

Organic matter sources for fish larvae and juveniles in a marine-estuarine interface (Mar Chiquita lagoon, Argentina)

Daniel O. Bruno · Luciana Riccialdelli ·
Florencia Botto · Eduardo M. Acha

Received: 16 May 2017 / Accepted: 5 September 2017
© Springer Science+Business Media B.V. 2017

Abstract The aim of this study was to analyze the organic matter (OM) origin in the nearshore and the surf zones adjacent to Mar Chiquita lagoon, in order to determine the importance of allochthonous estuarine detritus and in situ marine phytoplankton as carbon (C) sources for young fishes prior to entering the lagoon. Water samples from both the nearshore and the surf zones were collected for estimation of Chlorophyll *a* concentration, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the particulate organic matter (POM). Isotopic composition of the

zooplankton and fish larvae from both zones and fish juveniles from the surf zone were also estimated. The contribution of potential OM sources was quantified by Bayesian stable isotope mixing models (SIAR). SIAR models revealed that the POM composition in the coastal area close to Mar Chiquita lagoon comprised a mix of primary producers (terrestrial and marine). The cordgrass *Spartina densiflora* that develops in the saltmarshes bounding the lagoon, contributed most to the POM of the surf zone, being important as a C source for zooplankton from the same zone. Towards deeper waters (10–12 m, ~2.5 km offshore) with higher chlorophyll *a* concentrations, phytoplankton contributed most to the POM. *Spartina densiflora* was not relevant as a C source for larval and juvenile fishes. However, it was of importance to the group of primary consumers, which apparently sustain other zooplankton organisms that fish fed on. In this sense, the OM derived from *S. densiflora* and exported to the coastal area contributes to sustaining the prey for young fishes outside Mar Chiquita.

D. O. Bruno · L. Riccialdelli
Laboratorio de Ecología, Fisiología y Evolución de Organismos Acuáticos (LEFyE), Centro Austral de Investigaciones Científicas (CADIC-CONICET), Bernardo Houssay 200, V9410CAB Ushuaia, Tierra del Fuego, Argentina

D. O. Bruno (✉) · L. Riccialdelli
Instituto de Ciencias Polares, Ambiente y Recursos Naturales, Universidad Nacional de Tierra del Fuego (ICPA-UNTDF), Los Ñires 2382, V9410CAB Ushuaia, Tierra del Fuego, Argentina
e-mail: dobruno.ush@gmail.com

F. Botto
Laboratorio de Ecología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata (UNMdP), CC 573 Correo Central, B7600WAG Mar del Plata, Argentina

F. Botto · E. M. Acha
Instituto de Investigaciones Marinas y Costeras (IIMyC-UNMdP-CONICET), Deán Funes 3350, (B7602AYL) Mar del Plata, Argentina

E. M. Acha
Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paseo Victoria Ocampo N° 1, CC 175, (B7602HSA) Mar del Plata, Argentina

Keywords Young fishes · Organic matter · Estuarine environment · Stable isotopes · SIAR model

Introduction

Identification of the relative importance of different primary producers supporting marine, coastal and estuarine food webs has gained much attention in the last decades. For instance, food webs in coastal and beach

ecosystems are mainly based on marine sources, such as phytoplankton (Defeo and McLachlan 2005; McLachlan and Brown 2006; Bergamino et al. 2011). For estuarine ecosystems, on the other hand, several important carbon sources have been identified, like *Spartina* spp. and benthic microalgae (Sullivan and Moncreiff 1990), or macroalgae and phytoplankton (Deegan and Garritt 1997), or marsh macrophytes (Howe and Simenstad 2015), or the combination of these inputs (Botto et al. 2005). The variability of carbon sources found in these systems relies on the fact that estuarine environments are transitional areas that are subject to a significant supply of nutrients, detritus and organisms from terrestrial, fluvial and marine environments (Polis et al. 1997; Kneib 2002). The ecotone feature (a zone of transition between adjacent ecological systems; Holland 1988) of estuarine environments has encouraged researchers to understand the mechanisms of, and responses to, cross-ecosystem transport of organic matter (OM), nutrients, and organisms (e.g., Vizzini and Mazzola 2006; Vinagre et al. 2011; Howe and Simenstad 2015).

The exchange of non-living materials and organisms between estuaries and the sea can be classified into those that are passively driven by physical forces (Jansson 1988; Polis et al. 1997) and/or those that are the active result of the behavior of the organisms (Jansson 1988; Kneib 2002). Both passive and active transport can result in the movement of materials from the sea to the estuary (inwelling), and from the estuary to the sea (outwelling) (Dame and Allen 1996). In estuarine systems, the transport of suspended particulate material is frequently governed by the flux of tidal waters (Kjerfve and Magill 1989). If ebb velocities substantially exceed flood ('ebb dominance'), this will result in a seaward transport of suspended sediments (Dame and Allen 1996). In addition, the opposite has been observed (i.e., 'flood dominance'), resulting in a net displacement of suspended material in a landward direction (Dame and Allen 1996).

Although the hydrodynamics in most estuaries worldwide is largely influenced by tidal cycles, in coastal lagoons with a long, narrow and shallow inlet channel (choked lagoons, *sensu* Kjerfve and Magill 1989) winds play a major role because the inlet channel acts as a dynamic filter which significantly reduces tidal fluctuations or tidal currents (Kjerfve and Magill 1989; Kjerfve 1994). 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 semidiurnal low amplitude (< 1 m) tides (Reta et al. 2001). Strong (> 10 m s⁻¹) offshore winds (N, NW) increase the discharge of this lagoon even during the flood, while strong onshore winds (SW, S, SE, and E) increase saltwater intrusion into the lagoon (Reta et al. 2001). Therefore, the inwelling or outwelling in this estuarine system is driven by winds and not by a more predictable force, such as the tidal cycle. In addition, recruitment of young fishes into the lagoon has been demonstrated to be mediated by the wind effect, being onshore winds determinant in the success of the recruitment of larval (Bruno et al. 2014) and juvenile (Bruno et al. 2015) stages. Given the larger unpredictability of the wind force and its role on recruitment dynamics of young fishes into the lagoon, it has been proposed that the coast adjacent to the inlet acts as an accumulation area for fish early life history stages until conditions allow their entrance (Bruno and Acha 2015).

Understanding the origin and pathway of OM in food webs is significant for comprehension of food webs structures, and the analysis of stable isotopes [e.g., carbon (C) and nitrogen (N) stable isotopes; $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$] is a useful methodology to achieve it (Michener and Schell 1994). C and N stable isotopes are incorporated into an animal's body via diet and are passed in natural pathways (DeNiro and Epstein 1978, 1981). Therefore, isotopic measurements can indicate the natural pathways and energy flow from the producers to the consumers (Fry and Sherr 1984; Peterson and Fry 1987). In the case of C isotopes, different producers may be recognized by their different $\delta^{13}\text{C}$ values (Lajtha and Michener 1994), for example, benthic algae are on average ¹³C-enriched by about 5 ‰ compared to sympatric phytoplankton (France 1995). Whilst, $\delta^{15}\text{N}$ values depend on the external origin of the N and are also affected by internal biogeochemical transformations, such as N-fixation, nitrification and/or denitrification process (Minagawa and Wada 1984; Kendall 1998; Montoya 2007). In addition, the C:N ratio gives valuable information for tracing the OM (Kendall et al. 2001; Wissel et al. 2005). For example, particulate OM (POM) derived from terrestrial plants (either C3 or C4) showed C:N values between 15 and 50, whereas POM derived from phytoplankton showed values between 5 and 8 (Kendall et al. 2001).

For instance, food webs of some SW Atlantic estuaries, including inner areas of Mar Chiquita lagoon are supported by different sources, such as *Spartina densiflora*, benthic microalgae and phytoplankton

(Botto et al. 2005) in agreement with several studies conducted on similar estuarine systems (e.g., Sullivan and Moncreiff 1990; Currin et al. 1995; Garcia et al. 2007). These three sources of organic matter in the Mar Chiquita lagoon show distinct $\delta^{13}\text{C}$ values and are therefore useful for assessing the sources of energy for this system's food web. Botto et al. (2005) argued that there is a strong influence of *S. densiflora* and benthic microalgae in intertidal sediments of Mar Chiquita lagoon according to the $\delta^{13}\text{C}$ values recorded (between -12.6 and -15.5‰). On the other hand, the C isotopic signature of consumers (zooplankton, razor clams, polychaetes, crabs, and fish) showed that the three sources of organic matter were important to support the food web.

Therefore, it is expected that larval and early juvenile fishes entering Mar Chiquita system obtain their food from the same sources. However, and given that the coast adjacent to the lagoon's inlet acts as an accumulation area for fish early life stages (Bruno and Acha 2015) the question that arises is whether the sources of OM that sustain food webs within the lagoon are the same that hold these fish stages that remain outside Mar Chiquita. We hypothesize that the main source of OM for the trophic web at the nearshore and surf zones is the detritus of *S. densiflora* originated within the estuarine environment of the Mar Chiquita lagoon. An alternative hypothesis is that the OM that sustains the trophic web is the local phytoplankton production near Mar Chiquita's inlet.

Given that mortality rates in fish are maximal during early life stages (Cushing and Horwood 1994; Houde 2002), it is of great importance to understand both the role of nursery habitats used by fish larvae and juveniles and the possible sources that sustain them during these critical stages. Therefore, the aim of this study was to assess the importance of allochthonous (estuarine detritus) versus autochthonous (phytoplankton) sources for the trophic web sustaining fish larvae and juveniles in the nearshore and surf zones adjacent to Mar Chiquita's inlet.

Material and methods

Study area

The study area includes a sampling site in the inlet (E1) and covers the adjacent surf zone (S1, S2) to Mar Chiquita lagoon, and the marine nearshore zone (M1-M6) (Figs. 1a, b).

Mar Chiquita coastal lagoon, 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). Mudflats and surrounding marshes dominated by the cordgrass *S. densiflora* (e.g., Isacch et al. 2006) and the burrowing crab *Neholice granulata* (e.g., Iribarne et al. 1997) characterize this very shallow lagoon. The latter species is known for affecting sediments in the area by increasing the OM content due to its burrowing activity (Botto et al. 2005).

The area where the lagoon discharges to the sea is characterized by sandy beaches (Merlotto and Bertola 2009) with surf zones of moderate energy for the most part of the year (Bertola 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 Bertola 2009).

A sandy substratum of moderate slope characterizes the seabed from the surf zone to deeper nearshore waters up to a depth of 6 m (< 1 km from the coast) from where the slope largely decreases (Reta et al. 2001). Marine waters in the region are of sub-Antarctic origin, with salinities in the range of 33.5 to 33.8 PSU, and are subjected to seasonal variability (Lucas et al. 2005). Water temperature range from 9 °C to 10 °C in autumn-winter months and from 12 °C to 21 °C in spring-summer months showing also a seasonal trend (Lucas et al. 2005).

Sampling design

Sampling was conducted fortnightly in the surf zone between February and March 2012 (late austral summer) since previous studies showed a high abundance of larval and juvenile fishes during this season (e.g., Bruno et al. 2014, 2015). Only one survey in February 2012 at the nearshore zone was possible to achieve due to bad weather.

In each sampling site, (i.e., E1, S1, S2, M1-M6; Fig. 1b) water samples were collected in duplicate with plastic bottles (previously washed with distilled water) for chlorophyll *a* (500 ml) and particulate organic matter (POM) (5 L) analysis. Mesozooplankton (hereafter zooplankton) and fish larvae were collected in duplicate by a conical net with 0.15 m² mouth area and 300 μm mesh span net towed with a 60 HP boat against the prevailing current at 2 knots for 10 min at the nearshore sampling

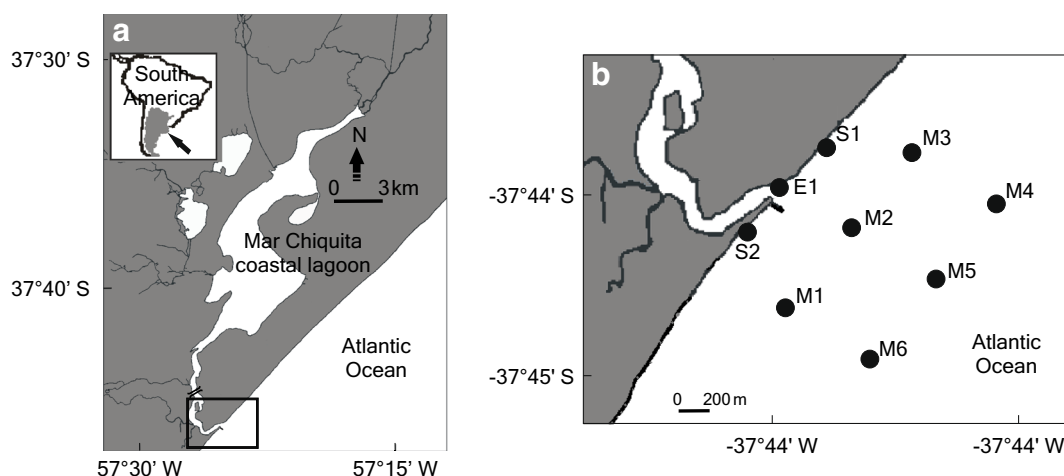


Fig. 1 Study area. **a** Mar Chiquita coastal lagoon (Argentina), **b** location of sampling sites in the surf zone (S1, S2) including the inlet (E1) and in the nearshore zone (M1 – M6)

sites. In this zone, depth ranged from 5 to 6 m (~0.6 km offshore; M1-M3) to 10–12 m (~2.5 km offshore; M4-M6) (Fig. 1b). The same net was employed to collect zooplankton and fish larvae in the sampling sites of the surf zone, but in this case, the net was pulled (five replicates) against the prevailing current for 50 m parallel to the shoreline at ~1 m depth. Also, in the sampling sites of the surf zone, a 4 m long and 1 m height nylon beach seine-net with a 5 mm stretch mesh size and a 2 m cod-end was pulled (five replicates) against the current for 50 m parallel to shoreline at ~1 m depth in order to collect juvenile fishes.

Once in the laboratory, the water samples collected for chlorophyll *a* detection were filtered until clogged onto pre-combusted (400 °C for 4 h) filters (Microclar, grade GF/F fiberglass nominal pore size 0.5 μm), which required an average volume of 302.5 ml (± 96.1) per sample. Filters were stored at -40 °C and then treated with 100% methanol and sonicated (30 s). From the resulting extract, previously centrifuged to remove particles and filter debris, Chlorophyll *a* determinations were made with a spectrum fluorometer FR-10AXL by fluorescence excitation (at 440 nm) and emission (at 650 nm) following Holm-Hansen et al. (1965) at the National Institute for Fisheries Research and Development (INIDEP, Argentina).

POM was obtained by filtering 5 L water samples until clogged onto pre-combusted (400 °C for 4 h) filters (Microclar, grade GF/F fiberglass nominal pore size 0.5 μm), first discarding material >100 μm. From plankton samples, fish larvae were sorted and identified under a stereoscopic microscope to the lowest possible taxon, guts

were removed and yolk-sac larvae were excluded according to Leite et al. (2002). Composites, whenever possible, of at least three individuals of each species, were made to decrease variability in isotopic values of the samples. Once fish larvae were removed, zooplankton present in plankton samples were extracted under a stereoscopic microscope, discarding large organisms (e.g., euphausiids, large amphipods). The feeding process in marine food webs can be considered as opportunistic and less dependent on prey taxonomy rather than on prey size (Cury et al. 2003). Therefore, analyses of isotopic values from zooplankton correspond to a composite of several species of the same sample aiming to make interpretations on the C flux from the available zooplankton in the area to the fish rather than on specific isotopic values of zooplankton organisms. Juvenile fishes were sorted and identified to species level. To prevent that unassimilated food affects the measurement of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ estimations, only the white muscle of fishes was used. Similarly to fish larvae, composites of at least three individuals, whenever possible, of each species were made.

All samples (POM, zooplankton, fish larvae and fish juveniles) were dried at 60 °C for 72 h, ground to fine powder, and weighed and loaded into tin capsules. As all samples were used for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes analysis, acid was not used to remove inorganic carbonate (Bunn et al. 1995) because acidification may have detrimental effects on nitrogen values (Pinnegar and Polunin 1999). Indeed, several authors suggested that the use of acidification for samples of organisms with low content of calcareous structures is not necessary, for example in the case of fish (Carabel et al. 2006) or

zooplankton (Grey et al. 2001), if the dominant component lack of calcareous structures like in our case (see Results). In addition, we also measured the C:N ratio for all samples.

Isotope analysis was performed by a PDZ Europa 20–20 isotope ratio mass spectrometer in the stable isotope facility of the University of California Davis. The stable isotope ratios are expressed as δ values as parts per thousand (‰): $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$; where $X = {}^{13}\text{C}$ or ${}^{15}\text{N}$, and R is the corresponding ratio ${}^{13}\text{C}:{}^{12}\text{C}$ or ${}^{15}\text{N}:{}^{14}\text{N}$. Standards used were Vienna Pee Dee Belemnite for C, and N_2 air for N. Analytical precision was quantified via repeated analysis of internal reference standards. The analytical error was of 0.2‰ for ${}^{13}\text{C}$ and 0.3‰ for ${}^{15}\text{N}$.

Statistical analysis

The null hypothesis of no differences in chlorophyll *a* concentrations and in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of POM and zooplankton between zones (nearshore zone, surf zone) was evaluated by a *t*-Student test. If necessary, correction for differences in variances (t_c , Welch's approximation *t*-test; Zar 2010) was done. In a first attempt, differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fishes in both developmental stages (larvae and juveniles) were assessed considering their size. As there is scarce information about ontogenetic shifts in foraging activity for fishes inhabiting the study area (e.g., Martinetto et al. 2005; with only two species in common but with different size range), two size classes were considered as follows: for larvae, preflexion (pref.) and postflexion (post.) stages (Table 1) were considered as a potential shift in foraging due to a more active locomotion related to the caudal fin development (Fuiman 2002); in the case of juveniles, the total range collected for each species was split in order to obtain two classes, early juveniles (EJ) and juveniles (J) [or juveniles (J) and late juveniles (LJ) in the case of *Odontesthes argentinensis* and *Ramnogaster arcuata*] (Table 1). These preliminary analyses showed no differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between sizes (pref. and post. for larvae, EJ and J or J and LJ for juveniles) within each of the zones (Wilcox test, $p > 0.05$; see Results). Therefore, differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from fish larvae between zones were evaluated as described for POM and zooplankton.

Botto et al. (2005) stated that phytoplankton, benthic microalgae and *S. densiflora* are the three main sources of organic matter that support the food web within Mar Chiquita lagoon and each of them have distinct isotopic

values. Therefore, the contribution of these inputs (isotopic values were taken from Botto et al. 2005) to the POM of both zones (nearshore and surf zone) was quantified by the Bayesian stable isotope mixing model in the Stable Isotope Analysis in R (SIAR) package (Parnell et al. 2010). The appropriate number of interactions (up to $1 \cdot 10^7$) was chosen according to SIAR's convergence (Package SIAR in R) for running the mixing models. Although C ratios of primary producers in coastal and estuarine environments may vary both in space and time (Michener and Schell 1994), values recorded by Botto et al. (2005) were similar to those recorded at similar estuarine systems nearby (e.g., Botto et al. 2011; Derisio et al. 2014). Therefore, we considered that the data from Botto et al. (2005) were representative of the primary producers, which may contribute to the POM collected by us. Consumers (zooplankton, fish larvae, and fish juveniles) were grouped according to significant differences in $\delta^{13}\text{C}$ and in $\delta^{15}\text{N}$ between zones (see Results). In this sense, we obtained four groups of consumers, zooplankton from the nearshore zone, zooplankton from the surf zone, fish larvae and fish juveniles. Thus, SIAR models for each group of consumers were performed considering different potential inputs. Trophic discrimination factors (TDFs) and associated variances were incorporated into the models (except for POMs). Since the specific discrimination factor for all the species analyzed is unknown, we applied a general TDF estimated for marine organisms of 1.0 ‰ (0.5 ‰ SD) and 3.4 ‰ (0.5 ‰ SD) for $\delta^{13}\text{C}$ and in $\delta^{15}\text{N}$, respectively (Minagawa and Wada 1984; Post 2002). Trophic level (TL) was also estimated considering the general TDF ($\delta^{15}\text{N} = 3.4$). We used the mean (\pm SD) $\delta^{15}\text{N}$ value of the filter feeder razor clam *Tagelus plebeius* (12.1 ‰ \pm 0.1; data from Botto et al. 2005) as a baseline $\delta^{15}\text{N}$ value for the food web given that large primary consumer have stable tissue isotopic signatures because of their slower nitrogen turnover compared to plankton organisms (Cabana and Rasmussen 1996). We assumed that this species occupied a TL of 2 and then, estimation of TLs for each consumer to determine a mean TL and variance was performed. To do that, we use the equation proposed by Vander Zanden et al. (1997): $TL_i = [(\delta^{15}\text{N}_i - \delta^{15}\text{N}_{\text{baseline}}) / \text{TEF}] + TL_{\text{baseline}}$; where the TL_i is the TL of each species considered, $\delta^{15}\text{N}_i$ is the nitrogen isotope composition of the species *i*, $\delta^{15}\text{N}_{\text{baseline}}$ and TL_{baseline} are the mean nitrogen isotope composition and the trophic level, respectively, of the baseline

Table 1 Mean (SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for the potential sources of OM and consumers, number of individuals and total body length (TBL, mm) range for fish species in larval and juvenile stages

collected in the surf zone and at the nearshore zone adjacent to Mar Chiquita lagoon. Mean (SD) C:N ratios and Trophic Levels (TL) are also given without considering class sizes for fishes

	Stage	N	TBL (mm)	$\delta^{13}\text{C}$	$\delta^{14}\text{N}$	Zone	C:N	TL
POM				-14.7 (1.8)	8.1 (2.1)	surf zone	10.9 (1.5)	-
				-17.4 (1.3)	9.9 (0.5)	nearshore zone	8.7 (0.7)	-
Zooplankton				-19.2 (3.5)	12.4 (2.1)	surf zone	9.7 (3.4)	2.1 (0.4)
				-17.5 (1.2)	15.7 (1.1)	nearshore zone	6.8 (0.4)	3.1 (0.3)
Fish larvae								
<i>Brevoortia aurea</i>	pref	4	7.99–8.18	-17.2 (1.1)	15.2 (0.4)	surf zone	3.9 (0.1)	2.9 (0.1)
	post	7	18–20.7	-18.6 (0.2)	15.1 (0.4)	surf zone		
<i>Cynoscion guatucupa</i>	post	6	10.06–23.44	-16.9 (0.3)	15.6 (1.0)	nearshore zone	4.5 (0.1)	3.1 (0.3)
<i>Gobiosoma parri</i>	pref	6	2.6–3.3	-17.4 (0.7)	15.4 (0.9)	nearshore zone	6.0 (0.9)	2.6 (0.1)
	post	3	5.33–10.92	-18.7 (0.5)	14.2 (0.2)	nearshore zone		
	pref	6	2.6–3.3	-16.5 (0.1)	16.4 (0.1)	surf zone	4.3 (0.1)	3.3 (0.1)
<i>Engraulidae</i>	post	1	10.92	-17.7	13.8	surf zone	3.7 (0)	2.5 (0)
<i>Micropogonias furnieri</i>	post	6	6.86–17.32	-18.2 (0.4)	14.5 (0.1)	nearshore zone	5.5 (0.2)	2.7 (0.1)
<i>Odontesthes argentinensis</i>	post	4	24–25	-17.6 (0.1)	16.2 (0.1)	surf zone	4.0 (0.1)	3.0 (0.3)
Fish juveniles								
<i>Brevoortia aurea</i>	EJ	4	25–37	-16.2 (1.4)	14.2 (0.3)	surf zone	3.7 (0.2)	2.6 (0.1)
	J	7	42–53	-17.7 (2.3)	14.2 (0.2)	surf zone		
<i>Lycengraulis grossidens</i>	J	2	63	-18.1 (0.1)	14.3 (0.1)	surf zone	3.8 (0.1)	2.6 (0.1)
<i>Micropogonias furnieri</i>	EJ	9	27–38	-17.5 (0.1)	14.2 (0.1)	surf zone	3.8 (0.1)	2.8 (0.1)
	J	9	41–65	-17.3 (0.1)	14.2 (0.2)	surf zone		
<i>Odontesthes argentinensis</i>	J	3	50–68	-16.4 (1.2)	15.3 (0.5)	surf zone	4.0 (0.2)	2.8 (0.2)
	LJ	4	90–124	-17.6 (1.6)	14.4 (0.8)	surf zone		
<i>Ramnogaster arcuata</i>	J	9	29–41	-17.4 (0.1)	16.3 (0.1)	surf zone	3.8 (0.1)	3.2 (0.1)
	LJ	7	45–53	-17.5 (0.3)	16.2 (0.3)	surf zone		

Abbreviations: *pref* preflexion; *post* postflexion; *EJ* early juvenile; *J* juvenile; *LJ* late juvenile

considered *T. plebeius*. A Kruskal-Wallis rank sum (homoscedasticity of variances was not met - Cochran test; Underwood 1997) and the Steel-Dwass-Critchlow-Fligner (SDCF) post hoc comparison tests were used to analyze differences in TLs estimated among groups of consumers.

All statistical analyses were performed using R software (R version 3.2.2; R Development Core Team 2015) and Addin-soft XLSTAT.

Results

Chlorophyll *a* concentration

Chlorophyll *a* concentration differed significantly between zones (t-test; $t = -2.54$, $df = 22$, $p < 0.05$). Values

recorded in the surf zone ($3.60 \text{ mg m}^{-3} \pm 2.84$; range = 1.04–9.41) were lower than those recorded in the nearshore zone ($7.21 \text{ mg m}^{-3} \pm 3.01$; range = 2.23–10.57).

Isotopes signatures

$\delta^{13}\text{C}$ values from POMs collected at the surf zone ranged between -16.7 and -11.8 ‰ and were significantly higher to those collected nearshore (-19.2 to -15.7 ‰) ($t = 3.03$, $df = 10$, $p < 0.05$) (Table 1, Fig. 2). Conversely, no significant differences were observed in mean $\delta^{15}\text{N}$ values between zones ($t_c = -2.01$, $df = 5.54$, $p = 0.09$) (Fig. 2). C:N average values were higher in the surf zone (9.3 ± 1.4) than those in the nearshore zone (7.4 ± 0.7) (Table 1).

Gammaridean amphipods dominated the zooplankton samples from the surf zone. Copepods and crab zoeas likely of *N. granulata* and/or *Cyrtograpsus angulatus* were present but in low proportions. From these samples, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ranged between -23.68 and -15.1 ‰, and between 10.9 and 15.56 ‰, respectively (Table 1, Fig. 2). On the other hand, chaetognaths and copepods dominated the zooplankton samples collected nearshore in which amphipods and crab zoeas were less abundant. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ estimated from these samples ranged between -18.3 and -15.7 ‰, and between 15.16 and 17.3 ‰, respectively (Table 1, Fig. 2). No significant differences in mean $\delta^{13}\text{C}$ values were observed between zones ($t = -0.92$, $df = 6$, $p = 0.39$), but zooplankton collected at the nearshore zone were significantly enriched in $\delta^{15}\text{N}$ than those collected at the surf zone ($t = -2.80$, $df = 6$, $p < 0.05$).

Larval stages of four fish taxa were collected in the surf zone while three fish taxa were collected nearshore (Table 1). *Gobiosoma parri* was the only species present as larvae in both zones. Mean values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were not significantly different between sizes (preflexion and postflexion) neither for fish larvae collected in the surf zone (Wilcox test, $p > 0.05$; Table 2) nor for those collected at the nearshore zone (Wilcox test, $p > 0.05$; Table 2). Therefore, comparisons of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fish larvae between zones were made without considering sizes. This analysis showed no

significant differences neither in mean $\delta^{13}\text{C}$ ($t = 0.83$, $df = 16$, $p = 0.42$) nor in mean $\delta^{15}\text{N}$ ($t = 1.89$, $df = 16$, $p = 0.76$) values between zones. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fish larvae collected at the whole study area ranged between -19.2 ‰ and -16.5 ‰ and between 13.8 ‰ and 16.6 ‰, respectively (Fig. 2).

Five fish species in juvenile stage were collected in the surf zone (Table 1) of which four are the most frequent and abundant according to previous results (Bruno et al., 2015). *Brevoortia aurea* were more enriched in $\delta^{13}\text{C}$ (Table 1, Fig. 2) and more depleted in $\delta^{15}\text{N}$ (Table 1, Fig. 2). Conversely, *Lycengraulis grossidens* were more depleted in $\delta^{13}\text{C}$ values while *R. arcuata* were more enriched in $\delta^{15}\text{N}$ (Table 1, Fig. 2). Mean values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were not significantly different between sizes (Wilcox test, $p > 0.05$; Table 2).

Stable isotope mixing models and trophic level estimation

From all possible sources analyzed that could contribute to the POM, the isotopic mixing models showed that *S. densiflora* contributed most to the POM of the surf zone (Fig. 3a, Table 3) while phytoplankton contributed most to the POM of the nearshore zone (Fig. 3b, Table 3). The POM from both zones contributed evenly as a C source for zooplankton organisms of the surf zone

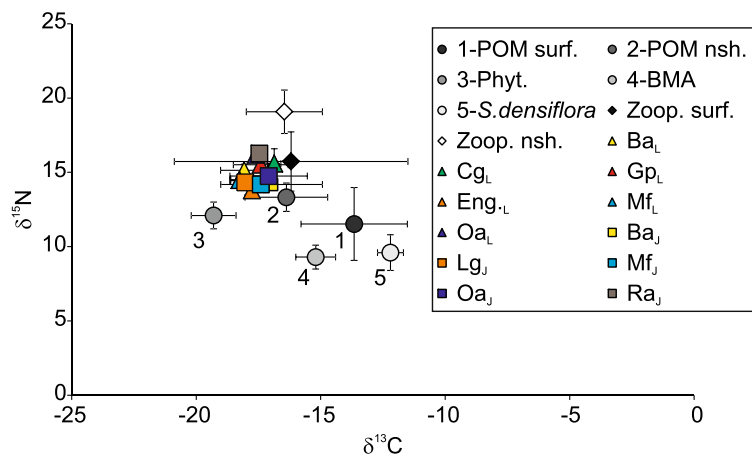


Fig. 2 $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ (mean \pm SD) values of the potential sources of OM (enumerated white circles) and consumers (diamonds, triangles, and squares) collected at the coast adjacent to Mar Chiquita lagoon. Abbreviations: surf, surf zone; nsh, nearshore zone; Phyt., phytoplankton, BMA, benthic micro-algae; Zoop., zooplankton. Abbreviations for fish species: Ba, *Brevoortia aurea*; Cg, *Cynoscion guatucupa*; Gp, *Gobiosoma parri*; Eng.,

Engraulidae; Lg, *Lycengraulis grossidens*; Mf, *Micropogonias furnieri*; Oa, *Odontesthes argentinensis*; Ra, *Ramnogaster arcuata*. Subscripts: J: juvenile; L: larva. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for OM sources 3, 4 and 5 were taken from Botto et al. (2005). Mean isotope values of OM sources and zooplankton have been corrected for trophic discrimination by adding $+1\%$ in $\delta^{13}\text{C}$ and $+3.4\%$ to $\delta^{15}\text{N}$ values

Table 2 Wilcox test comparisons between size classes considered for fish larvae and juveniles for each of the zones sampled in the coast close to Mar Chiquita lagoon

	Source	Zone	$\delta^{13}\text{C}$		$\delta^{14}\text{N}$				
			<i>W</i>	<i>p</i>	<i>W</i>	<i>p</i>			
Fish larvae	pref vs. post	surf zone	24	0.0719	ns	19	0.4121	ns	
	pref vs. post	nearshore zone	7.5	0.7374	ns	12.5	0.4347	ns	
Fish juveniles									
	<i>Brevoortia aurea</i>	EJ vs. J	surf zone	5	0.5000	ns	4	0.7500	ns
	<i>Micropogonias furnieri</i>	EJ vs. J	surf zone	0	0.2500	ns	3	1	ns
	<i>Odontesthes argentinensis</i>	J vs. LJ	surf zone	5	0.400	ns	5	0.400	ns
	<i>Ramnogaster arcuata</i>	J vs. LJ	surf zone	7	0.6250	ns	6	0.8750	ns

ns not significant

Abbreviations: *pref* preflexion; *post* postflexion; *EJ* early juvenile; *J* juvenile; *LJ* late juvenile

Fig. 3 SIAR boxplots showing the contribution of organic matter sources to the composition of (a) POM of the surf zone, (b) POM of the nearshore zone, (c) zooplankton of the surf zone, (d) zooplankton of the nearshore zone, (e) fish larvae, (f) fish juveniles. In each case, the three superimposed gray boxes represent Bayesian credibility intervals (50, 75 and 95%) for 1 10⁷ iterations. See Fig. 2 for abbreviations

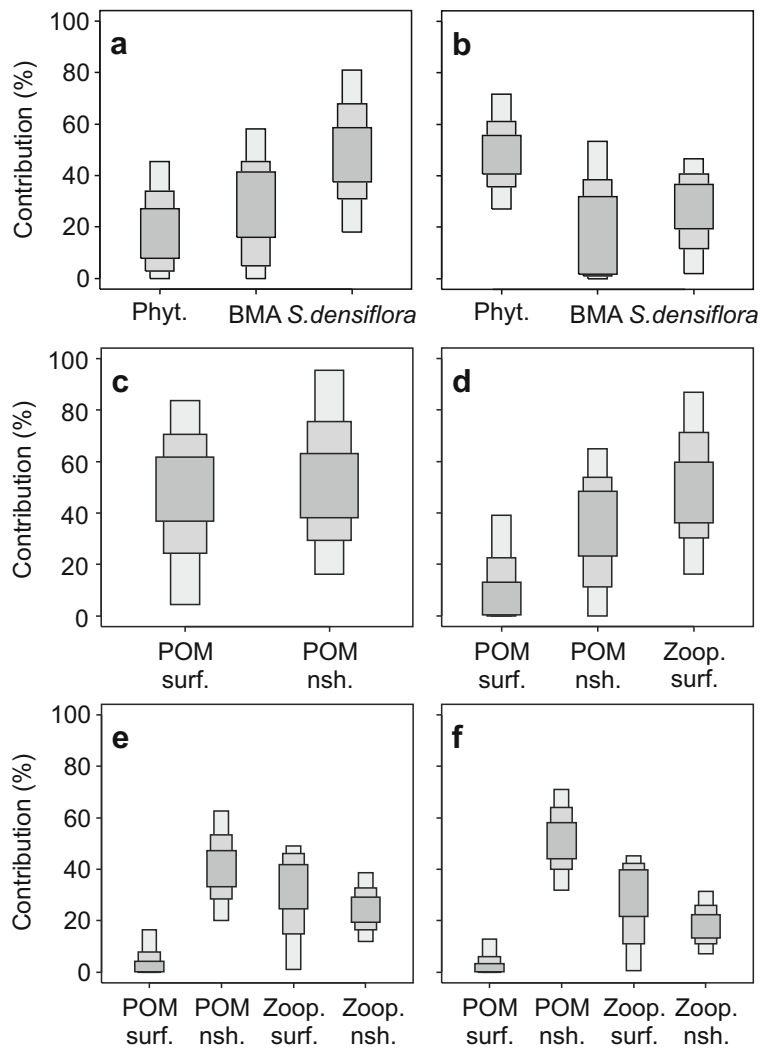


Table 3 Relative contribution of organic matter sources to the composition of POM, zooplankton, larval fish and juvenile fishes in the adjacent coast of Mar Chiquita lagoon

	POM surf.	POM nsh.	Zoop. surf	Zoop. nsh.	Fish larvae	Fish juveniles
Phyt.	22.1 (13.27)	48.95 (11.35)	–	–	–	–
BMA	29.12 (17.06)	25.13 (16.29)	–	–	–	–
<i>S. densiflora</i>	48.78 (15.99)	25.92 (11.94)	–	–	–	–
POM surf.	–	–	47.42 (19.76)	15.33 (12.26)	5.66 (5.28)	4.37 (10.3)
POM nsh.	–	–	52.57 (19.76)	34.41 (18.06)	40.69 (10.82)	51.23 (12.78)
Zoop. surf	–	–	–	50.27 (17.68)	28.62 (13.03)	25.48 (6.33)
Zoop. nsh.	–	–	–	–	25.02 (6.95)	18.92 (21.92)

Stable isotope mixing model results (SIAR) are shown as mean contribution (%), ±SD). See Fig. 2 for abbreviations

(Fig. 3c, Table 3) while POM of the surf zone was of less importance for zooplankton organisms of the nearshore zone (dominated by chaetognaths) (Fig. 3d, Table 3). For this latter group, and according to the SIAR model, zooplankton of the surf zone (dominated by amphipods) contributed most as a C source followed by POM of the nearshore zone (Fig. 3d, Table 3). The isotopic mixing model also revealed that POM of the nearshore zone and zooplankton of the surf zone contributed most as C sources for fishes in both developmental stages (Fig. 3e, f; Table 3).

The TLs estimated for the group of consumers considered revealed that zooplankton of the surf zone was composed of primary consumers (TL = 2, Table 1) while zooplankton of the nearshore zone and larval and juvenile fish have a TL = 3 (Table 1). The TLs estimated were significantly different among groups ($\chi^2 = 18.81$, df = 3, $p < 0.01$) and the TL of the zooplankton of the surf zone was lower than TLs of the rest of the groups (SDCF test, $p < 0.05$) (Table 4).

Discussion

Potential sources of OM in the coast nearby to mar Chiquita lagoon

Our study revealed that the POM composition in the coastal area close to Mar Chiquita lagoon is comprised by a mix of primary producers, though the proportions varied between the surf zone and the nearshore zone.

The detritus of *S. densiflora* contributed most (~49%; SIAR results) to the POM of the surf zone while phytoplankton contributed most (~49%; SIAR results) to the POM of the nearshore zone, showing that the influence

of the lagoon on the coastal trophic web reaches some hundreds of meters at the most. In addition, the higher contribution of phytoplankton to the POM of the nearshore zone was in accordance with chlorophyll *a* results. Considering the C:N ratio, the POM of the surf zone had a mean value of 10.86, which is close to those reported for the POM derived from terrestrial plants (C:N = 15–50; Kendall et al. 2001; Wissel et al. 2005). On the other hand, POM of the nearshore zone had a mean C:N ratio of 8.66, a value mainly related to marine phytoplankton (C:N = 5–8; Kendall et al. 2001) though with some detritus influence. Moreover, the large confidence intervals around our estimations of OM sources contributions with SIAR (Fig. 3) in both zones may be related to the variability of water exchange between the lagoon and the sea which seems to be ruled mainly by wind direction and intensity (Reta et al. 2001). The large confidence intervals may be also related to the mixing effect of the wave action in the surf zone, which results in a resuspension of material available in the water

Table 4 Steel-Dwass-Critchlow-Fligner (SDCF) pair-wise comparisons among TLs estimated for the group of consumers collected in the surf zone and at the nearshore zone adjacent to Mar Chiquita lagoon

	W_{ij}	p -value	
Zoop. surf. vs. Zoop. nsh.	3.770	0.047	*
Zoop. surf. vs. Fish larvae	5.091	0.002	**
Zoop. surf. vs. Fish juveniles	5.280	0.001	**
Zoop. nsh. vs. Fish larvae	1.080	0.870	ns
Zoop. nsh. vs. Fish juveniles	2.000	0.490	ns
Fish larvae vs. Fish juveniles	2.360	0.341	ns

* $p < 0.05$; ** $p < 0.01$

ns not significant. See Fig. 2 for abbreviations

column, even kilometers off the coast due to reflux currents.

The relative importance of *Spartina* spp. detritus as a food source relies on its high productivity (Mann 1988). Furthermore, a high proportion of *Spartina* spp. production is transported and accumulated in sediment and can be used as a food source for deposit feeders (Mann 1988; Créach et al. 1997). Within Mar Chiquita lagoon, *S. densiflora* supports one of the dominant species in SW Atlantic estuaries, the burrowing crab *N. granulata* (Botto et al. 2005). The importance of the activity of *N. granulata* for this micro-tidal estuarine system is significant due to its effects on sediment dynamics (Botto and Iribarne 2000), benthic communities (Botto and Iribarne 1999), shorebirds (Botto et al. 1998; Palomo et al. 2003) and juvenile fishes (Martinetto et al. 2005, 2007). Burrowing areas of *N. granulata* can occupy up to 80% of intertidal zones in estuaries of the SW Atlantic (Botto et al. 2005) and are, therefore, large macro-detritus retention areas that work as sinks for OM (mostly derived from *S. densiflora* detritus) that otherwise would be exported to the adjacent coastal system (Iribarne et al. 1997; Botto and Iribarne 2000; Botto et al. 2006). Recently, Fanjul et al. (2015) stated that *N. granulata* burrowing activity modifies the OM processing at intertidal soft bottoms and the ways in which carbon is exported to coastal waters. The authors suggested that *S. densiflora* detritus are efficiently remineralized at this bioturbated sediment, and then quickly exported to the water column as CO₂ and dissolved organic carbon (DOC) with an important contribution to sustaining coastal food webs. Despite the effective OM retention by *N. granulata*'s caves (Iribarne et al. 1997, Botto and Iribarne 2000; Botto et al. 2006), the results obtained during this study agree to Fanjul et al. (2015) proposal, suggesting that if the proportion exported is substantially lower compared to what is retained, it is enough to constitute an important component to the POM available on the surf zone close to the lagoon's inlet.

Sources of OM that sustain fish early life stages and trophic relationships

The importance of the coast adjacent to Mar Chiquita lagoon as an accumulation area for fish early life stages awaiting optimal conditions to move into the lagoon has previously been stated (Bruno and Acha 2015). The present study adds a trophic dimension to the role

proposed in two senses: OM inputs and trophic level of fish developmental stages (Fig. 4). For fish, stable isotope analysis is a complementary approach to traditional diet studies (e.g., stomach contents) because it represents an integrative record of the food that has really been assimilated by the fish during a period prior to the sampling (e.g., Winemiller et al. 2007; Pasquaud et al. 2010). Larval fish tend to exhibit isotopic values most similar to plankton while larger juveniles and adults tend to reflect values associated with the benthic environment (Wells et al. 2008).

Our results revealed that in this accumulation area for young fishes, POM of the nearshore zone, with a high contribution of phytoplankton, constituted a major C source for all consumers considered, thus rejecting our first hypothesis. Nevertheless, these results allowed us to develop a conceptual model of the C flux dynamics in the marine-estuarine interface of Mar Chiquita lagoon (Fig. 4) that could be extrapolated to other similar estuarine environments used as nursery ground for fish. POM of the surf zone, composed of almost 50% of *S. densiflora* detritus (Fig. 4), constituted an important C source for zooplankton of the surf zone, which according to SIAR models, contributed to the diet of zooplankton of the nearshore zone and of young fishes in both developmental stages (Fig. 4). The different trophic position of zooplankton between both zones was also reflected in the markedly higher $\delta^{15}\text{N}$ values of the zooplankton of the nearshore zone compared to those of the surf zone, reaching the same position as larval and juvenile fishes (Fig. 4). Such differences may be due to forage habits of the dominant species for each zone. For instance, amphipods of the Suborder Gammaridea, which are grinding detritus and mesoherbivores (Duffy and Hay 2000; Mancinelli 2012) dominated the surf zone, while chaetognaths, which are organisms with more predatory habits compared to amphipods (Canino and Grant 1985; Sato et al., 2011), dominated the nearshore zone.

Despite that the source of OM with more contribution of *S. densiflora* was not relevant as a C source neither for larvae (~4%; SIAR results) nor for juveniles (~6%; SIAR results) stages, it was of importance to the group of primary consumers which apparently sustain other zooplankton organisms that fish fed on (Fig. 4). In this sense, the OM derived from *S. densiflora* detritus and exported to the coastal area (Fanjul et al. 2015) in this micro-tidal estuarine system contributes, indirectly, to the growth of young fishes. The similar isotopic values

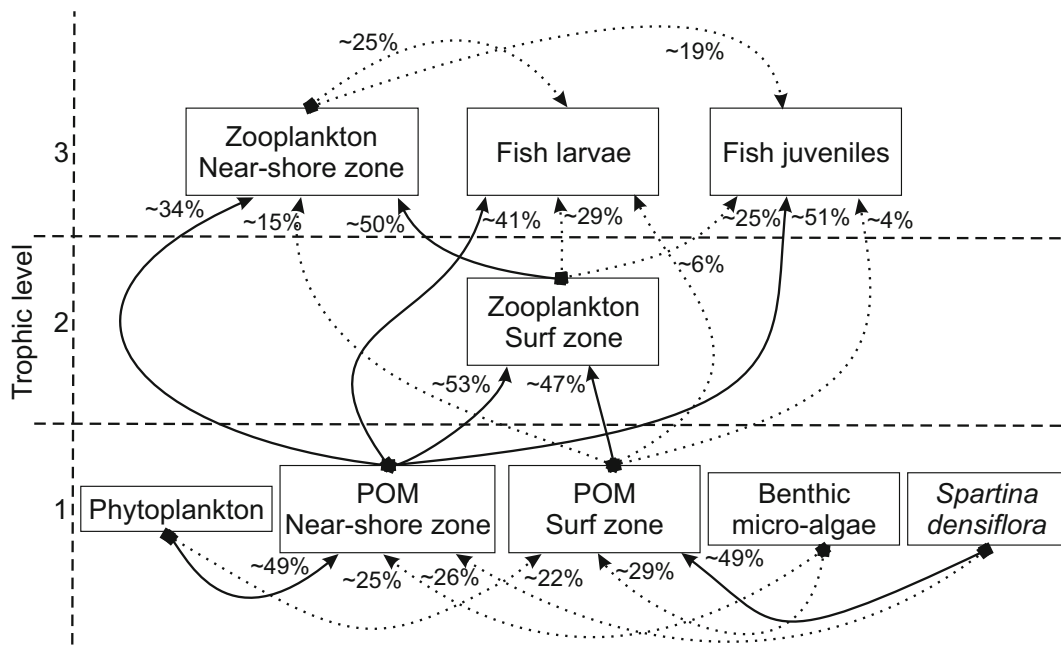


Fig. 4 Conceptual model of the OM flow from potential sources to larval and juvenile fishes in the adjacent coast of Mar Chiquita lagoon according to the SIAR models. Solid arrows represent main fluxes between functional groups and dashed arrows represent

minor flows. The mean proportional contribution (%) of each source estimated by SIAR and the estimated trophic level for each trophic group are also given

of $\delta^{15}\text{N}$ between larval and juvenile fishes indicate that both developmental stages are at the same level in this estuarine environment's food web (Fig. 4) sharing the same resource.

In proportion, zooplankton of the nearshore zone contributed more as a C source for fish larvae than for juveniles, conversely to the contribution of zooplankton of the surf zone (Fig. 4). The higher relative proportion of contribution of "marine" sources to larvae than to juveniles may be related to the fact that most fish inhabiting Mar Chiquita lagoon are of marine origin (Bruno et al. 2014). As fish move towards the coast and spend more time in there, where continental inputs are more abundant, the contribution of OM sources vary and fish begin to reflect the typical estuarine isotopic values. Also, the development of jaw musculature and the increases in size and in mouth gap during growth allow juvenile stages to consume bigger prey with harder exoskeletons (Russo et al. 2007), like amphipods (dominant in the surf zone of the study area) which mainly fed on detritus (Duffy and Hay 2000).

In conclusion, this work shows that the POM composition in the coastal area close to Mar Chiquita lagoon is comprised of a mix of primary producers including

S. densiflora detritus originated within the lagoon and marine phytoplankton. The exchange of water between Mar Chiquita lagoon and the sea and fish recruitment is ruled by the wind effect (Bruno and Acha 2015). That is, strong onshore winds allow the entrance of young fishes into Mar Chiquita by pushing seawater into inner areas of the lagoon while strong offshore winds restrict the entry of sea water and, consequently, the entry of young fishes which remain outside Mar Chiquita (Bruno and Acha 2015). These offshore winds may also favor the water discharge from the lagoon to the sea, inducing the export of small stages, with low motility, which have been entered in Mar Chiquita's inlet and also part of the OM derived from *S. densiflora* detritus originated within the lagoon. In this sense, Mar Chiquita lagoon seems to act as an outwelling estuary with a net OM flux towards the sea (sensu Dame and Allen 1996), as far as a few kilometers at least. This exported OM could be beneficial in two ways. Firstly, it will sustain zooplankton organisms and, subsequently, young fishes waiting to enter and/or exported from Mar Chiquita; and secondly, it possibly may act as olfactory cues, which are critical for the orientation of fish early life stages (e.g., Whitfield 1994) with marine origin in the recruitment process to this micro-tidal estuarine system.

Acknowledgements We are deeply grateful to J.M. Díaz de Astarloa and E. Mabragna (BIMOPE, UNMdP, Argentina) for partially supporting the sampling; to Buenos Aires Province Ministry of Agrarian Subjects' authorities, M. Iza and J. Mangiarotti (forest guard of Mar Chiquita Biosphere Reserve) for sampling permission; to S.M. Delpiani, C. Rumbold, A. Martínez, J.J. Rosso, D. Castellini and N. Lajud for field assistance; to D.A. Cucchi-Colleoni for chlorophyll *a* analysis, and to G.I. Álvarez, E. Fanjul and E.N. Gaitán for laboratory assistance. We thank the staff of the UC Davis Stable Isotope Facility for invaluable sample processing services and acknowledge the useful suggestions made by D.L.G. Noakes and two anonymous reviewers on an early draft. This study was supported by grant EXA 647/14 to E.M. Acha, and CONICET PIP 112-200901-00942 to J.M. Díaz de Astarloa and E. Mabragna. D.O.B. was supported by fellowships from CONICET (Argentina). This is part of D.O.B.'s Ph.D. thesis.

References

- Bergamino L, Lercari D, Defeo O (2011) Food web structure of sandy beaches: temporal and spatial variation using stable isotope analysis. *Estuar Coast Shelf Sci* 91:536–543. <https://doi.org/10.1016/j.ecss.2010.12.007>
- Bertola GR (2006) Morfodinamica de playas del sudeste de la provincia de Buenos Aires (1983 a 2004). *Lat Am J Sedimentol Basin Anal* 13:31–57
- Botto F, Iribarne O (1999) Effect of the burrowing crab *Chasmagnathus granulata* (Dana) on the benthic community of a SW Atlantic coastal lagoon. *J Exp Mar Biol Ecol* 241: 263–284. [https://doi.org/10.1016/S0022-0981\(99\)00089-1](https://doi.org/10.1016/S0022-0981(99)00089-1)
- Botto F, Iribarne O (2000) Contrasting effects of two burrowing crabs (*Chasmagnathus granulata* and *Uca uruguayensis*) on sediment composition and transport in estuarine environments. *Estuar Coast Shelf Sci* 51:141–151. <https://doi.org/10.1006/ecss.2000.0642>
- Botto F, Iribarne OO, Martínez MM, Delhey K, Carrete M (1998) The effect of migratory shorebirds on the benthic species of three southwestern Atlantic Argentinean estuaries. *Estuaries* 21:700. <https://doi.org/10.2307/1353274>
- Botto F, Valiela I, Iribarne O, Martinetto P, Alberti J (2005) Impact of burrowing crabs on C and N sources, control, and transformations in sediments and food webs of SW Atlantic estuaries. *Mar Ecol Prog Ser* 293:155–164. <https://doi.org/10.3354/meps293155>
- Botto F, Iribarne O, Gutierrez J, Bava J, Gagliardini A, Valiela I (2006) Ecological importance of passive deposition of organic matter into burrows of the SW Atlantic crab *Chasmagnathus granulatus*. *Mar Ecol Prog Ser* 312:201–210. <https://doi.org/10.3354/meps312201>
- Botto F, Gaitán E, Mianzan H, Acha M, Giberto D, Schiariti A, Iribarne O (2011) Origin of resources and trophic pathways in a large SW Atlantic estuary: an evaluation using stable isotopes. *Estuar Coast Shelf Sci* 92:70–77. <https://doi.org/10.1016/j.ecss.2010.12.014>
- Bruno DO, Acha EM (2015) Winds vs. tides: factors ruling the recruitment of larval and juvenile fishes into a micro-tidal and shallow choked lagoon (Argentina). *Environ Biol Fish* 98: 1449–1458. <https://doi.org/10.1007/s10641-014-0371-3>
- Bruno DO, Delpiani SM, Cousseau MB, Díaz de Astarloa JM, Blasina GE, Mabragna E, Acha EM (2014) Ocean-estuarine connection for ichthyoplankton through the inlet channel of a temperate choked coastal lagoon (Argentina). *Mar Freshw Res* 65:1116–1130. <https://doi.org/10.1071/MF13128>
- Bruno DO, Cousseau MB, Díaz de Astarloa JM, Acha EM (2015) Recruitment of juvenile fishes into a small temperate choked lagoon (Argentina) and the influence of environmental factors during the process. *Sci Mar* 79:1–13
- Bunn SE, Loneragan NR, Kempster MA (1995) Effects of acid washing on stable isotope ratios of C and N in penaeid shrimp and seagrass: implications studies using multiple stable isotopes. *Limnol Oceanogr* 40(3):622–625
- Cabana G, Rasmussen JB (1996) Comparison of aquatic food chains using nitrogen isotopes. *Proc Natl Acad Sci U S A* 93:10844–10847. <https://doi.org/10.1073/pnas.93.20.10844>
- Canino MF, Grant GC (1985) The feeding and diet of *Sagitta tenuis* (Chaetognatha) in the lower Chesapeake Bay. *J Plankton Res* 7:175–188. <https://doi.org/10.1093/plankt/7.2.175>
- Carabel S, Godínez-Domínguez E, Verísimo P, Fernández L, Freire J (2006) An assessment of sample processing methods for stable isotope analyses of marine food webs. *J Exp Mar Biol Ecol* 336(2):254–261
- Créach V, Schricke MT, Bertru G, Mariotti A (1997) Stable isotopes and gut analyses to determine feeding relationships in saltmarsh macroconsumers. *Estuar Coast Shelf Sci* 44: 599–611. <https://doi.org/10.1006/ecss.1996.0147>
- Currin CA, Newell SY, Paerl HW (1995) The role of standing dead *Spartina alterniflora* and benthic microalgae in salt-marsh food webs - considerations based on multiple stable-isotope analysis. *Mar Ecol Ser* 121:99–116. <https://doi.org/10.3354/meps121099>
- Cury P, Shannon L, Shin YJ (2003) The functioning of marine ecosystems: a fisheries perspective. In: Sinclair M, Valdimarson G (eds) *Responsible Fisheries in the Marine Ecosystem*. FAO Fisheries Technical Paper N°400, pp 103–123
- Cushing H, Horwood JW (1994) The growth and death of fish larvae. *J Plankton Res* 16(3):291–300
- Dame RF, Allen DM (1996) Between estuaries and the sea. *J Exp Mar Biol Ecol* 200:169–185. [https://doi.org/10.1016/S0022-0981\(96\)02642-1](https://doi.org/10.1016/S0022-0981(96)02642-1)
- Deegan LA, Garritt RH (1997) Evidence for spatial variability in estuarine food webs. *Mar Ecol Prog Ser* 147:31–47. <https://doi.org/10.3354/meps147031>
- Defeo O, McLachlan A (2005) Patterns, processes and regulatory mechanisms in sandy beach macrofauna: a multi-scale analysis. *Mar Ecol Prog Ser* 295:1–20. <https://doi.org/10.3354/meps295001>
- DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim Cosmochim Acta* 42(5):495–506
- DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45(3):341–351
- Derisio C, Braverman M, Gaitán E, Hozbor C, Ramírez F, Carreto J, Mianzan H (2014) The turbidity front as a habitat for *Acartia tonsa* (Copepoda) in the Río de la Plata, Argentina-Uruguay. *J Sea Res* 85:197–204

- Duffy JE, Hay ME (2000) Strong impacts of grazing amphipods on the organization of a benthic community. *Ecol Monogr* 70:237–263. [https://doi.org/10.1890/0012-9615\(2000\)070\[0237:SIOGAO\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2000)070[0237:SIOGAO]2.0.CO;2)
- Fanjul E, Escapa M, Montemayor D, Addino M, Alvarez MF, Grela MA, Iribarne O (2015) Effect of crab bioturbation on organic matter processing in south West Atlantic intertidal sediments. *J Sea Res* 95:206–216. <https://doi.org/10.1016/j.seares.2014.05.005>
- France RL (1995) Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Mar Ecol Prog Ser* 124:307–312. <https://doi.org/10.3354/meps124307>
- Fry B, Sherr EB (1984) $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contrib Mar Sci* 27:13–47
- Fuiman LA (2002) Chapter 1: special considerations of fish eggs and larvae. In: Fuiman LA, Werner RG (eds) *Fishery science: the unique contributions of early life stages*. Blackwell Science, Oxford, pp 1–32
- Garcia AM, Hoenighaus DJ, Vieira JP, Winemiller KO (2007) Isotopic variation of fishes in freshwater and estuarine zones of a large subtropical coastal lagoon. *Estuar Coast Shelf Sci* 73:399–408. <https://doi.org/10.1016/j.ecss.2007.02.003>
- Grey J, Jones RI, Sleep D (2001) Seasonal changes in the importance of the source of organic matter to the diet of zooplankton in loch ness, as indicated by stable isotope analysis. *Limnol Oceanogr* 46(3):505–513
- Holland MM (1988) SCOPE/MAB technical consultations on landscape boundaries: report of a SCOPE/MAB workshop on ecotones. *Biol Inter Special Issue* 17:47–106
- Holm-Hansen O, Lorenzen CJ, Holmes RW, Strickland JDH (1965) Fluorometric determination of chlorophyll. *J du ...* 30:3–15. doi: <https://doi.org/10.1093/icesjms/30.1.3>
- Houde ED (2002) Chapter 3: mortality. In: Fuiman LA, Werner RG (eds) *Fishery science: the unique contributions of early life stages*. Blackwell Science, Oxford, pp 64–87
- Howe ER, Simenstad CA (2015) Using stable isotopes to discern mechanisms of connectivity in estuarine detritus-based food webs. *Mar Ecol Prog Ser* 518:13–29. <https://doi.org/10.3354/meps11066>
- Iribarne O, Bortolus A, Botto F (1997) Between-habitat differences in burrow characteristics and trophic modes in the southwestern Atlantic burrowing crab *Chasmagnathus granulata*. *Mar Ecol Prog Ser* 155:137–145. <https://doi.org/10.3354/meps155137>
- Isacch JP, Costa CSB, Rodríguez-Gallego L, Conde D, Escapa M, Gagliardini DA, Iribarne OO (2006) Distribution of saltmarsh plant communities associated with environmental factors along a latitudinal gradient on the south-west Atlantic coast. *J Biogeogr* 33:888–900. <https://doi.org/10.1111/j.1365-2699.2006.01461.x>
- Jansson BO (1988) *Coastal-offshore ecosystem interactions*. Springer-Verlag, New York
- Kendall C (1998) Tracing nitrogen sources and cycling in catchments. In: Kendall C, McDonnell JJ (eds) *Isotope tracers in catchments hydrology*. Elsevier Science, Amsterdam, pp 519–575
- Kendall C, Silva SR, Kelly VJ (2001) Carbon and nitrogen isotopic compositions of particulate organic matter in four large river systems across the United States. *Hydrol Process* 15: 1301–1346. <https://doi.org/10.1002/hyp.216>
- Kjerfve B (1994) *Coastal lagoons*. Elsevier Oceanogr Ser 60:1–8
- Kjerfve B, Magill KE (1989) Geographic and hydrodynamic characteristics of shallow coastal lagoons. *Mar Geol* 88: 187–199. [https://doi.org/10.1016/0025-3227\(89\)90097-2](https://doi.org/10.1016/0025-3227(89)90097-2)
- Kneib RT (2002) Salt marsh ecoscapes and production transfers by estuarine nekton in the southeastern United States. In: Weinstein MP, Kreeger DA (eds) *Concepts and controversies in tidal marsh ecology*. Kluwer Academic Publisher, New York, pp 267–291
- Lajtha K, Michener R (1994) Introduction. In: Lajtha K, Michener R (eds) *Stable isotopes in ecology and environmental science*. Blackwell Scientific Publishers, Oxford, pp XI–XIX
- Leite RG, Araújo-Lima C, Vitória R, Martinelli L (2002) Stable isotope analysis of energy sources for larvae of eight fish species from the Amazon floodplain. *Ecol Freshw Fish* 11: 56–63. <https://doi.org/10.1034/j.1600-0633.2002.110106.x>
- Lucas AJ, Guerrero RA, Mianzán HW et al (2005) Coastal oceanographic regimes of the northern argentine continental shelf (34–43°S). *Estuar Coast Shelf Sci* 65:405–420. <https://doi.org/10.1016/j.ecss.2005.06.015>
- Mancinelli G (2012) On the trophic ecology of Gammaridea (Crustacea: Amphipoda) in coastal waters: a European-scale analysis of stable isotopes data. *Estuar Coast Shelf Sci* 114: 130–139. <https://doi.org/10.1016/j.ecss.2011.12.003>
- Mann KH (1988) Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. *Limnol Oceanogr* 33:9–930. https://doi.org/10.4319/lo.1988.33.4_part_2.0910
- Martinetto P, Iribarne O, Palomo G (2005) Effect of fish predation on intertidal benthic fauna is modified by crab bioturbation. *J Exp Mar Biol Ecol* 318:71–84. <https://doi.org/10.1016/j.jembe.2004.12.009>
- Martinetto P, Ribeiro P, Iribarne O (2007) Changes in distribution and abundance of juvenile fishes in intertidal soft sediment areas dominated by the burrowing crab *Chasmagnathus granulatus*. *Mar Freshw Res* 58:194–203. <https://doi.org/10.1071/MF06079>
- McLachlan A, Brown AC (2006) *The ecology of Sandy shores*. Academic Press, USA, Burlington
- Merlotto A, Bertola GR (2009) Coastline evolution at Balneario Parque Mar Chiquita, Argentina. *Ciencias Mar* 35:271–286
- Michener RH, Schell DM (1994) Stable isotopes ratios as tracers in marine aquatic food webs. In: Lajtha K, Michener RM (eds) *Stable isotopes in ecology and environmental science*. Blackwell Scientific Publishers, Oxford, pp 138–157
- Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim Cosmochim Acta* 48:1135–1140. [https://doi.org/10.1016/0016-7037\(84\)90204-7](https://doi.org/10.1016/0016-7037(84)90204-7)
- Montoya JP (2007) Natural abundance of ^{15}N in marine planktonic ecosystems. In: Michener RM, Lajtha K (eds) *Stable isotopes in ecology and environmental science*. Blackwell Publishing Ltd, Oxford, pp 176–201
- Palomo G, Botto F, Navarro D, Escapa M, Iribarne O (2003) Does the presence of the SW Atlantic burrowing crab *Chasmagnathus granulatus* Dana affect predator-prey interactions between shorebirds and polychaetes? *J Exp Mar Biol Ecol* 290(2):211–228
- Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. *PLoS One* 5(3):e9672

- Pasquaud S, Pillet M, David V, Sautour B, Elie P (2010) Determination of fish trophic levels in an estuarine system. *Estuar Coast Shelf Sci* 86:237–246. <https://doi.org/10.1016/j.ecss.2009.11.019>
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18:293–320
- Pinnegar JK, Polunin NVC (1999) Differential fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among fish tissues: implications for the study of trophic interactions. *Funct Ecol* 13(2):225–231
- Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu Rev Ecol Syst* 28:289–316. <https://doi.org/10.1146/annurev.ecolsys.28.1.289>
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703–718. <https://doi.org/10.2307/3071875>
- R Development Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing (Version 3.2.2). <http://www.R-project.org/>
- Reta R, Martos P, Perillo GME, Piccolo MC, Ferrante A (2001) Características hidrográficas del estuario de la laguna Mar Chiquita. In: Iribarne O (ed) Reserva de Biósfera Mar Chiquita: Características físicas, biológicas y ecológicas. Editorial Martín, Mar del Plata, pp 31–52
- Russo T, Costa C, Cataudella S (2007) Correspondence between shape and feeding habit changes throughout ontogeny of gilthead sea bream *Sparus aurata* L., 1758. *J Fish Biol* 71(3):629–656
- Sato NE, Hernández D, Viñas MD (2011) Hábitos alimentarios de *Sagitta friderici* Ritter-Zahony en las aguas costeras de la provincia de Buenos Aires, Argentina. *Bol Invest Mar Cost* 40(1):59–74
- Sullivan M, Moncreiff C (1990) Edaphic algae are an important component of salt marsh food-webs: evidence from multiple stable isotope analyses. *Mar Ecol Prog Ser* 62:149–159. <https://doi.org/10.3354/meps062149>
- Underwood AJ (1997) Experiments in ecology. Their logical design and interpretation using analysis of variance. Cambridge University Press, UK
- UNESCO (1996) Nine new biosphere reserves designated by the MAB bureau. *Biosphere Reserves: Bull World Network* 4:6–10
- Vander Zanden MJ, Cabana G, Rasmussen JB (1997) Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}\text{N}$) and literature dietary data. *Can J Fish Aquat Sci* 54:1142–1158. <https://doi.org/10.1139/f97-016>
- Vinagre C, Salgado J, Cabral HN, Costa MJ (2011) Food web structure and habitat connectivity in fish estuarine nurseries—impact of river flow. *Estuar Coasts* 34:663–674. <https://doi.org/10.1007/s12237-010-9315-0>
- Vizzini S, Mazzola A (2006) Sources and transfer of organic matter in food webs of a Mediterranean coastal environment: evidence for spatial variability. *Estuar Coast Shelf Sci* 66(3):459–467
- Wells RJD, Cowan JH, Fry B (2008) Feeding ecology of red snapper *Lutjanus campechanus* in the northern Gulf of Mexico. *Mar Ecol Prog Ser* 361:213–225
- Whitfield AK (1994) Abundance of larval and O+ juvenile marine fishes in the lower reaches of 3 southern African estuaries with differing freshwater inputs. *Mar Ecol Prog Ser* 105:257–268. <https://doi.org/10.3354/meps105257>
- Winemiller KO, Akin S, Zeug SC (2007) Production sources and food web structure of a temperate tidal estuary: integration of dietary and stable isotope data. *Mar Ecol Prog Ser* 343:63–76. <https://doi.org/10.3354/meps06884>
- Wissel B, Gaçe A, Fry B (2005) Tracing river influences on phytoplankton dynamics in two Louisiana estuaries. *Ecology* 86:2751–2762. <https://doi.org/10.1890/04-1714>
- Zar JH (2010) Biostatistical analysis. Prentice Hall, New Jersey