groups defined by pairwise PERMANOVAs, using SIMPER analysis

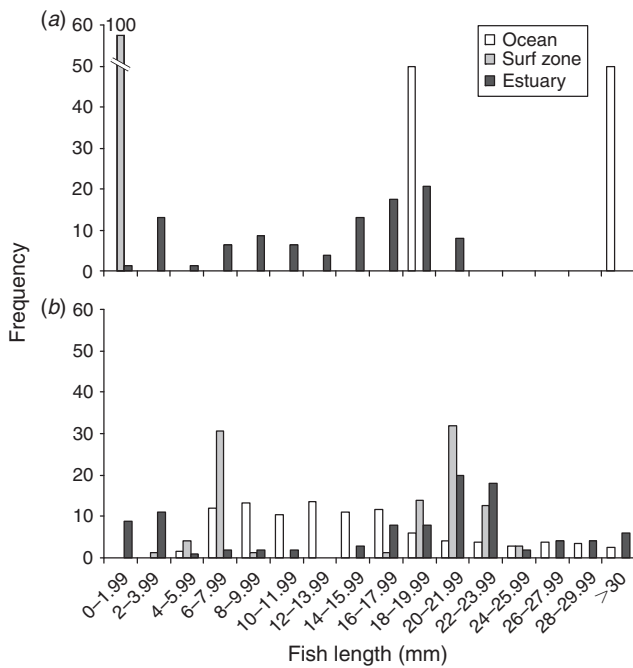|	Early summer	Late summer		
	Ocean *v.* Estuary	Ocean *v.* Surf zone	Ocean *v.* Estuary	Surf zone *v.* Estuary
Average dissimilarity (%)	92.77	96.28	92.85	78.75
Species contribution (%)				
Anchoa marinii	–	7.82	7.73	1.15
Brevoortia aurea	34.49	9.57	11.39	30.3
Cynoscion guatucupa	3.79	13.13	15.16	4.32
Engraulidae	4.99	20.9	18.94	5.05
Gobiosoma parri	–	19.1	18.62	2.46
Hypleurochilus fissicornis	28.95	–	4.33	10.52
Macrodon ancylodon	3.79	0.98	0.99	–
Micropogonias furnieri	5.12	9.96	10.1	–
Paralichthys orbignyanus	2.11	10.02	0.75	24.94
Stromateus brasiliensis	9.51	–	–	–
Umbrina canosai	–	4.79	4.84	–

Fig. 6.   Temporal variation on fish larvae length–frequency for (*a*) Early summer and (*b*) Late summer by zones sampled along the ocean–estuarine gradient in Mar Chiquita coastal lagoon.

Fig. 7.   Ordination diagram (triplot) of the CCA analysis. Arrows represent environmental variables. Principal species incorporated in CCA are abbreviated as: Ba, *Brevoortia aurea*; Eng, Engraulidae family; Hf, *Hypleurochilus fissicornis*; Mf, *Micropogonias furnieri*; Po, *Paralichthys orbignyanus*; Am, *Anchoa marinii*; Gp, *Gobiosoma parri*, Cg, *Cynoscion guatucupa* and Uc, *Umbrina canosai*.

Chiquita's inlet (Delpiani *et al.* 2012). Since a muddy substrate characterised the inlet channel, reproductive events of *H. fissicornis* within Mar Chiquita seems not to be feasible. However, the species might be taking advantage of cavities within the jetty close to Mar Chiquita's inlet (Fig. 1), and then larvae could be dragged inwards by currents.

Spawning at sea and the subsequent eggs and early larvae entering inside the lagoon is also the most common life cycle for those fishes inhabiting the Patos Lagoon (southern Brazil) (Muelbert and Weiss 1991). Despite the larger size area of Patos
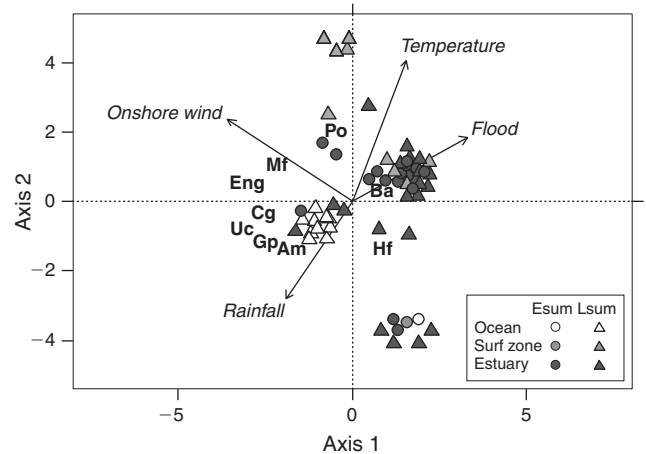
Lagoon (10 360 km^2) compared with Mar Chiquita coastal lagoon (46 km^2), both systems have a very similar shape, host a common ichthyofauna (e.g. Cousseau *et al.* 2001; Garcia *et al.* 2003; González-Castro *et al.* 2009), and the dominant reproductive strategy for fishes (i.e. the 'saltwater spawner' *sensu* Whitfield 1999) is the same. In between both lagoons, the Río de la Plata estuary (35°S) is characterised because spawning activity by fishes laying planktonic eggs is a rather common event (e.g. Acha *et al.* 2008). Several fish species from both Patos and Mar Chiquita lagoons that spawn at sea, spawn well inside the estuary in the Río de la Plata, in which the existence of retention mechanisms for plankton has been proposed (Acha *et al.* 1999; Simionato *et al.* 2008; Braverman *et al.* 2009). All this evidence illustrates how behavioural flexibility may give to the individuals of the same species the ability to respond effectively to different local environmental conditions.

Patterns of diversity and abundance

A knowledge of the coupling between nearshore waters and estuaries is necessary to understand the variability in estuarine recruitment patterns (Harris *et al.* 2001), but can also aid in our understanding of estuarine dependence and nursery habitats (Harris *et al.* 2001). A high to low species diversity along the ocean–estuarine gradient is expected in estuaries where the fish community is dominated by species with a marine origin (e.g. Muelbert and Weiss 1991; Harris *et al.* 2001). Although all fish species collected during this study were of marine origin, there was no clear gradient in fish larvae density, species richness and diversity as observed, for example, by Harris *et al.* (2001) in the ocean–estuarine gradient of St. Lucia estuary (South Africa). Despite average number of species were significantly higher in the Ocean zone than in the Estuary, overall species richness was slightly higher in the Estuary (Table 3). Moreover, five species (of a total of 19): *E. anchoita*, *P. paru*, *P. porosissimus*, *S. brasiliensis* and *U. canosai*, were restricted to the Ocean zone. All these evidences indicate that a high number of fish species use Mar Chiquita lagoon as nursery ground for larvae. On the other hand, the Surf zone presented the lowest average values of fish density, number of species and diversity (Table 1). The dynamic nature of the surf zones creates a highly heterogeneous habitat (Watt-Pringle and Strydom 2003), with increased levels of environmental stress (disturbance), which have generally been considered to decrease diversity (Harris and Cyrus 2000). Moreover, the fact that all species collected in the Surf zone were also present in the Estuary zone and/or the Ocean zone, account for an area that is not used as a complementary nursery ground, but as a transient corridor for fish larvae between the offshore spawning ground and the estuarine nursery ground within Mar Chiquita. Although there is evidence of the use of surf zones adjacent to estuaries' mouth as nursery ground for fish larvae (e.g. Whitfield 1989*b*; Harris *et al.* 2001; Watt-Pringle and Strydom 2003), Kjerfve and Magill (1989) stated that choked lagoons (like Mar Chiquita) are usually found along coasts with high wave energy and significant littoral drift. So, the harshness of this particular system may be not suitable for the retention of fish larvae, as was observed by Neira and Potter (1992) for the Wilson inlet (Australia) and by Cowley *et al.* (2001) for the East Kleinemonde estuary (South Africa).

Within Mar Chiquita lagoon, *B. aurea* larvae were dominant, followed by Engraulidae and *M. furnieri* larvae. Ichthyoplankton communities in South-western Atlantic estuaries appear to be strongly structured around Clupeidae or Engraulidae and Sciaenidae (Muelbert and Weiss 1991; Berasategui *et al.* 2004; Hoffmeyer *et al.* 2009), in agreement with our results. Although Clupeidae is also a dominant group in similar estuaries of Australia (Gaughan *et al.* 1990) and South Africa (Harris and Cyrus 1995; Harris *et al.* 1999), Gobiidae is the principal component in larval fish assemblages, which in our case study, was a dominant group outside the Mar Chiquita lagoon. All those examples corroborate the fact that these families use inner coastal systems during their life cycle, despite of their spatial scale and water exchange mechanisms with the sea (Macedo-Soares *et al.* 2009).

Coastal larval fish assemblages are identifiable but are dynamic with both their boundaries and composition changing over time (Cowen *et al.* 1993). Seasonal trends were evident in the composition of fish larvae at the ocean–estuarine gradient of Mar Chiquita, although the sampling period spanned four months only. During the first two months of sampling (i.e. Early summer) lower densities and number of species were collected in the Ocean zone and the Surf zone in comparison to the following two months (i.e. Late summer). For the former period, higher fish larvae densities were collected in the Estuary zone, mainly of *B. aurea* and *H. fissicornis*, which at the Ocean zone, were absent and lower, respectively. The higher values of fish larvae density collected during Late summer months have also been reported for similar worldwide estuaries (Muelbert and Weiss 1991; Neira and Potter 1994; Cowley *et al.* 2001). These temporal peaks tend to coincide with greater planktonic food sources and higher water temperatures (Dickey-Collas *et al.* 1996).

Also a seasonal variation in fish larvae length was observed, with dominant yolk sac and preflexion stages for the Early summer months and a dominance of postflexion stages during Late summer months. For the former period, *H. fissicornis* ($<2\,mm$) and both *H. fissicornis* ($<3\,mm$) and *B. aurea* ($<7\,mm$) were the dominant species in the Surf zone and the Estuary zone, respectively. This provides strong evidence that peak spawning by these species must occur over a similar period, as it was observed in the Swan estuary (Australia) for the dominant fish larvae species (Gaughan *et al.* 1990).

Migration into the lagoon

Two major phases of movements for recruitment into estuaries by species spawned offshore are recognised. The first is accumulation in the coastal zone. The second is the aggregation near inlets and estuary mouths and eventual passage through them (Boehlert and Mundy 1988). Aggregations of estuarine associated fish larvae in the inshore zone have been mainly related to winds, tides, river runoff and longshore currents (Boehlert and Mundy 1988; Raynie and Shaw 1994; Sanvicente-Añorve *et al.* 2000). The subsequent recruitment of fish larvae to temperate shallow estuaries have been related to tidal effects or to water properties such as temperature, salinity and/or turbidity (see Table 6 for references).

Several variables were selected to explain the recruitment process of fish larvae to Mar Chiquita lagoon (Fig. 7). Among them, salinity did not contributed significantly to the CCA ordination diagram. Although this variable was significantly different between the Ocean zone and the Estuary zone, our results may indicate that the ocean–estuarine salinity gradient in the study area is not important in the fish larvae recruitment process. The importance of salinity in this process has been established in several studies (see Table 6 for references), Whitfield (1994) also indicated that salinity gradients were the most important factor for larval fishes immigration into several estuaries of South Africa. However he suggested that olfactory cues associated with riverine inputs and hence estuarine outflow stimulate immigration of euryhaline fishes into estuaries and not salinity *per se*, so this could be the case in Mar Chiquita lagoon.

Rainfall, temperature, tidal stage and wind direction were of significant contribution to the CCA ordination diagram (Fig. 7). Five species (*A. marinii*, *C. guatucupa*, *U. canosai*, *H. fissicornis* and *G. parri*) of the nine incorporated in the analysis were

Table 6.   Main environmental factors related to fish eggs and larvae recruitment to and/or spatial distribution in selected estuaries worldwide

Estuary	Lat.	Region	Size of estuary (km^2)	Type of estuary	Environmental factors	Reference
Galveston Bay (USA)	30°N	Temperate	1550	Leaky lagoon	Tide, salinity	Fore and Baxter 1972; Glass *et al.* 2008;
Indian River Lagoon System (USA)	26°N	Subtropical	830	Three semi-isolated estuarine basins	Temperature	Reyier and Shenker 2007;
Araruama lagoon (Brazil)	22°S	Tropical	210	Choked lagoon	No spatial nor seasonal variations	De-Castro *et al.* 1999;
St. Lucia (South Africa)	28°S	Subtropical	325	Estuarine lake seasonally open	Temperature, salinity, turbidity	Harris *et al.* 1999; Harris *et al.* 2001;
Swan Estuary (Australia)	32°S	Temperate	53	Choked lagoon seasonally closed	Tidal current	Neira *et al.* 1992;
Patos lagoon (Brazil)	32°S	Temperate	10 360	Choked lagoon	Temperature, wind direction and intensity	Muelbert and Weiss 1991; Martins *et al.* 2007;
East Kleinemondi (South Africa)	33°S	Temperate	17.5	Coastal lagoon	Overwash events	Cowley and Whitfield 2001; Cowley *et al.* 2001;
Lake Macquarie (Australia)	33°S	Temperate	120	Coastal salt lake	Tidal current	Trnski 2001;
Wilson inlet (Australia)	35°S	Temperate	48	Coastal lagoon intermittently open	Tidal current	Neira and Potter 1992; Neira and Potter 1994;
Nornalup-Walpole (Australia)	35°S	Temperate	13	Coastal lagoon permanently open	Tidal current	Neira and Potter 1994;
Mar Chiquita (Argentina)	37°S	Temperate	46	Choked lagoon	Onshore winds	Present study

associated to cooler and rainy conditions. In our study, rainfall contribution to species ordination may be related to freshwater inputs. The river discharge, through its effect on estuarine water temperature, turbidity and salinity could also have a major influence on fish recruits (Whitfield 1994). The Vivoratá stream is one of the largest tributaries of Mar Chiquita lagoon. It is the only one reaching the channel (see Fig. 1) and its volume discharge depends on rainfall (Reta *et al.* 2001). Marcovecchio *et al.* (2006) stated that heavy rains can provide inorganic nutrients to Mar Chiquita lagoon due to the use of fertilizers on the surrounding fields for farming, and the consequent leaching of the soils by freshwater runoff. The five species mentioned above, except *G. parri* are all of marine origin. Given the fact that salinity was not of significant contribution, and that these species were mainly collected on the Ocean zone (with salinity values recorded between 30 and 34), it is possible that the association found to rainy conditions is merely related to an increase of olfactory cues related to the inorganic nutrients supply.

Temperature gradients have been also recognised as an important stimuli to facilitate estuarine recruitment (see Table 6), mainly because fishes show temperature tolerances and preferences (Boehlert and Mundy 1988). Given the fact that no significant differences in water temperature among zones were observed in this study, it may be assumed that temperature gradients in this particular estuarine system are weak during summer months. Nevertheless, it may be argued that preferences of temperature differed among larval fish species that inhabit Mar Chiquita lagoon and its surrounding coastal area., *A. marinii*, *C. guatucupa*, *U. canosai*, *H. fissicornis* and *G. parri* were associated to cooler conditions while *B. aurea*, *M. furnieri*, *P. orbignyanus* and Engraulidae larvae were associated to warmer conditions.

Wind direction was the parameter that best contributed to explain data variability (Fig. 7) supporting our hypothesis. Indeed, most species were associated to it. Tidal stage was also of significant contribution in the CCA triplot. However most of the species were associated to ebb and only two (*B. aurea* and *H. fissicornis*) were associated to flood. This mean that the wind effect would be imposed upon the tidal effect in this microtidal choked lagoon. This is the opposite of what was observed on several microtidal estuaries worldwide (see Table 6), where fish larvae recruitment depends on currents related to tidal cycles.

The wind effect on fish larvae recruitment and distribution into shallow estuaries worldwide could be underestimated (see Table 6). It have been incorporated only on numerical models that coupled biological and physical information to study fish and/or invertebrate larvae transport through the continental shelf (e.g. Blanton *et al.* 1999; Epifanio and Garvine 2001; Santos *et al.* 2004) and large estuaries (e.g. Simionato *et al.* 2008). It was also employed to study fish eggs dispersion at the Patos Lagoon estuary (Martins *et al.* 2007). In all cases, the authors concluded that the transport of particles is controlled by wind action. Also, Martins *et al.* (2007) argued that fish productivity inside estuarine systems (like the Patos estuary, Brazil) is highly dependent on the passage of weather fronts during Spring months when fish eggs are more abundant in the ocean. According to Reta *et al.* (2001) wind zonal component (W-E) is the main force responsible for Mar Chiquita's water level oscillations. Strong winds from the sea (SW, S, SE, E) during spring tides help the marine waters to enter into the lagoon several kilometers from the mouth (Reta *et al.* 2001). The association to onshore winds by most of the species in larval stage (Fig. 7) would be indicating that winds, in addition to pushing seawater into the lagoon, contribute to species

colonisation of the inlet area of Mar Chiquita in order to accomplish the second phase of recruitment. Moreover, wave period and height may be influenced by wind action (Knauss 1997). The surrounding coasts of Mar Chiquita lagoon are characterised by a moderate to high wave energy (Martos *et al.* 2004; Merlotto and Bértola 2009). This would explains why fish larvae move into Mar Chiquita lagoon once they are pushed into the coast, instead of remaining in a highly turbulent environment like the surf zone.

Therefore, the inorganic nutrients supply from the surrounding fields of Mar Chiquita (Marcovecchio *et al.* 2006) that may act as olfactory cues coupled with the variable entrance/discharge of water depending on wind direction (Reta *et al.* 2001) may be a critical combination for the orientation of fish early life stages in order to accomplish the first phase of accumulation.

Why recruit to Mar Chiquita coastal lagoon?

Mar Chiquita coastal lagoon is bounded by two major nursery grounds for coastal fishes, the Río de la Plata estuary to the north and the El Rincón-Bahía Blanca estuary to the south. Notwithstanding, species persistently attempt to recruit to this small coastal lagoon, characterised by a narrow inlet and unpredictable water dynamics. Three hypotheses can be proposed to asses the meaning of such behaviour. First we can consider an opportunistic behaviour by fishes. Coastal species could reproduce all along the coastal system and if larvae or juveniles find some estuarine environment simply take advantage of it. Due to their characteristics, coastal lagoons are usually among those marine habitats with the highest biological productivity (Agostini *et al.* 2002; Pérez-Ruzafa *et al.* 2007), functioning as nurseries and feeding grounds for opportunistic marine-estuarine fish (Pérez-Ruzafa *et al.* 2007). Second, we can think in density-dependent habitat selection (e.g. MacCall 1990): if habitat suitability is depleted because of an increase in the numerical density of individuals (i.e. interspecific competition is intensified in a crowded population), suboptimal habitats (Mar Chiquita lagoon in our case) become more attractive. However, high fishing pressure on coastal stocks in our region has diminished fish populations (e.g. Jaureguizar and Milessi 2008), and probably individuals' density in the major nursery grounds. Third, we need to consider that present-day estuaries are geologically ephemeral coastal features. Sea level rise and fall events have occurred regularly during the past few million years, causing shifts in the position of coastlines worldwide, and in the locations of estuaries. Moreover, once formed, estuaries quickly fill with sediments and essentially disappear (Snedden *et al.* 2013). The species and types of biological communities that presently exist in estuaries have certainly existed for much longer than the estuaries themselves. Even though particular estuaries are relatively short lived, estuarine organisms and estuarine ecosystems are very old (Day *et al.* 2013). So, in some way species are able to cope with the short-lived nature of the estuaries. Spawning inside or in the nearby of all the estuaries in the species' distributional area can be seen as a spread-risk strategy assuring that any time some group of individuals find an appropriate reproductive and/or nursery ground; and this could be the meaning (at evolutionary time-scales) of those nursery grounds located at such small coastal lagoons in a region where major estuaries do exist. Finally, natural variability of estuaries may be augmented by processes related to climate change. Any change in either the ocean or the watershed of the estuary due to climate change has the potential to affect estuaries. Currently, climate change is affecting both the oceans (i.e. rising sea level) and watersheds (i.e. changes in freshwater runoff) (Rybczyk *et al.* 2013). In this context, a spread-risk strategy may contribute to improve species' resiliency to face natural variability and that induced by human activities.

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