



The turbidity front as a habitat for *Acartia tonsa* (Copepoda) in the Río de la Plata, Argentina-Uruguay

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ABSTRACT

Acartia tonsa is one of the most abundant copepod species in estuaries worldwide. In the Río de la Plata, its highest densities appear to occur in an area of low quality food (detritus): the turbidity front (TF). The objective of this study was to understand how trophic and oceanographic drivers contribute to the high densities of *A. tonsa* in the Río de la Plata TF. The patterns of spatial distribution and density of this species were analyzed in relation to oceanographic and biological attributes of the system. The egg production rate (EPR) in the TF was evaluated as a measure of fitness, and a stable isotope analysis indicated the possible sources of organic matter in the species' diet. This study confirmed that the highest observed densities of *A. tonsa* were mostly associated with the TF, where high suspended matter and low Chl-*a* occur. Immediately offshore from the TF, decreased copepod densities and the maximum Chl-*a* values were found. Females close to the estuarine turbidity maximum (ETM) had a lower EPR than those closer to the high Chl-*a* concentrations. Within the TF, *A. tonsa* apparently fed on detritus close to the ETM and phytoplankton close to the edge of the TF. The report includes a discussion of how retention processes, two layered flow and the life history strategy of *A. tonsa* could be contributing to the development of high densities (more than 10,000 ind m⁻³) of this species in the inner estuarine zone, despite the poor quality of food available for development in that area. *A. tonsa* can live and prosper in areas with high turbidity and low chlorophyll concentrations. This trait exemplifies the plasticity of this species and helps explain why it is a key species in many worldwide estuaries.

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1. Introduction

The calanoid copepod *Acartia tonsa* is one of the most abundant species in estuaries worldwide. This eurythermal, euryhaline and omnivorous species can ingest foods such as phytoplankton and microzooplankton, as well as large amounts of detritus (e.g., David et al., 2005; Diodato and Hoffmeyer, 2008; Irigoien and Castel, 1995; Kleppel et al., 1998; White and Roman, 1992). Food quality is known to affect the fecundity of this species, with phytoplankton promoting higher egg production than detritus (Calliari et al., 2004; Diodato and Hoffmeyer, 2008; White and Roman, 1992). Other factors such

as temperature and salinity also affect egg production (Castro-Longoria, 2003; Holste and Peck, 2006; White and Roman, 1992). *A. tonsa*'s maximum population growth and fecundity rates are reached in warm, polyhaline waters with high phytoplankton density or a mixture of food sources (Calliari et al., 2004; Castro-Longoria, 2003; Holste and Peck, 2006; Irigoien and Castel, 1995; White and Roman, 1992). High environmental tolerance and omnivory facilitate the colonization of a broad range of estuarine environments by *A. tonsa*. Although this species may inhabit any part of such ecosystems, the highest concentrations may be restricted to the inner sector of estuaries, close to and immediately outside of the estuarine turbidity maximum (ETM) when present, where the concentration of suspended matter is lower and phytoplankton density and salinity values are optimal for the species' development (e.g., David et al., 2005; Irigoien and Castel, 1995).

The adult and larval stages of *A. tonsa* are considered key items in the Río de la Plata estuarine food web (Calliari et al., 2004; Mianzan et al., 2001). Some evidence shows that *A. tonsa* reaches its greatest densities in the inner sector of the estuarine zone (Mianzan et al.,

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2001), matching the offshore boundary of the ETM, specifically the turbidity front (TF). The head of the estuarine zone is characterized by a well-developed TF (Framiñan and Brown, 1996), which is important in the ecology of many estuarine species (Acha et al., 2008). Maximum salinity gradients characterize this area and high turbidity constrains photosynthesis, leading to poor phytoplankton production. Immediately offshore from the TF where waters become less turbid, a high chlorophyll-*a* (Chl-*a*) signal is observed with values as high as 15.50 mg m^{-3} (e.g., Carreto et al., 2008; Mianzan et al., 2001).

Low-quality food (detritus) and highly variable salinity would be expected to make the TF a suboptimal region for *A. tonsa*; however, their highest densities appear to occur there. On the other hand, the TF has been recognized as a retention area for plankton in this area (Acha et al., 2008; Simionato et al., 2008). This is important because due to the net seawards transport of estuarine waters, copepods are at risk of export from the estuarine zone to coastal waters (Castel and Veiga, 1990; Morgan et al., 1997; Naylor, 2010; Roman et al., 2001; Schmitt et al., 2011). This could be especially detrimental for broadcast spawners, such as *A. tonsa* (Mauchline, 1998). The objective of this work was to understand how trophic and oceanographic drivers may lead to the high densities of *A. tonsa* in Río de la Plata turbidity front.

To confirm this pattern, an analysis of a multi-year database of copepod densities and environmental variables that covered the entire Río de la Plata estuarine zone was performed. Next, the conditions with the potential to regulate the *A. tonsa* population in the TF were analyzed. Egg production rate (EPR) was used as a measure of fitness, and stable isotopes indicated the possible sources of organic matter contributing to *A. tonsa*'s diet. A conceptual framework for the success of *A. tonsa* in the TF was developed considering the results of this work, the hydrodynamics of the system, and the biology of this species.

2. Materials and methods

2.1. Study area

The Río de la Plata (Fig. 1A), located between Argentina and Uruguay (35°S, 56°W), is one of the largest coastal plains and permanently open estuarine zone in the world (270 km long with a

width of up to 230 km at the mouth). The average discharge of the river into the Atlantic Ocean is approximately $22,000 \text{ m}^3 \text{ s}^{-1}$ with low seasonality, creating a large (38,000 km²), shallow (maximum depth approx. 25 m) estuarine zone. It is characterized by a low tidal amplitude (microtides < 1 m), high susceptibility to atmospheric forcing, and a salt wedge regime with two-layered flow (Guerrero et al., 1997; Mianzan et al., 2001; Simionato et al., 2008). The mixohaline area is characterized by a salt wedge that generates a frontal system. The maximum salt wedge scope, controlled by topography, defines a bottom salinity front that coincides with a bottom bar called the Barra del Indio shoal between Montevideo and Punta Piedras (Guerrero et al., 1997). Framiñan and Brown (1996) analyzed satellite images over long time scales and defined the mean position of a turbidity front (TF). The front corresponds to the highest horizontal turbidity gradient. It occurs near the landward limit of the salt intrusion and is marked by an abrupt change in the color of the water. See Acha et al. (2008) and Mianzan et al. (2001) for a complete description of the system.

2.2. Mean distribution pattern of *A. tonsa* in the whole area

Data from 29 cruises were used to determine the mean distribution patterns of *A. tonsa* adults, chlorophyll-*a* (Chl-*a*) and suspended particulate matter (SPM). Most of this historical information was obtained from unpublished data with the exception of some *A. tonsa* data, which were taken from different bibliographic sources (Akselman et al., 1986; Berasategui et al., 2006; Ramírez, 1966). The cruises were conducted from 1968 to 2006 during the spring–summer period in the Río de la Plata estuarine zone and its adjacent coastal waters. Mean surface salinity values were taken from Guerrero et al. (1997). A total of 176 plankton stations, 208 water samples for Chl-*a*, and 95 water samples for SPM were analyzed (Fig. 1A). Water samples were collected at 0 and 10 m depths with a plastic bucket and Niskin bottles, respectively. Chl-*a* concentrations (mg m^{-3}) were estimated in the laboratory using the fluorometric method (Holm-Hansen et al., 1965). Before measurement, filters were extracted in 90% acetone, stored overnight at -20°C , sonicated, centrifuged, and read in a Perkin Elmer LS3 spectrofluorometer (calibrated against pure Chl-*a*—Sigma Ltd). Chl-*a* values from the two depths (0 and 10 m) were averaged to map the mean distribution of

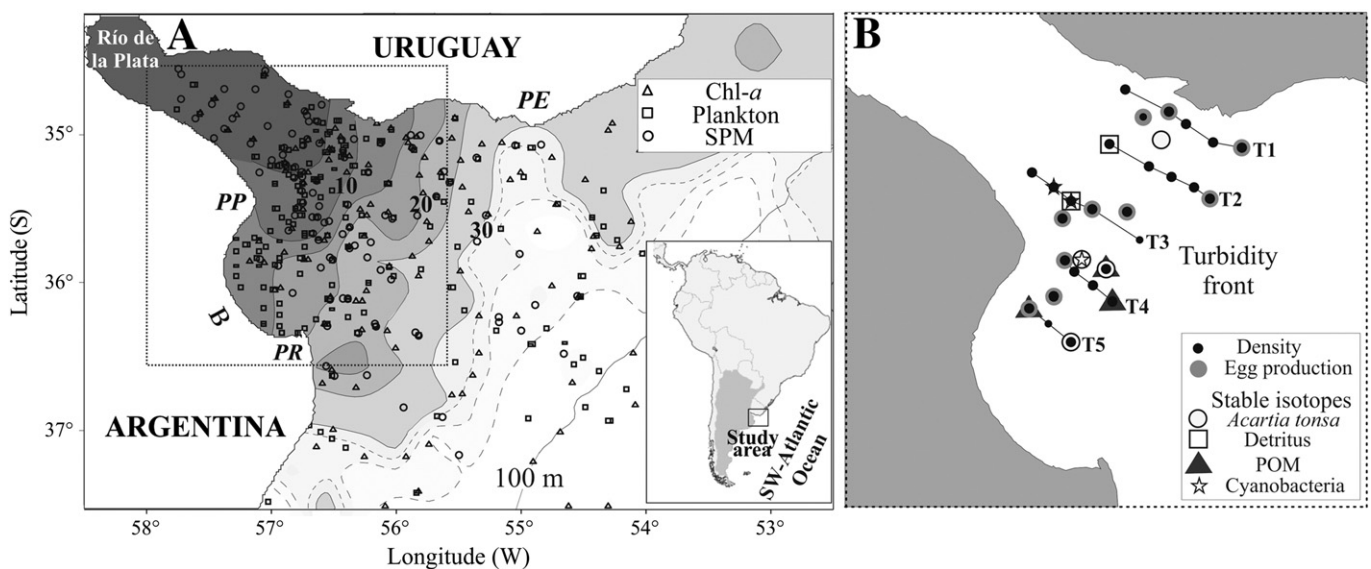


Fig. 1. A) The Río de la Plata estuarine zone and neighbor shelf waters. Mean surface salinity distribution for spring–summer. Symbols represent historical sampling effort (samples: Chl-*a*, plankton and SPM). PP: Punta Piedras, SB: Samborombón Bay, PR: Punta Rasa, PE: Punta del Este. B) Sampling stations in the turbidity front during 10–20 March 2006. Copepod densities were measured at all stations, and *Acartia tonsa* egg production and stable isotopes were measured at some stations. Transects (T1–5). A, redrawn from Guerrero et al. (1997).

Chl-*a*. To measure suspended matter, water samples were filtered and the concentration was calculated based on the difference in sample weight before and after filtering (mg m^{-3}). Complementary data on Chl-*a* ($n = 16$) and SPM (30 stations) collected in the tidal river region (CARP, 1989) were added to cover the whole system.

Plankton samples were collected with different nets (Nackthai, Multinet, Hensen, 20 cm bongo, and Motoda samplers) equipped with digital flowmeters and operated in stratified or whole-water-column tows. Nets had 150 to 300- μm mesh sizes, all of which were capable of efficiently collecting *A. tonsa* adult specimens (e.g., Aronés et al., 2009; Hoffmeyer, 1994). All samples were preserved in 4% buffered

formalin. Individuals of *A. tonsa* were identified and counted in the laboratory with the aid of a binocular microscope. Samplers were not intercalibrated; instead, data were arranged into broad density scales (0; >0–100; >100–1000; >1000–10,000; >10,000 copepods m^{-3}). Because the aim was to describe the general pattern of *A. tonsa* horizontal distribution, data from different depths at the same sampling station were averaged.

To study *A. tonsa*'s distribution and its possible association with the TF, this region was delineated by considering the frontal density estimated by Framiñan and Brown (1996) from satellite images, defined as the highest probability of frontal occurrence (with values higher than $5 \times 10^{-5} \text{ km}^{-2}$ of frontal density) (Fig. 2B). The TF is located between freshwater (FW) and the outer estuary (OE) (Fig. 2). *A. tonsa* density estimates and the mean distribution patterns of Chl-*a* and SPM were mapped in relation to these areas. Data are shown as the mean \pm standard deviation. Because not all of the historical data on *A. tonsa* coincided in space and time with the environmental variables, these data were estimated at points not sampled by interpolating onto a 0.3° latitude \times 0.3° longitude grid using an inverse distance squared algorithm (SURFER version 8.02, Golden Software Inc.). Next, a non-parametric and non-linear generalized additive model (GAM) (Wood, 2006) was constructed to detect pairwise relationships between *A. tonsa* distribution and environmental variables (salinity, Chl-*a* and SPM). *A. tonsa* abundance (ind m^{-3}) was $\log_{10}(x + 1)$ transformed to fit the requirements of the statistical analysis. The model was fitted using Gaussian errors with identity as a link function.

2.3. *A. tonsa* in the turbidity front (TF)

High-resolution sampling, focused on the region where the highest *A. tonsa* densities were detected, was conducted during a cruise along the TF during 10–20 March 2006 (late summer). To confirm the location of the TF, a satellite image was obtained with TERRA-MODIS on 19 March 2006 that was representative of the distribution of turbidity during the cruise. In this study area, samples were collected at 26 stations (Fig. 1B) where salinity was measured with a Seabird-911 CTD (conductivity–temperature–depth profiler). At each station, plankton was sampled using a Motoda net with a 60-cm mouth diameter (see Wiebe and Benfield, 2003 for description) equipped with a mechanical closing device, a mechanical flowmeter and a 200- μm meshnet. Samples were taken above and below the halocline, when present. When the water column was homogeneous, plankton samples were taken in the upper ($2.5 \pm 1.1 \text{ m}$ depth) and lower ($6.2 \pm 1.4 \text{ m}$ depth) layers. Samples were preserved in 4% buffered formalin for subsequent laboratory analysis. *A. tonsa* and other copepod species were identified and counted to determine the density (ind m^{-3}) of each species in the area. Copepod densities across the TF were plotted in vertical salinity sections for five transects that included 22 stations (Fig. 1B).

2.3.1. Egg production rates (EPRs)

To assess the fitness of *A. tonsa* in the TF zone, the egg production rates of 220 females were estimated at 11 stations (Fig. 1B). Specimens were collected with vertical tows (maximum depth approx. 3–5 m) with a plankton net (30-cm mouth diameter and 200- μm mesh) at stations located in the TF and immediately offshore from it. Onboard the ship, *A. tonsa* adult females were identified and transferred with a large-mouthed pipette into incubation jars filled with surface water filtered with 40- μm mesh. One female per jar was incubated with in situ water for 24 h (20 females were incubated per station). In each jar, 200- μm mesh netting was used to separate the female from liberated eggs to prevent egg cannibalism. Jars were placed in a bath on the deck with running water to stabilize the temperature (mean $22.5^\circ \text{C} \pm 0.5^\circ \text{C}$). After incubation, the number of females that produced eggs was recorded. The contents of the egg-collecting chambers were preserved in Lugol's solution and the eggs counted with a stereomicroscope. Egg production rates (EPRs) for the egg-producing

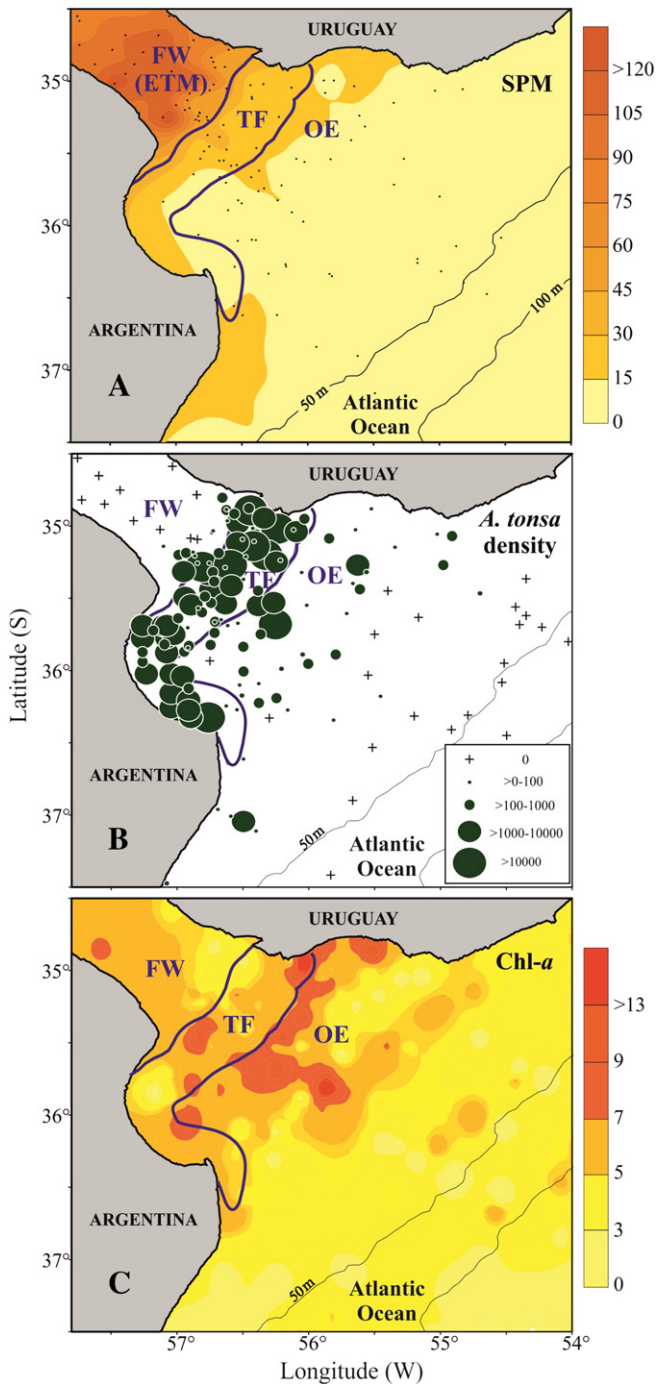


Fig. 2. A) Spatial pattern of SPM (scale bar in mg m^{-3}) in the Río de la Plata turbidity front, B) *Acartia tonsa* (ind m^{-3}) density, and C) Chl-*a* concentration (scale bar in mg m^{-3}). Thick lines border the four defined regions: FW: freshwater, ETM: estuarine turbidity maximum; TF: turbidity front, OE: outer estuary.

females were averaged by station (eggs female⁻¹ day⁻¹). A cluster analysis (Bray–Curtis similarity index) grouped stations with similar eggs production values. Differences among station groups were tested with a t-student test (or its non-parametric equivalent the Mann–Whitney test) for the EPR, the number of females that spawned, *A. tonsa* density, and salinity. A Spearman correlation tested the relationship between EPR and salinity (Zar, 1999).

2.3.2. Stable isotope analysis

To determine the origin of the resources consumed by *A. tonsa*, stable isotopes of carbon (C) and nitrogen (N) from samples of *A. tonsa*'s main potential food sources were analyzed at 9 stations in the TF (Fig. 1B). Particulate organic matter (POM) samples were obtained at three stations that coincided with the mean pattern of Chl-*a* maximum. Thus, the isotopic signal of POM samples was considered to be composed primarily of phytoplankton. Water samples (1 L) were pre-filtered through a 200- μ m mesh to remove large organisms and then filtered through pre-combusted (450 °C, 2 h) glass fiber filters (Whatman GF/F, 0.45- μ m pore size). Finally, filters were dried at 60 °C for 72 h and kept frozen until analysis. Detritus was collected together with surface plankton samples in two stations located in the inner sector of the TF. "Detritus" was considered to include any form of non-living organic matter, including different types of plant and animal tissues, dead microbes, feces, as well as all related microflora. Detritus was separated from the rest of the plankton with the aid of a binocular microscope. In addition, *A. tonsa* specimens were sorted from surface samples from three different stations in the TF (Fig. 1B). Several hundred copepods per sample were pooled to obtain an adequate amount of material for analysis. Detritus and copepod fractions were rinsed with distilled water, dried at 60 °C for 72 h and homogenized with a mortar and pestle. Mats of the cyanobacterium *Microcystis aeruginosa* were collected via surface plankton tows and processed in the same way as the detritus. Samples were analyzed using continuous flow isotope ratio mass spectrometry at the University of California–Davis Stable Isotope facility to determine $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Isotope ratios were expressed in the δ notation: δ (‰) = $(R_{\text{sample}} / R_{\text{standard}} - 1) \times 1000$, where δ (‰) is $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ and R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratios of the sample and a standard. The stable isotope compositions of C and N and the C:N ratio (mg C/mg N in sample) were analyzed from these samples to obtain ancillary information on the samples' origin (Kendall et al., 2001). Data from detritus, POM, cyanobacteria, and *A. tonsa* were grouped as for the EPR stations. ANOVA and Tukey's post-hoc comparison tests were used to analyze differences in the C/N ratio among resources (Zar, 1999).

3. Results

3.1. Mean distribution pattern across the whole area

A. tonsa was distributed throughout the study region and was recorded in 78.4% of the sampled stations (138 of 176) within a salinity range of 0.38–33 units. The highest *A. tonsa* density (up to 48,711 ind m⁻³, mean 3329 \pm 6858 ind m⁻³) was largely constrained to the TF. The TF presented a strong suspended particulate matter (SPM) gradient (3–163 mg m⁻³, mean 37 \pm 40) and low Chl-*a* values (0–8.6 mg m⁻³, mean 4.1 \pm 2.4) (Fig. 2A–C). *A. tonsa* densities decreased towards both the freshwater (FW) and outer estuary (OE) (Fig. 2B). In the FW region, maximum values of SPM were observed (the ETM) (74–170 mg m⁻³, mean 104 \pm 24) (Fig. 2A). By contrast, SPM was low in the OE region (0–22 mg m⁻³, mean 4.6 \pm 5.3), and the maximum values of Chl-*a* were found immediately offshore from the TF (7.2–16 mg m⁻³, mean 11 \pm 3.2) (Fig. 2C). Regarding the three environmental variables considered (salinity, Chl-*a* and SPM), a significant relationship between *A. tonsa* abundance and SPM was found ($P < 0.001$). *A. tonsa* abundance

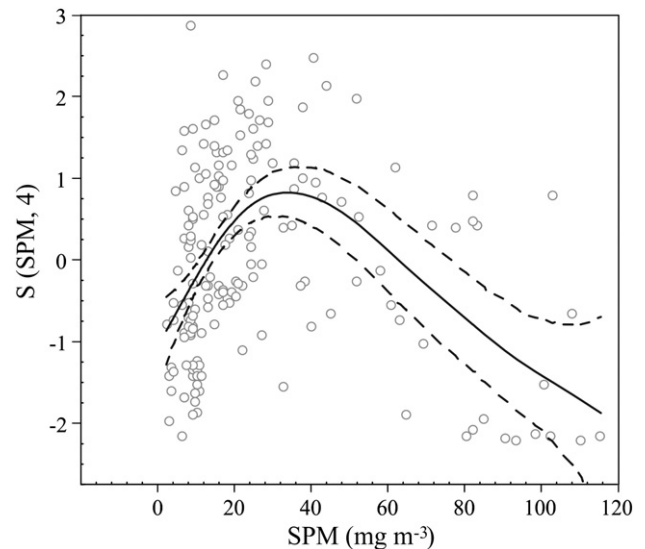


Fig. 3. Relationship (solid line) between *Acartia tonsa* abundance [$\log_{10}(x + 1)$] and SPM obtained by generalized additive model. Dotted line indicates confidence bands (95%). Circles correspond to the observed values. S on the y-axis represents the smooth function (spline) for *A. tonsa* abundance and the number next to the variable name is the estimated degrees of freedom. The model explained 46.5% of the total variance.

presented a non-linear relationship with SPM, peaking between 20 and 60 mg m⁻³ (Fig. 3), which spatially coincides with the TF.

3.2. *A. tonsa* in the turbidity front (TF)

The TF was characterized by a wide salinity range (0.1 to 23.5 units) and by temperatures between 18 and 23.9 °C. The isohaline distribution (Fig. 4) included the tip of the salt wedge, especially in transects 1 and 3; salinity stratification significantly decreased towards the head of the estuarine zone. *A. tonsa* was the most abundant copepod species in nearly all of the stations along the TF, especially those with salinities above 4 (Fig. 4), with more than 90% frequency of occurrence and a greater prevalence than other marine or freshwater species. Other typical marine copepod species, such as *Labidocera fluviatilis*, *Corycaeus amazonicus*, *Eucalanus monachus*, *Centropages furcatus*, and *Paracalanus parvus*, were found in these salinities in lower proportions (<10%, except on transect 4). In turn, the freshwater species *Pseudodiaptomus richardi*, *Argynodiaptomus* sp., *Notodiaptomus* sp., and Fam. Cyclopoidea predominated at the lowest salinity (Fig. 4, transects 1 and 2). *A. tonsa* presented a nearly homogenous distribution across the whole water column, even at stations with strong stratification such as the offshore stations in transects 1 and 3 (Fig. 4). In the surface layer, *A. tonsa* was found in 95% of the stations (21 of 22), with a maximum density of 27,781 ind m⁻³ (mean = 6306 ind m⁻³, SD = 7031). In the bottom layer, it was found in 89% of the stations (18 of 22), reaching 16,698 ind m⁻³ (mean = 4702 ind m⁻³, SD = 5346).

3.2.1. Egg production rates (EPRs)

A. tonsa egg production rates (EPRs) ranged from 2.4 to 14.9 eggs female⁻¹ day⁻¹ (mean = 8.6 eggs female⁻¹ day⁻¹). The cluster analysis identified two significantly different groups of EPR values ($t = 1309.5$, $p < 0.001$). Group A was formed by the stations (1–5) with the lowest EPRs, coinciding with the highest turbidity values (near the ETM). Stations in group B (6–11) were located in the boundary between the TF and the OE, where turbidity was lower (Table 1 and Fig. 5); this zone was near the maximum values of Chl-*a* (see Fig. 2C). The number of females that spawned eggs in group A was significantly lower than in Group B ($t = 3.5$; $p = 0.007$). The *A. tonsa* densities of these two groups did not differ

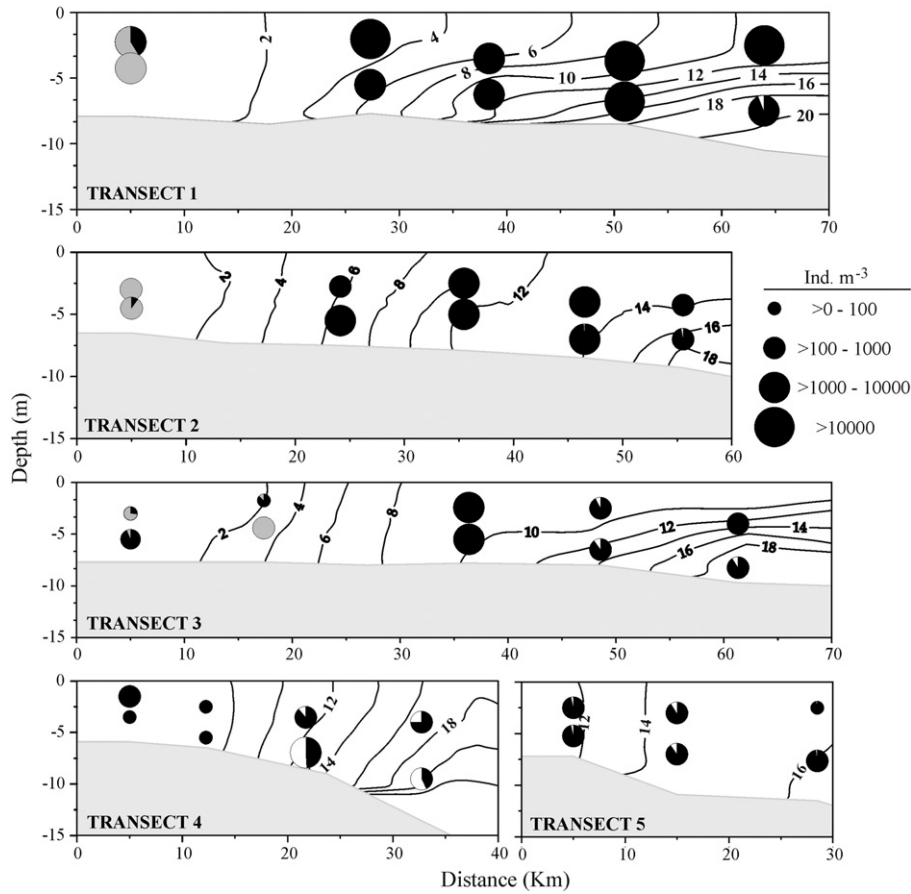


Fig. 4. Copepod densities (values proportional to symbol size) across the turbidity front in a salinity section sampled during a 10–20 March 2006 cruise. Pie charts illustrate the relative densities of copepod groups at the respective sampling depths (black: *Acartia tonsa*. White: marine copepod species. Light gray: freshwater copepod species).

significantly ($t = 28$; $p = 0.8$). Mean salinity was significantly higher in group B ($t = -3.8$, $p = 0.004$) than in group A (Table 1).

3.2.2. Stable isotope analysis

Stable isotope analysis showed that of the three organic sources considered in the TF, *A. tonsa* only used detritus and POM (primarily composed of phytoplankton). Near the ETM, where detritus was the dominant source, the $\delta^{13}C$ signal of *A. tonsa* was similar to that of detritus, whereas near of the zone with maximum Chl-*a* values, the $\delta^{13}C$ signal of *A. tonsa* was similar to that of POM. Cyanobacteria had a relatively more enriched $\delta^{13}C$ signal, suggesting that this food source was not utilized by *A. tonsa* (Fig. 6). The $\delta^{15}N$ values of *A. tonsa* were

similar for both location groups (Fig. 4); however, the $\delta^{15}N$ values of POM were more enriched than expected considering the fractionation of 3.4%. The C/N ratio exhibited significant differences among sources ($F = 143.9$, $df = 7$, $p < 0.05$). Detritus (mean 13.1 ± 1.3) differed from POM (mean 5.0 ± 0.3) (Tukey’s test $p < 0.001$).

4. Discussion

This study confirmed that the highest densities of *A. tonsa* were largely associated with the turbidity front (TF), a specific portion of the system near the most upriver penetration of the salt wedge. The TF region was characterized by strong turbidity and salinity gradients, high SPM concentration and low Chl-*a* values. *A. tonsa* was numerically dominant over the other copepod species in the TF.

In other estuaries where *A. tonsa* is present, the maximum saline intrusion is marked by the presence of the estuarine turbidity maximum (ETM) (e.g., David et al., 2005; Hoffmeyer, 1994; Kimmel and Roman, 2004). In the Río de la Plata, however, the ETM appears to occur mostly in the freshwater part of the estuarine zone and the TF is offshore from it (Fig. 2A). The ecological features of the Río de la Plata TF are similar to those usually reported for ETMs in other estuaries, including, e.g., high bacterial productivity, low biodiversity, high biomass of organisms, fish spawning and nursery areas (Acha et al., 2008; Crump and Baross, 1996; Islam et al., 2005; North and Houde, 2006; Roman et al., 2001).

In the Río de la Plata TF, *A. tonsa* EPR was low (<15 eggs female⁻¹ day⁻¹), as expected for such environments. In optimum conditions of salinity, temperature, and food quality, the species EPR can be as high as 50 eggs female⁻¹ day⁻¹ (e.g., Holste and Peck, 2006; Kleppel et al., 1998 and references).

Table 1

Acartia tonsa eggs production rates (EPRs) in the Río de la Plata estuarine zone. Groups A and B correspond to the cluster analysis in Fig. 5. N_s = number of station, N = number of females incubated, N_e = number of females incubated that released eggs, S_s = surface salinity. Density refers to that estimated in the plankton station where females for incubation were caught.

Group	N_s	N	N_e	Mean EPRs (s.d.)	EPR range	S_s	Density (ind m^{-3})
A	1	20	9	6.3 (4.6)	1–15	10.6	10,599
	2	20	6	3.5 (3.2)	1–10	3.7	12,768
	3	20	7	2.4 (1.2)	1–4	1.9	264
	4	20	11	4.4 (2.4)	1–8	3.4	1192
	5	20	10	3.1 (2.6)	1–9	7.3	2895
B	6	20	11	14.9 (4.7)	6–24	13	1372
	7	20	13	11.0 (8.1)	2–34	11.1	80,816
	8	20	13	12.7 (5.6)	5–24	8.9	27,781
	9	20	10	11.8 (6.3)	1–25	11.7	267
	10	20	14	12.4 (5.8)	1–24	12.7	372
	11	20	14	12.4 (6.1)	2–25	11.7	3958

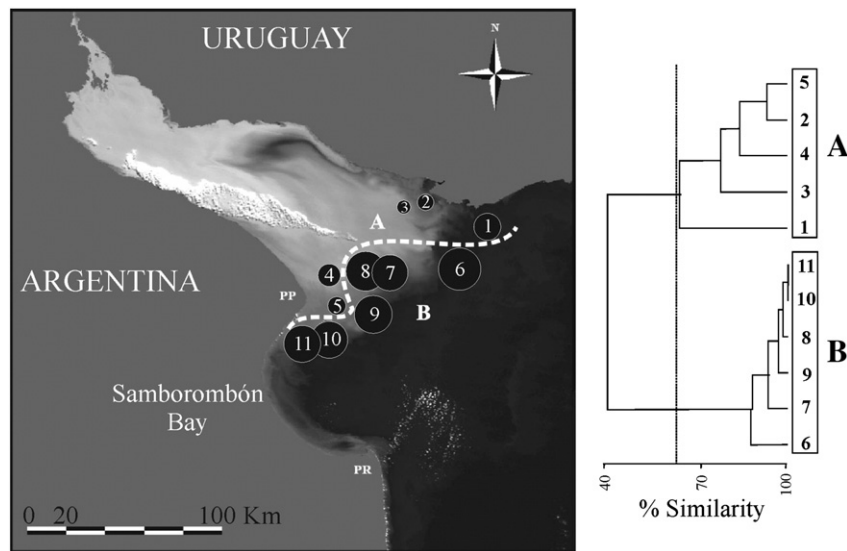


Fig. 5. Satellite image of the Río de la Plata turbidity front obtained with TERRA-MODIS on 19 March 2006. Groups of stations (A and B) with symbol sizes proportional to egg production rates (range: 2.4 to 14.9 eggs female⁻¹ day⁻¹). The dendrogram shows the clustering of the two groups of stations (A and B) at a 65% similarity level. PP = Punta Piedras, PR = Punta Rasa.

The Río de la Plata TF is wide enough (30–70 km, Fig. 3) to detect that *A. tonsa* EPR was unevenly distributed within it. Fewer females spawned and their EPR was lower near the ETM than closer to the high Chl-*a* further offshore. Food quality has a great influence on the fecundity of *A. tonsa* (Calliari et al., 2004; Kleppel et al., 1998; White and Roman, 1992); salinity also has an effect on egg production, presumably due to the costs of osmoregulation (Calliari et al., 2006; Holste and Peck, 2006). Stable isotope analysis supported the differences in EPR related to food quality. Given that phytoplankton typically exhibits different $\delta^{13}\text{C}$ values than detritus of terrestrial origin (Kendall et al., 2001), the origins of primary resources can be linked to *A. tonsa*. In the TF, detritus dominated the samples near the ETM, whereas POM (primarily phytoplankton) was most important close to the high Chl-*a* zone. Hence, individuals of *A. tonsa* near the ETM and with $\delta^{13}\text{C}$ values similar to detritus would have access to predominantly detritus-based food resources. Conversely, individuals near the sector with the highest Chl-*a* concentration exhibited $\delta^{13}\text{C}$ values suggesting that they are primarily incorporating POM. On the other hand, the high $\delta^{15}\text{N}$ values of POM could be due to a

mixture of phytoplankton and microzooplankton, which is abundant in this area (Acha et al., 2008). This is another possible reason for the high EPR close to the high Chl-*a* zone, given that the mix of phytoplankton and microzooplankton is a better diet for *A. tonsa* than one based on detritus (e.g., Calliari et al., 2004; Kleppel et al., 1998).

A. tonsa is omnivorous and may feed on almost any food source; it is usually assumed to feed primarily on the dominant available food (Kleppel et al., 1998; White and Roman, 1992). In fact, other stable isotope studies in estuaries demonstrate the existence of spatial variations in feeding mode (detritus-based feeding or algal-based feeding) related to a differential distribution of resources (Buskey et al., 1999). Although many copepod species are considered omnivorous, most of them can actively select food particles based on the particles' size and nutritional value (Adrian and Schneider-Olt, 1999; Tackx et al., 1989; Tackx et al., 2003). However, selectivity may be affected in environments with high turbidity levels such as estuaries, where phytoplankton production and food availability are strongly affected (Gonçalves et al., 2012 and references therein). Using fatty acid trophic markers (FATMS), Gonçalves et al. (2012) determined that several copepods, including *A. tonsa*, feed primarily on the available food, preferably SPM, in high turbidity environments. In this study, stable isotope analysis indicated that *A. tonsa* did not select its food, instead ingesting the dominant food regardless of its quality. This opportunistic behavior was also reflected in its EPR; *A. tonsa* EPR decreased where detritus (lower quality food) was dominant. Therefore, the use of a combination of both techniques (FATMS and stable isotopes) would likely allow a greater level of detail for determining dietary components.

Export from estuaries due to net offshore flow constitutes a problem for many organisms, and planktonic eggs are the most susceptible developmental stages to be exported (Naylor, 2010 and references therein). Copepods that live in the inner estuary need to be retained by physical and/or biological mechanisms. Water mass convergence was proposed as the primary physical mechanism of copepod aggregation/retention (e.g., Castel and Veiga, 1990; Morgan et al., 1997; Roman et al., 2001). However, physical forces alone are not enough, and some biological mechanisms, such as vertical movements in the water column, are also important in diminishing export and increasing retention (e.g., Morgan et al., 1997; Naylor, 2010; Schmitt et al., 2011). Generally, some life history strategies, such as eggs adhering to the substratum and/or parental transport, have been proposed as methods of diminishing export from estuaries (Dando, 1984; Day

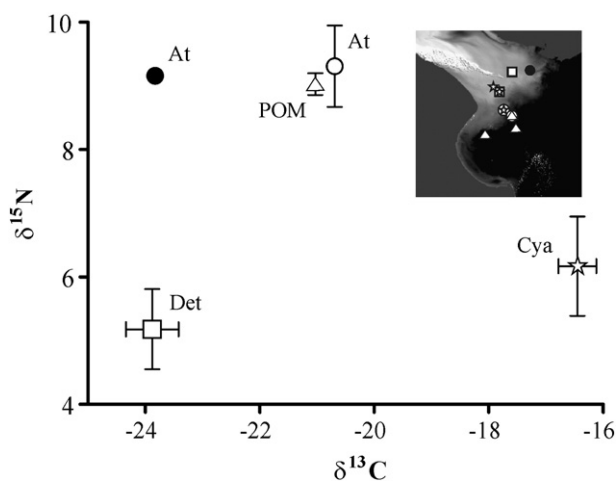


Fig. 6. Dual plots of the stable isotope values of *Acartia tonsa* and its possible food sources in the Río de la Plata turbidity front. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are expressed in ‰. At = *Acartia tonsa*. Black circles and white circles correspond to results near the estuarine turbidity maximum and the opposite side, respectively. Cya = cyanobacteria (star), Det = detritus (square), POM = particulate organic matter (triangle).

et al., 1989; Hempel, 1979; Roman et al., 2001). The epibentic *Eurytemora affinis*, one of the most abundant species in many estuaries worldwide, uses such methods (e.g., Morgan et al., 1997; Naylor, 2010 references therein; Schmitt et al., 2011).

Unlike *E. affinis*, *A. tonsa* releases free planktonic eggs (Mauchline, 1998) that would be more likely to be exported from ETM areas (Roman et al., 2001). In the Río de la Plata estuarine zone, several of the dominant species that spawn and/or inhabit the TF area have pelagic eggs and/or larvae (Acha et al., 2008 and references therein). The confinement of larger densities of organisms and/or inert particles to a narrow band coinciding with the TF suggests that physical retention plays an important role in the estuarine zone (Braverman et al., 2009; Schiariti et al., 2006; Simionato et al., 2008). The convergence of freshwater and estuarine water masses may concentrate organisms around the TF, but dynamic retention by winds may be the primary forcing factor keeping organisms inside the estuarine zone (Simionato et al., 2008). *A. tonsa* in this region are distributed throughout the water column, so both mechanisms could aid in their retention. Moreover, active behavior (e.g., vertical migration in a 2-layered flow) may also favor retention (Cuker and Watson, 2002; Menéndez et al., 2012). Retention of eggs would improve when individuals remain near the bottom in a salt wedge regime (e.g., Mann and Lazier, 1996). Although *A. tonsa* adults are also present in the upper, fresher layer, their eggs could achieve retention due to their high sinking rates ($>20 \text{ m day}^{-1}$) (Miller and Marcus, 1994; Tiselius et al., 2008). Sinking would carry the eggs to the upstream flow of the bottom layer, in which they would be transported again towards the TF. Nevertheless, frequent strong southeast wind events in the area throughout the year may provoke wind-induced vertical mixing and cause the disruption of the salt wedge (Acha et al., 2008; Mianzan et al., 2001). During such unfavorable events, adults, eggs, and larvae would be exposed to advection from the system with consequent population loss. To rebuild the population, benthic resting eggs would be important. *A. tonsa* releases resting eggs in response to adverse environmental conditions, such as low temperatures during winter (Drillet et al., 2008; Sullivan et al., 2007). The resting eggs of *A. tonsa* have not been studied in the Río de la Plata, but the TF has very high sedimentation rates (Acha et al., 2003) that would favor egg settlement to the bottom, and resting eggs could be an important mechanism of population replenishment. In spite of this study's results showing that *A. tonsa* individuals who live in different locations within the TF exhibit different food sources and egg production rates, a good indication that their life history has important consequences on their distribution, there is not enough information about how the *A. tonsa* population is maintained within the TF. Future studies considering interactions between currents, vertical movements and the egg distribution of *A. tonsa* in the Río de la Plata estuarine zone should be developed.

In summary, the high numerical density of *A. tonsa* in the TF indicates that this region is highly advantageous for the copepod's population. The high and constant supply of detritus enables the maintenance of high densities that are not limited by the spring phytoplankton bloom. In addition, high turbidity limits the efficiency of visual predators and increases copepod survival (Morgan et al., 1997 and references therein; Naylor, 2010 and references therein). The two-layered flow in the Río de la Plata estuarine zone and dynamic retention within the TF reduces the exportation of eggs and copepods, and benthic resting eggs may compensate for a share of losses to the population. Those advantages apparently outweigh the low EPR resulting from the poor quality of food in the TF. *A. tonsa* is a common species in several estuaries worldwide, where its highest densities are commonly associated with high chlorophyll values (e.g., David et al., 2005; Diodato and Hoffmeyer, 2008; Irigoien and Castel, 1995). However, *A. tonsa* can live and prosper in areas with high turbidity and low chlorophyll concentrations in the inner sections of estuaries, where retention processes may occur. This ability exemplifies the plasticity

of the species and helps explain why it is a key species in the trophic webs of many estuaries around the world.

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