



Diel variation of ichthyoplankton recruitment in a wind-dominated temperate coastal lagoon (Argentina)

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ABSTRACT

This study aimed to assess the diel changes of ichthyoplankton occurrence, during a known recruitment period, to a wind-dominated coastal lagoon (Argentina). We collected plankton samples at three sites of the lagoon's inlet area every 3 h during four 24 h cycles in mid austral summer. For each early-life history stage (eggs, yolk sac, preflexion larvae, postflexion larvae and early juveniles), the relationship between the abundance and possible combinations of the time of sampling, the wind effect, the wave period and the tidal state was evaluated by fitting generalized linear mix-effects models (GLMM). The wind effects depending on the time of sampling mainly affected fish abundance in all developmental stages. Overall, the highest abundances were collected at nocturnal hours when low-speed offshore winds blew. In addition, higher abundances of eggs, yolk sac and preflexion larvae were related to the incoming flood tide; whereas higher abundances of postflexion larvae and early juveniles were related to longer wave periods. We argued that the daily variation in the abundance of early-life history stages of fishes is related to the sea-land breeze cycle. Therefore, a conceptual framework of the recruitment process of eggs, larvae and early juveniles of fishes into this estuarine system considering the daily effect of winds is proposed.

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1. Introduction

Fishes vary their behavior and activity in response to rhythmic environmental cycles. For instance, teleost fishes perform cyclic changes in their position within the water column that occur with 24-h periodicity (diel), being often more evident during the first year of life (e.g., Neilson and Perry, 1990; Strydom and Wooldridge, 2005; Aceves-Medina et al., 2008; Primo et al., 2012; Nickols et al., 2013). Furthermore, tidal cycles are known to affect the structure of fish larvae assemblages in several estuarine environments (e.g.,

Neira and Potter, 1992; Trnski, 2001; Strydom and Wooldridge, 2005; Bonecker et al., 2009).

Estuarine environments are essential habitats for many fish species for reproduction, serving as important nursery areas (Aceves-Medina et al., 2008). In the case of estuaries and/or coastal lagoons, this raises a special interest in understanding the strategies fish larvae display for successful recruitment and maintenance in inlets in the face of the advection processes resulting from flood and ebb tides and alongshore currents (Boehlert and Mundy, 1988). Marine larval fish are planktonic and depend on hydrodynamic processes, among other factors, for dispersal and transport into suitable nursery grounds (Dege and Brown, 2004). As early-life history stages of fishes have limited ability for swimming long distances, some researchers have suggested that the recruitment

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mechanisms to inlets are entirely passive (Rijnsdorp et al., 1985). However, others have suggested that this underdeveloped ability to swim is enough to allow early-life history stages of fishes to do some deliberate movements. In those estuaries deep enough to allow for stratification, vertical movements, which are closely related to diel and tidal rhythms, enable them to reach or remain in certain favorable areas to control passive drift (Weinstein et al., 1980; Boehlert and Mundy, 1988; Joyeux, 1999; Primo et al., 2012). For shallow estuaries, on the other hand, active swimming against ebb currents, especially at dark periods, has been proposed (Trnski, 2001; Strydom and Wooldridge, 2005; Patrick and Strydom, 2014).

Although the hydrodynamics in most estuaries worldwide are largely influenced by tidal cycles, in coastal lagoons with a long, narrow and shallow inlet channel (choked lagoons, *sensu* Kjerfve and Magill, 1989) the wind effect is significant. This is mainly due to a decrease in tidal energy along the inlet channel because of its morphology (Kjerfve, 1994; Kjerfve and Magill, 1989). Considered as an UNESCO Biosphere Reserve (UNESCO, 1996), Mar Chiquita Lagoon (37°32'S, 57°19'W; Argentina), is a small (46 km²) and very shallow (0.80–3 m) choked lagoon affected by semi-diurnal small amplitude (<1 m) tides (Reta et al., 2001). Strong (>10 m s⁻¹) offshore winds (N and NW) increase the discharge of this lagoon even during the incoming flood tide, while strong onshore winds (SW, S, SE and E) increase saltwater intrusion into the lagoon (Reta et al., 2001). Recruitment of young fishes into the lagoon has been demonstrated to be mediated by the wind effect rather than by tides (Bruno and Acha, 2015). Most of the eggs and larvae occurring in the lagoon are believed to be spawned at sea and the subsequent entry inside the lagoon is aided by onshore winds (Bruno et al., 2014; Bruno and Acha, 2015). However, to reach the lagoon early-life history stages of fishes must cross through a surf zone characterized by moderate-energy wave action (Bértola, 2006). Because such feature was argued to not be very effective for the retention of fish larvae (Bruno et al., 2014), the immediate sea area off the surf zone was proposed to act as an accumulation area for early-life history stages of fishes until optimal conditions (e.g., onshore winds, low-energy wave action) to facilitate the entry into the lagoon are presented (Bruno and Acha, 2015).

At certain scales, winds may behave in a more predictable way, as is the case of the sea-land breeze. Under particular synoptic conditions, such as high land insolation, very mild synoptic winds and low cloud cover (Pattiaratchi et al., 1997; Gassmann et al., 2002) the sea-land breeze cycle develops. This cycle consists of a strong onshore breeze (sea breeze) from midday to the late afternoon and then an offshore breeze (land breeze) of much lower intensity from dusk to the next morning (Pattiaratchi et al., 1997; Reta et al., 2001; Gassmann et al., 2002). At a temporal scale of several days/weeks the recruitment of early-life history stages of fishes to Mar Chiquita Lagoon is wind-mediated (Bruno et al., 2014, 2015; Bruno and Acha, 2015). However, this lagoon is under the effects of a marked sea-land breeze cycle during summer months (Reta et al., 2001; Gassmann et al., 2002), which could induce diel variations in the ichthyoplankton occurrence in the estuary.

Therefore, the aim of this study was to assess diel changes in the ichthyoplankton occurrence in the lagoon inlet area. We hypothesized that, in the context of a wind-dominated system, ichthyoplankton abundance varies according to wind rhythms related to the diel cycle. We expected higher abundances of larvae and early juveniles at nocturnal rather than diurnal hours, as observed in similar estuarine systems (e.g., Trnski, 2001; Strydom and Wooldridge, 2005; Patrick and Strydom, 2014), due to the sea-land breeze cycle.

2. Materials and methods

2.1. Study area

The Mar Chiquita Coastal Lagoon is located in the southeastern coast of the Buenos Aires Province (Argentina) (Fig. 1a). The lagoon has an elongated shape with a general NNW-SSE direction (Fig. 1b) and receives the freshwater discharges of several streams and canals (Reta et al., 2001). Mudflats and surrounding marshes dominated by the cordgrass, *Spartina densiflora* (Family: Poaceae) (e.g., Isacch et al., 2006), and the burrowing crab, *Neohelice granulata* (Family: Varunidae) (e.g., Iribarne et al., 1997) characterize this very shallow lagoon. The lagoon is connected to the sea by means of a 6-km-long and 200-m-wide inlet channel with a sandy-muddy bottom and a depth ranging from 0.8 to 3.0 m. This inlet channel



Fig. 1. Map of the study area. (a) Location of Mar Chiquita Coastal Lagoon (Argentina) in South America, (b) the region of Mar Chiquita Coastal Lagoon under study and (c) location of the sampling sites in the surf zone, in the mouth and in the inlet channel of Mar Chiquita Coastal Lagoon.

extends from the mouth to a bridge (about 5 km upstream) built at the head of the inlet. Tidal effect is perceived up to the bridge and, therefore, the inlet channel is the portion of the lagoon that has distinctly estuarine features (Reta et al., 2001). Upstream of the bridge, tidal effects are negligible (Reta et al., 2001). The adjacent marine environment where the lagoon discharges is characterized by sandy beaches (Merlotto and Bértola, 2009) with surf zones of moderate energy for most of the year (Bértola, 2006). However, strong southeasterly storms, which may last from one to six days and which peak in early spring and mid-summer, enhance the energy of the surf zones (Merlotto and Bértola, 2009).

The study area includes three sampling sites: in the surf zone (E01), in the mouth of the lagoon (E02) and in the middle portion of the inlet channel (E03) (Fig. 1c).

2.2. Biological and environmental sampling

A high-frequency sampling design was performed because diel changes in ichthyoplankton abundance is believed to act over short time periods (Castillo-Rivera et al., 2010). Moreover, samples were taken during the mid-austral-summer, because the highest abundance of fish larvae were previously reported between January and February (mid-austral-summer) (Bruno et al., 2014; Bruno and Acha, 2015). This sampling period was appropriate to cover the reproductive season of most fish species cited for the area, which range from early spring to late summer (Cousseau and Perrotta, 2004). Therefore, ichthyoplankton samples were collected at 3-h intervals during four 24 h cycles in January 2011 (07, 14, 21 and 28/01/2011) starting at 08:00 h and finishing at 05:00 h of the next day at three sampling sites (Fig. 1). A conical net with a 0.15 m² mouth area and a 300- μ m mesh span net was pulled twice against the prevailing current for 50 m parallel to shoreline at ~1 m depth at each site. The mean volume filtered in each tow was ~16 m³. The semidiurnal tidal regime in the area allowed us for sampling during ebb and flood tides at diurnal and at nocturnal hours in each 24 h sampling period. Samples were fixed and preserved in 4% buffered formalin-seawater solution and transported to the laboratory. Fish larvae and eggs 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). Eggs were counted and larvae were counted and measured to the nearest 0.01 mm using an ocular micrometer. Notochord length (NL) was measured for all preflexion and flexion larvae and total length (TL) for all postflexion larvae (Fuiman, 2002). These were termed as 'body length' (BL) for all species caught. The guild approach (Potter et al., 2015) was used to classify fishes comprising of four categories, marine, estuarine, diadromous and freshwater. For this study only the former two was applicable with the marine category being further divided into marine estuarine-dependent (MED), marine estuarine-opportunist (MEO) and marine stragglers (MS); with the estuarine category only divided into solely estuarine (SE).

Before each tow, water temperature (°C) and salinity were registered. The wave period (seconds between consecutive waves) was also recorded at the surf zone as a proxy for the turbulent energy and water pushed into the inlet area. Wind data were registered by the Mar del Plata Aero Meteorological station located 26 km northwest of Mar Chiquita (37,56°S - 57,4°W) and provided by the National Weather Service (Argentina). This meteorological station is the closest to the study area and, despite it is located several kilometers far from the coast, Gassmann et al. (2002) found it appropriate for recognizing the sea-land breeze phenomenon. Mean wind speed and mode wind direction during the sampling hour and the 2 h preceding sampling were calculated for statistical analysis. In order to evaluate the wind effect, wind direction and

speed were combined and turned into a four level categorical variable following Reta et al. (2001) and Bruno and Acha (2015). Winds from SW, S, SE and E were classified as "onshore winds" while winds from NE, N, NW and W were classified as "offshore winds". Wind speed was considered as low ($\leq 5 \text{ m s}^{-1}$) and moderate (> 5 and $\leq 10 \text{ m s}^{-1}$) following Reta et al. (2001).

2.3. Data analysis

Differences in water properties (temperature and salinity) among sites were evaluated with a Kruskal-Wallis test (K), followed by Steel-Dwass-Critchlow-Fligner (SDCF) post hoc test (W_{ij}). In addition, differences in these parameters and in wind speed and wave period between diurnal and nocturnal hours were evaluated by a Wilcoxon rank sum test (W).

A three-way PERMANOVA using Bray-Curtis distances with 10000 permutations of matrix data (Anderson, 2001) was used to test the null hypothesis of no differences in the log ($x+1$)-transformed density (ind. 100 m⁻³) of fishes among developmental stages (yolk sac, preflexion, postflexion and early juvenile) by the hour of sampling (diurnal and nocturnal hours), the guild classification (marine estuarine-dependent (MED), marine estuarine-opportunist (MEO), and solely estuarine (SE), *sensu* Potter et al. (2015)), the sampling site (surf zone, mouth and inlet channel) and their interactions. Eggs were not included in the analysis because identification to species a level could not be achieved and, therefore, guild classification either.

To test the hypothesis that the abundance of ichthyoplankton is higher during nocturnal hours due to the sea-land breeze cycle, a multiple-hypothesis model approach was adopted (Franklin et al., 2001; Johnson and Omland, 2004). The abundance of all taxa by each developmental stage (i.e., eggs, yolk sac, preflexion, postflexion and early juvenile) was pooled and the guild classification was not considered (see PERMANOVA results). For each fish developmental stage, generalized linear mix-effects models (GLMM; Zuur et al., 2009) (Package lme4; Bates et al., 2015) were built with the number of fish captured as the response variable and the hour (eight levels), the wind direction (onshore, offshore) combined with the wind speed (low, moderate) and the tidal stage (flood, ebb) as explanatory fixed variables. The sampling sites are morphologically different among each other and water salinity was observed to also differ among them; therefore, and despite differences in fish density among sites were not observed, site was included in the models as a random factor to control for non-independence. According to previous results (Bruno and Acha, 2015), temperature and salinity were not considered as explanatory variables but wave period was included in the analysis. Therefore, models with possible combinations of the above indicated environmental factors were also fitted. Finally, a model without any of the independent variables (i.e. null model) was built to test the hypothesis that none of the variables tested had an effect on the fish abundance. Since models had large variance-mean relationships and many zero values characterized the samples, a negative binomial error distribution and a log link were specified (Crawley, 2005). Model selection was based on Akaike's information criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002, 2004) and the model with the lowest AICc was selected as the best. Models with a Δ AICc value less than 2 were considered to be 'equally good' following Burnham and Anderson (2002). Each model was weighed against the others using AICc weights (ω), which gives an estimation of the likelihood of the model's fit according to the data used (Burnham and Anderson, 2002, 2004).

All statistical analysis were done using R 3.3.1 software (R Core Team, 2016) and Addin-soft XLSTAT.

3. Results

3.1. Physical environment

No differences in water temperature was observed among sites ($K = 4.23$, $df = 2$, $p = 0.1205$) but values were in accordance to diel heat variation (Fig. 2), with warmer temperatures during diurnal rather than nocturnal hours ($W = 7650$, $p < 0.0001$). Water salinity varied among sites ($K = 5.99$, $df = 2$, $p < 0.0001$) with higher salinity at the mouth of the lagoon compared to the surf zone ($W_{ij} = 3.85$, $p = 0.0180$) and at the inlet channel ($W_{ij} = 6.40$, $p < 0.0001$). However, salinity did not vary significantly between diurnal and nocturnal hours ($W = 5320$, $p = 0.0568$) although a decrease in salinity was observed at 2:00 and 5:00 h on 21 of January (Fig. 2c).

Low wind speeds and calm periods, were dominant during the nocturnal hours ($W = 58892$, $p < 0.0001$) as expected, though wind direction was in accordance to the sea-land breeze cycle in just two of the four days sampled (Fig. 2). That is, low offshore winds blew at nocturnal hours on every day of sampling as expected (Fig. 2); but, during diurnal hours, moderate offshore winds blew on 07 and 21 of January (Fig. 2a and c) whereas moderate onshore winds blew on

14 and 28 of January (Fig. 2b and d). The typical conditions of wind direction for the sea-land breeze cycle were only reflected on the last two days mentioned.

Wave energy in the inlet area was clearly related to the wind intensity. Wave period in all four days of sampling was shorter during diurnal hours ($W = 2484$, $p < 0.0001$) with moderate winds while wave period was longer during nocturnal hours with low winds (Fig. 2).

3.2. Ichthyoplankton abundance and relationship with environmental variables

Planktonic eggs of *Brevoortia aurea* and an unidentified group occurred in all of the three sampling sites during the study period. Egg abundances were lower at diurnal than at nocturnal hours (Table 1).

Early developmental stages of twelve taxa were collected during the study period, (Table 1). Identification to the species level of larvae within the Engraulidae Family by means of morphological or meristic diagnosis was not possible due to a lack of specific dissimilarities. Therefore, the Engraulidae category (Table 1) includes unidentified individuals of likely *Anchoa marinii*, *Engraulis anchoita*

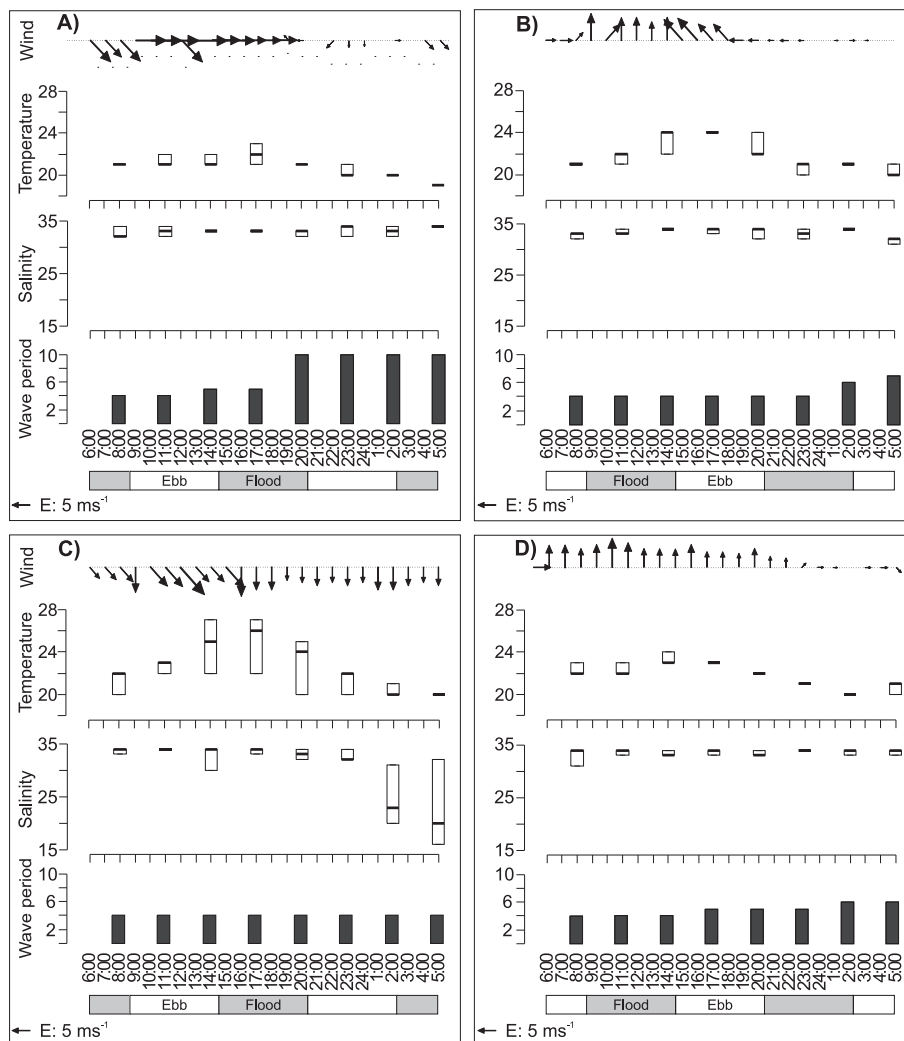


Fig. 2. Diel variation in the mode direction and the mean intensity ($m s^{-1}$) of the wind at the hour of sampling and the 2 h preceding sampling, water temperature ($^{\circ}C$) and salinity (line: median; box: 25th to 75th percentiles; whiskers: minimum to maximum value range), wave period (seconds) and tidal state registered at the study area on a) 07/01/2011, b) 14/01/2011, c) 21/01/2011 and d) 28/01/2011. Below each figure the scale of the wind direction and intensity is given.

Table 1

Taxa composition and guild classification (MED, marine-estuarine dependent; MEO, marine-estuarine opportunist; MS, marine straggler, SE, solely estuarine; *sensu* Potter et al., 2015) of early-life history stages of the fishes collected at the study area of the Mar Chiquita Coastal Lagoon. Total density (ind. 100 m⁻³) by developmental stage, the body length (BL) in mm (range) and the sites (S, surf zone; M, mouth; C, channel) of occurrence are given for diurnal and nocturnal hours.

Family	Taxa	Guild	Eggs					Site	Nocturnal hours					Site		
			Diurnal hours	Yolk sac	Pre-flexion	Post-flexion	Early juvenile		BL range (mm)	Yolk sac	Pre-flexion	Post-flexion	Early juvenile		BL range (mm)	
Engraulidae	Engraulidae	MEO	–	–	–	37.5	31.25	8.18–28.39	M/C	–	–	–	6.2	–	9.85	C
Clupeidae	<i>Brevoortia aurea</i>	MED	6.2	–	–	2881.2	1831.2	11.86–34	S/ M/C	18.7	–	–	8687.5	3893.7	8.85–34	S/ M/C
Gobiidae	<i>Gobiosoma parri</i>	SE	–	100.0	–	–	–	1.65–2.31	S/ M/C	–	493.7	50.0	–	–	1.77–2.82	S/ M/C
Mugilidae	<i>Mugil liza</i>	MEO	–	–	–	–	462.5	23–29	S/ M/C	–	–	–	–	393.7	24–28	S/ M/C
Blenniidae	<i>Hypleurochilus fissicornis</i>	MEO	–	56.2	131.2	–	–	1.65–2.16	S/M	–	187.5	868.7	–	–	1.53–2.61	S/ M/C
Atherinopsidae	<i>Odontesthes argentinensis</i>	MEO	–	–	6.2	–	75.0	5.34–32	S/ M/C	–	–	6.2	9.0	1206.2	5.52–34	S/ M/C
Paralichthyidae	<i>Paralichthys orbignyanus</i>	MED	–	–	–	37.5	–	6.68–7.51	M	–	–	–	18.7	–	6.01–7.68	S/ M/C
Cynoglossidae	<i>Symphurus jenynsii</i>	MEO	–	–	–	–	–	–	–	–	–	–	6.2	–	10.52	M
Trichiuridae	<i>Trichiurus lepturus</i>	MS	–	–	–	–	–	–	–	6.2	–	–	–	–	–	S
Sciaenidae	<i>Cynoscion guatucupa</i>	MED	–	–	6.2	–	–	4.17	C	–	–	–	12.5	–	7.51	M/C
	<i>Micropogonias furnieri</i>	MED	–	–	–	6.2	–	9.52	S	–	–	6.2	162.5	25.0	4.68–31	S/ M/C
	<i>Umbrina canosai</i>	MEO	–	–	–	6.2	–	16.20	C	–	–	–	31.2	–	8.35–19.54	M/C
Unidentified	Unidentified	–	87.5	–	6.2	–	–	2.10	S/ M/C	1575.0	–	–	–	–	–	S/ M/C

and/or *Lycengraulis grossidens*, which are known to occur in the study area (Cousseau and Perrotta, 2004). Almost all taxa were present at diurnal and nocturnal hours. However, overall abundance was higher at nocturnal than diurnal hours, except for the Engraulidae fish Family, *Mugil liza* and *Paralichthys orbignyanus* which were more abundant at diurnal hours (Table 1).

The hour of sampling and the guild classification were significant for the differences observed in the fish density by developmental stage (PERMANOVA results, Table 2). Overall, the density of fishes of all three guild classification and in every developmental stage was higher in nocturnal than in diurnal hours (Fig. 3). In addition, the developmental stages were represented by different guilds. For instance, the yolk sac stages collected were dominated by solely estuarine (SE) fishes, preflexion stages were mostly MEO fishes and postflexion and early juvenile stages were mostly MED fishes (Fig. 3).

According to the models used (Table 3), fish abundance for the very early developmental stages (i.e., eggs, yolk sac and preflexion larvae) in the inlet area of the Mar Chiquita Lagoon were mainly

affected by the hour, wind direction and speed and tidal changes. High abundances of eggs were collected when the combination of the flood tide and low-speed offshore winds occurred between 20:00 and 05:00 h, peaking at 20:00 h (Fig. 4a and b). Similarly, highest abundances of yolk sac and preflexion larva occurred on the flood tide during low-speed offshore winds but highest abundances were collected at 23:00 h (Fig. 4c–f). Postflexion larvae and early juveniles, on the other hand, were mainly affected by the hour, wind direction and wind speed and wave period, according to the models (Table 3). High abundance of fishes in both developmental stages was collected when the combination of low-speed offshore winds and long wave period (8–10 s) occurred between 20:00 and 05:00 h, with a peak at 23:00 h (Fig. 4g–j).

Table 2

Summary results from the three-way PERMANOVA testing for differences in the log (x+1)-transformed density (ind. 100 m⁻³) of fishes among developmental stages (yolk sac, preflexion, postflexion and early juvenile) by the hour of sampling (diurnal and nocturnal hours), the guild classification (marine estuarine-dependent (MED), marine estuarine-opportunist (MEO), and solely estuarine (SE), *sensu* Potter et al. (2015)), the sampling site (surf zone, mouth and inlet channel) and their interactions. Mean sq., Mean square; df, degrees of freedom. **p < 0.01; ***p < 0.001.

Source	df	Mean Sq.	Pseudo F	P (perm)	
hour (A)	1	0.752	4.013	0.0096	**
guild (B)	2	9.557	50.985	1.00E-04	***
site (C)	2	0.085	0.454	0.8267	
A x B	2	0.157	0.838	0.5339	
A x C	2	0.257	1.372	0.2276	
B x C	4	0.304	1.622	0.0929	
A x B x C	4	0.189	1.009	0.4367	
Residuals	199	0.187			
Total	216				

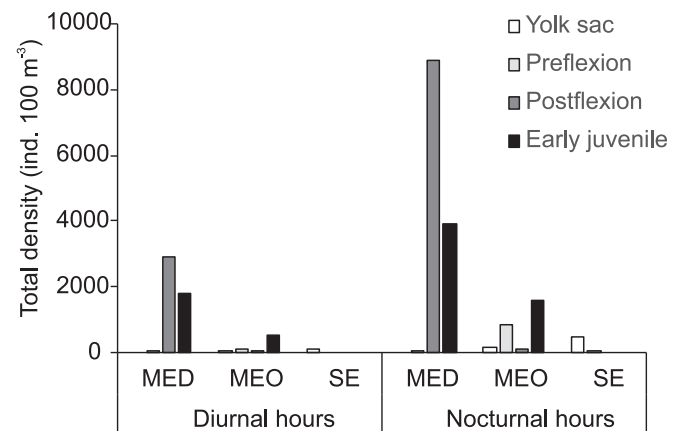


Fig. 3. Total density (ind. 100 m⁻³) by developmental stage of fishes collected during diurnal and nocturnal hours considering the guild classification (MED, marine-estuarine dependent; MEO, marine-estuarine opportunist; SE, solely estuarine dependent) from Potter et al. (2015) at the study area of the Mar Chiquita lagoon.

Table 3
Competing models for explaining the recruitment of fish developmental stages to Mar Chiquita lagoon. For each model, Akaike Information Criterion corrected for small sample size (AICc), degrees of freedom (df), the difference between AICc of the current model and the most parsimonious model (in bold) (Δ AICc), and the Akaike weight (ω) are given. Abbreviations: wavep, wave period.

Model	Eggs				Yolk sac				Preflexion				Postflexion				Early juvenile			
	AICc	df	Δ AICc	ω	AICc	df	Δ AICc	ω	AICc	df	Δ AICc	ω	AICc	df	Δ AICc	ω	AICc	df	Δ AICc	ω
Null	438.3	3	48.3	<0.001	311.8	3	11.4	0.0025	341.2	3	23.8	<0.001	735.9	3	89.6	<0.001	881.8	3	51.6	<0.001
hour	392.3	10	2.2	0.157	315.7	10	15.2	<0.001	330.4	10	13.1	0.0014	711.1	10	64.9	<0.001	856.1	10	25.9	<0.001
wind	417.5	6	27.4	<0.001	308.4	6	7.9	0.0134	335.9	6	18.5	<0.001	711.8	6	65.6	<0.001	863.7	6	33.5	<0.001
tide	439.7	4	49.6	<0.001	316.3	4	15.8	<0.001	335.4	4	18	<0.001	725.4	4	79.1	<0.001	877.3	4	47.1	<0.001
hour + wind	391.9	13	2.1	0.168	302.5	13	2.1	0.2538	328.9	13	11.6	0.003	709.9	13	63.6	<0.001	850.7	13	20.6	<0.001
hour + tide	393.9	11	3.8	0.072	317.3	11	16.9	<0.001	317.3	11	6.8	0.0321	712.3	11	66.1	<0.001	858.3	11	28.2	<0.001
hour + wind + tide	390.1	14	0	0.504	300.5	14	0	0.7129	324.1	14	0	0.9621	712	14	65.8	<0.001	853	14	22.9	<0.001
hour + wind + wavep	393.9	14	3.9	0.07	316.8	14	16.3	<0.001	332.1	14	8	<0.001	646.3	14	0	0.75	830.2	14	0	0.7268
wind + tide	419.5	7	29.5	<0.001	308.8	7	8.3	0.0112	330.7	7	13.3	0.0012	709.8	7	63.6	<0.001	863.8	7	33.7	<0.001
wind + wavep	419.5	7	29.5	<0.001	310.1	7	9.6	0.0057	337	7	19.6	<0.001	669.8	7	23.5	<0.001	841.2	7	11	0.0065
hour + wind + tide + wavep	395.7	15	5.6	0.029	317.1	15	16.6	<0.001	334.3	15	10.2	<0.001	648.5	15	2.2	0.25	832.3	15	2.1	0.2667

4. Discussion

4.1. Diel variation of the physical environment

With the exception of salinity, all environmental parameters recorded during the present study showed a diel variation cycle. Salinity showed almost no variation among sampling hours but for two events of very low values at 02:00 and 05:00 h on 21/01/2011, at the end of the sampling period. Moderate offshore winds blew throughout the day, and consistent with strong winds sustained over time, they may have increased the discharge of the lagoon even during the flood tide (Reta et al., 2001). Therefore, the low salinity values registered may be a consequence of the continuous discharge of continental water to the inlet area during that day rather than diel variations.

Water temperature showed a clear trend in relation to solar radiation with higher values during diurnal hours, peaking between 14:00 and 17:00 h during all four sampling events. Wave period also showed a diel variation. Such variation might be related to the diel variation of the wind intensity, as the wave period was longer during nocturnal hours with low-speed winds while wave period was shorter during diurnal hours when wind speed was higher. Wave period (and height) is known to be controlled by wind action (Knauss, 1997), and winds contribute to the moderate high wave energy which characterizes the surf zone close to Mar Chiquita Lagoon (Martos et al., 2004; Merlotto and Bértola, 2009). This highly turbulent environment was proposed to act as a transient corridor between the sea and the lagoon rather than an accumulation area for fish larvae (Bruno et al., 2014) in contrast to other surf zones near similar estuarine systems (e.g., Neira and Potter, 1992; Cowley et al., 2001; Watt-Pringle and Strydom, 2003). However, the results obtained during this study allow us to infer that the role of the surf zone close to Mar Chiquita Lagoon may change between diurnal and nocturnal hours. When synoptic conditions promote the sea-land breeze cycle, which affects only the lowest part of the atmosphere (100–400 m), the sea breeze (diurnal) can achieve significant speeds of 40–50 km h⁻¹, 10 m above sea level (Pattiaratchi et al., 1997) promoting a turbulent environment as strong synoptic winds do (Bruno et al., 2014). However, during this phenomenon, winds decrease in speed at night, decreasing the wave period and thus decreasing the turbulence. In such a scenario, the surf zone close to Mar Chiquita Lagoon may be a suitable environment for accumulation of early-life history stages of fishes and enabling the subsequent recruitment to the lagoon of a much larger amount of fishes.

4.2. Diel variation of ichthyoplankton abundance and the best predictors for recruitment to the lagoon

Our results revealed that the recruitment of early-life history stages of fishes (from planktonic embryo to early juvenile) to Mar Chiquita Lagoon is ruled by a combination of factors that act at a fine-scale. Such factors were the diel variation in the wind regime (thus not rejecting our hypothesis), and tide state and wave period for the less developed and the more developed fishes, respectively. In this regard, it is notable to mention that every developmental stage considered for this work was mainly represented by a different group of fish species that differ from each other in the use of estuarine environments. MED and MEO fishes have been previously mentioned as the more frequent and abundant groups of fishes that use Mar Chiquita Lagoon as a nursery area for juveniles and as a stopover site along migratory routes (González-Castro et al., 2009; Valiñas et al., 2010). This work shows that these groups of fishes use the lagoon as a nursery in yet earlier stages of their life. It is well known that MEO species worldwide also frequently use coastal marine waters as an alternative nursery habitat (e.g., Potter et al., 2015). Thus, larvae or juveniles stages of these species may simply take advantage of estuarine environments present all along the spawning coastal system. 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 (Fig. 1a). Considered as a suboptimal environment compared to the two larger nursery grounds, the persistent occurrence of fish larvae in this small coastal lagoon was argued to be related to a spread-risk strategy that may contribute to improve species' resiliency by reducing density-dependent pressures (Bruno et al., 2014). In addition, it was recently found that the Particulate Organic Matter (POM) composition in the coastal area close to Mar Chiquita Lagoon is comprised of a mix of primary producers including the detritus of the cordgrass, *Spartina densiflora*, originated within the lagoon, and marine phytoplankton (Bruno et al., 2017). This exported organic matter was argued to be beneficial by sustaining zooplankton organisms, which serve as food for young fishes waiting to enter and/or recently exited from Mar Chiquita Lagoon. Furthermore, POM may act as a possible olfactory cue, critical for the orientation of the early-life history stages of fishes (e.g., Whitfield, 1994) with marine origin, in the recruitment process to this micro-tidal estuarine system (Bruno et al., 2017).

Nevertheless, the distribution of fishes within Mar Chiquita Lagoon related to the wind effect at larger scales has been reported. Wind patterns were employed to explain the occasional presence of

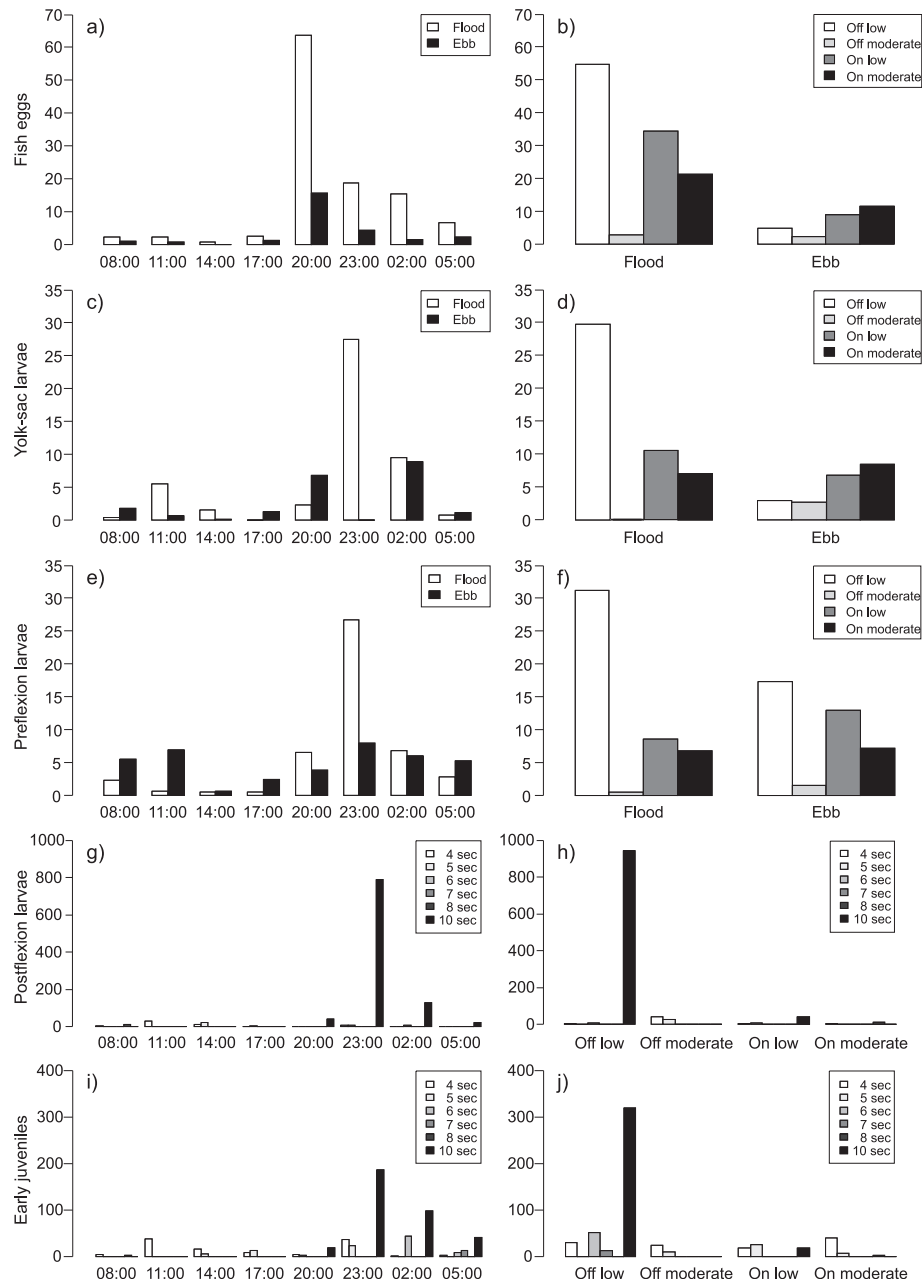


Fig. 4. Variation in the abundance of a-b) fish eggs, c-d) yolk sac larvae, e-f) prefixion larvae, g-h) postflexion larvae, and i-j) early juvenile fishes at the Mar Chiquita Coastal Lagoon, estimated by generalized linear mix-effects models (GLMM) with a log link and negative binomial error distribution.

tropical and subtropical marine teleost fishes (e.g., Díaz de Astarloa et al., 2000; Figueroa et al., 2000; González-Castro et al., 2006; Blasina et al., 2009; Bruno et al., 2011), the distribution of freshwater fishes from the tributary streams to the lagoon (Bruno et al., 2013) and the recruitment of larval and juvenile stages from the sea to the lagoon (Bruno et al., 2014, 2015; Bruno and Acha, 2015). Regardless of the season (spring or summer) in which fishes recruit to this system (Cousseau and Perrotta, 2004), strong onshore winds coupled with the penetration of seawater into inner estuarine areas of the lagoon are significant for the success of such entry (Reta et al., 2001; Bruno and Acha, 2015). We now show that winds act also at much shorter (diel) scales. Taking all this into account, we propose the following conceptual framework for the recruitment of early-life history stages of fishes into the lagoon.

In general, dispersal of coastal larvae is subject to the effects of a

coastal boundary layer, which is, in effect, a retention zone (Largier, 2003). Moreover, Bas et al. (2009) argued that several meters off the Mar Chiquita Lagoon, the winds generate a retention zone for crab zoea, which could also allow ichthyoplankton to be retained or minimize dispersion (Fig. 5, circular arrows off the inlet). In this context, early-life history stages of fishes remain in this accumulation area until environmental conditions facilitate their entrance into the lagoon. When synoptic moderate or strong onshore winds blow over a sustained period of time, whether during diurnal (Fig. 5a) or nocturnal (Fig. 5b) hours, ichthyoplankton is pushed onshore with the water mass, regardless of tidal state (Reta et al., 2001). However, the intensity of these winds increase the turbulence of the surf zone, and though some larvae can move into the lagoon (Bruno and Acha, 2015), such conditions are not the optimum for assuring fish recruitment. Conversely, when synoptic

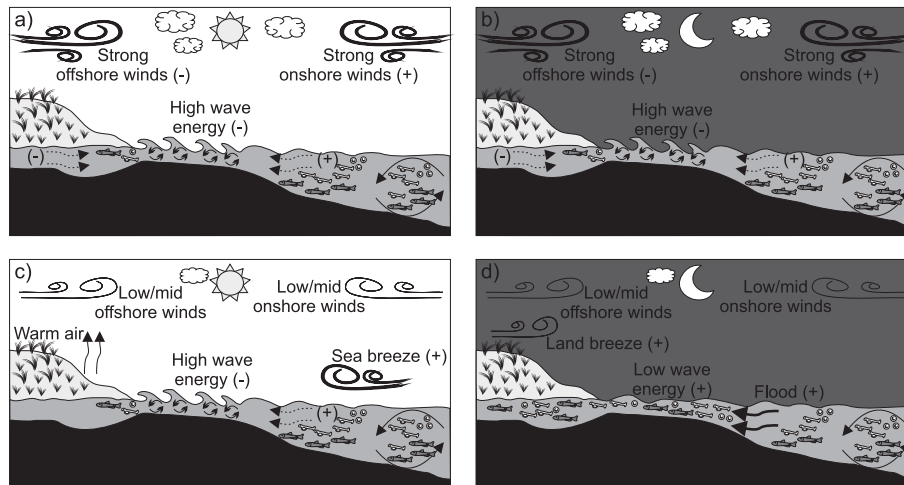


Fig. 5. Conceptual diagram of the wind effect (+ or -) on the recruitment of fishes to Mar Chiquita Coastal Lagoon during synoptic winds during the a) day and b) night and during the presence of the sea-land breeze phenomenon during the c) day and d) night. Dotted arrows show the movement of the water due to the wind effect. Small circular arrows denote the turbulence of the environment while large circular arrows show the potential accumulation area off the region of the mouth of the Mar Chiquita Coastal Lagoon. Black thick arrows show the direction of water during flood.

moderate or strong offshore winds blow continuously over time, the recruitment is inhibited (Fig. 5a and b) by preventing the entrance of seawater and by enhancing the lagoon discharge into the sea (Reta et al., 2001; Bruno and Acha, 2015).

Nevertheless, when synoptic conditions enable the generation of the sea-land breeze cycle (i.e. high thermal gradient between the water and the land, very low synoptic winds and low cloud cover; Pattiaratchi et al., 1997; Gassmann et al., 2002) the scenario significantly changes. During diurnal hours, the sea breeze, which blows with a moderate/strong intensity (Gassmann et al., 2002), generates the same effects of the strong onshore synoptic winds (Fig. 5c). But at dusk, the inverse thermal gradient generates a land breeze with lower intensity, and thus, the turbulence of the surf zone between the marine accumulation area and the mouth of Mar Chiquita Lagoon decreases (Fig. 5d). This less turbulent environment minimizes dispersal of fish larvae due to wave action, as reflected by the models proposed for postflexion and early juvenile stages, which explained higher fish abundances by the combination of longer wave periods and low-speed offshore winds occurring at nocturnal hours. Reta et al. (2001) suggested that when calm episodes or very low winds blow in the lagoon, tidal cycles should regulate the oscillation of the water level at the inlet channel. However, such conditions seem to be less frequent for diurnal hours (Bruno and Acha, 2015). On the other hand, at nights when the land breeze (with low intensity) is evident, flooding becomes an important factor for the less developed fish stages (i.e., eggs, yolk sac and preflexion larvae) according to the best models proposed. During flooding, seawater is pushed into the lagoon aiding the recruitment of the earliest stages of fishes.

5. Conclusions

We developed a mechanistic explanation for the recruitment process of marine fish larvae and early juveniles into a wind-dominated and very shallow coastal lagoon that could be extrapolated to other similar shallow estuarine systems. In a first step, the youngest fishes should be accumulated and retained near the mouth of the lagoon. The second is the most challenging step, in which larvae must cross the surf zone and penetrate into the lagoon. Winds, acting at different scales, play a dominant role to support the second step. At a large time scale, synoptic strong

offshore winds are inappropriate for ensuring the recruitment of fishes to the lagoon while strong onshore winds aid ichthyoplankton to reach the coast from the offshore. However, strong winds from both directions generate a highly turbulent environment at the surf zone, by intensifying the wave energy, which results in turning a non-suitable environment for the retention of young fishes. Conversely, when synoptic winds are of less magnitude, their effect can be as short as in the order of hours. At diurnal hours, a sea breeze develops by means of several synoptic conditions, which have the same effect as strong synoptic onshore winds. This breeze aids the ichthyoplankton to reach the coast from the sea but it also intensifies the wave energy of the surf zone. However, from dusk until the first hours of the next day, the wind intensity diminishes promoting a surf zone much favorable for the accumulation of young fishes. In such a scenario, without the masking effect of winds, the tide becomes a more relevant factor for the recruitment of fishes, as flood at nocturnal hours aids the less developed fishes to reach the shore and to move into the lagoon by pushing seawater shoreward.

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