

Top-Down Effects of an Exotic Serpulid Polychaete on Natural Plankton Assemblage of Estuarine and Brackish Systems in the SW Atlantic

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ABSTRACT

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The invasive reef-building polychaete *Ficopomatus enigmaticus* (Fauvel, 1923) has become well-established in many temperate brackish waters. To analyze preferences for different planktonic food sources, short-term (~1.5 h), grazing microcosm experiments were performed *in situ* ($n = 3$), at two water bodies, a coastal lagoon (Mar Chiquita, MC) and the mixohaline stretches of a coastal creek (La Tigra, LT), Argentina, in January 2007. Relative clearance rates of phytoplankton were assessed for chlorophyll *a* size-fractions and for different groups of nanoplanktonic and microplanktonic protists. The two locations showed significant differences in plankton community structure. Nanoeukaryotes were the dominant group at both locations; the second most-abundant groups were diatoms at MC and ciliates at LT. There were significant differences in chlorophyll-based clearance rates in relation to phytoplankton size-fraction. Clearance rates for pennate diatoms were significantly higher than for any other planktonic prey ($2.3 \text{ l h}^{-1} \text{ g DW}^{-1}$). *Ficopomatus enigmaticus* presented relatively high clearance rates for heterotrophic ciliates ($1.5 \text{ l h}^{-1} \text{ g DW}^{-1}$). Biomass removal by *F. enigmaticus* was high (>50% of initial standing stocks for all components), indicating that the serpulid was capable of regulating planktonic biomass. Significant differences in clearance for different components of the community suggest that *F. enigmaticus* has the potential to promote changes in plankton community structure and, hence, exerts strong top-down controls.

ADDITIONAL INDEX WORDS: *Ficopomatus enigmaticus*, *suspension-feeding*, *microplankton*, *nanoplankton*, *coastal lagoon*, *coastal creek*.

INTRODUCTION

The study of ecological benthic–pelagic coupling has traditionally focused on reproductive (reviewed by Strathmann, 1990) or trophic interactions. Through the latter, benthic suspension-feeding organisms are known to exert a dominant organizing role in shallow aquatic ecosystems by diverting production from the water column to the benthos (French McCay *et al.*, 2003). Benthic suspension-feeding organisms are known for the positive effects that they provide to coastal ecosystems (reviewed most notably for bivalve molluscs by Dame 1996; Lonsdale *et al.*, 2009; Newell, 2004; Prins, Smaal, and Dame, 1998). A number of studies comparing coastal systems that have experienced dramatic changes in abundances of suspension-feeding benthos (either through introductions or eliminations) have linked them to shifts in pelagic structure and function of the whole system (Caraco *et al.*, 1997; Jackson *et al.*, 2001; Mann, Harding, and Southworth, 2009; Pomeroy, D’Elia, and Schaffner, 2006). Serpulid polychaetes are suspension-feeders capable of filtering a wide range of particle sizes (1 to >50 μm ; Jordana *et al.*, 2001a). Although not as thoroughly

studied as bivalves, it has been documented that, through their grazing activity, serpulids might regulate seston concentration and planktonic biomass and productivity (Bruschetti *et al.*, 2008; Davies, Stuart, and de Villiers, 1989) of estuarine systems with limited circulation. Virtually no field or laboratory-based studies have addressed the differential effects that suspension-feeding of serpulids might have on discrete members of the plankton community.

Ficopomatus enigmaticus (Fauvel, 1923) is an exotic and invasive serpulid polychaete in several temperate, brackish water bodies (reviewed in Orensanz *et al.*, 2002). The success of its invasion is related to its ability to thrive in a wide range of temperature (9–27°C) and salinity (1.5–30.0; Fornós, Forteza, and Martínez-Taberner, 1997), and its high densities and reproductive output (Bianchi and Morri, 2001). It builds calcareous, circular coralliform reefs that can change sediment dynamics (Fornós, Forteza, and Martínez-Taberner, 1997; Schwindt, Iribarne, and Isla, 2004) and serve as refuge to other benthos (Etchegoin, Merlo, and Parietti, 2012). *F. enigmaticus* also alters biogeochemical cycles (Lopez, 2004), as the calcareous tubes bind phosphate, thus, representing a significant sink for phosphorus in estuarine systems.

In the SW Atlantic, *F. enigmaticus* was first reported from a freshwater creek in Uruguay in 1938 and then, in 1943, from Argentina’s Quequén River (Orensanz *et al.*, 2002 and references therein). Of particular interest is its occurrence in

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Mar Chiquita, a temperate coastal lagoon in Argentina, where a field survey carried out in 1964 (Olivier *et al.*, 1972) reported it as being a well-established component of the benthos. Obenat and Pezzani (1994) recognized it to be the dominant, benthic suspension feeder in the system; only two other benthic suspension feeders (the infaunal razor clam [*Tagelus plebeius*], and the intertidal mussel [*Brachidontes rodriguezii*] with a limited distribution) have been found at this coastal lagoon (Olivier *et al.*, 1972).

The present study considered two coastal systems, namely the above-mentioned Mar Chiquita coastal lagoon and a coastal creek and contrasted the *F. enigmaticus* filtration activity at both. Coastal lagoons occupy an estimated 13% of coastal areas worldwide (Kjerfve, 1994); the prevalence of wind stress coupled with typically shallow depths results in an intensified benthic–pelagic coupling (Kjerfve, 1994). This intensified benthic–pelagic coupling involves both physical (*e.g.*, the enhanced supply of seston to the benthic community through tidal currents) and biological mechanisms (*e.g.*, the diversion of pelagic primary productivity to the benthos through the feeding activity of suspension feeders). On the other hand, the course of coastal creeks in the area of our study has been carved into Holocene estuarine sequences (loessic sediments), seldom thicker than 2.4 m (Isla, Cortizo, and Schnack, 1996), and they experience seasonal influences from the adjacent coastal ocean due to changes in inlet configuration and storm events (Olivier *et al.*, 1972). Therefore, the consolidated sediments on the margins of the creeks, along with bridge and piling structures, provide a hard substrate for the settlement and development of reef-like aggregations of *F. enigmaticus*.

The coastal systems chosen for this study function differently, in the sense that one is a true estuary (*i.e.* Mar Chiquita is a tidally influenced coastal lagoon that exchanges water daily with the coastal ocean; see De Marco *et al.*, 2005 and references therein), whereas the other is only temporarily influenced by the coastal ocean (see Olivier *et al.*, 1972). Despite these differences, both systems have been successfully invaded by the serpulid, illustrating the plasticity of *F. enigmaticus* to colonize and thrive under a range of ecological conditions. The objectives of this research were to characterize the top-down effects of the exotic, invasive serpulid *F. enigmaticus* on the planktonic assemblage of estuarine and mixohaline water bodies. We examined how this suspension feeder processes different components of the plankton in short-term grazing experiments.

MATERIALS AND METHODS

Study Sites

Mar Chiquita (37°43' S, 57°24' W) is a temperate coastal lagoon in Buenos Aires Province, Argentina (Figure 1a). It is a vertically homogeneous system (De Marco *et al.*, 2005) with a mean tidal amplitude of 0.79 m, is connected to the Atlantic Ocean by a narrow inlet, and is separated by a coastal barrier of sand dunes and beaches. It has an area of ~60 km², with a tributary basin of ~10,000 km² (Lanfredi *et al.*, 1987). Based on dissolved nutrients and pigment distributions, De Marco *et al.* (2005) identified two different subsystems within the lagoon with characteristic ecological and environmental traits, one under marine influence, and the other under inland influence.

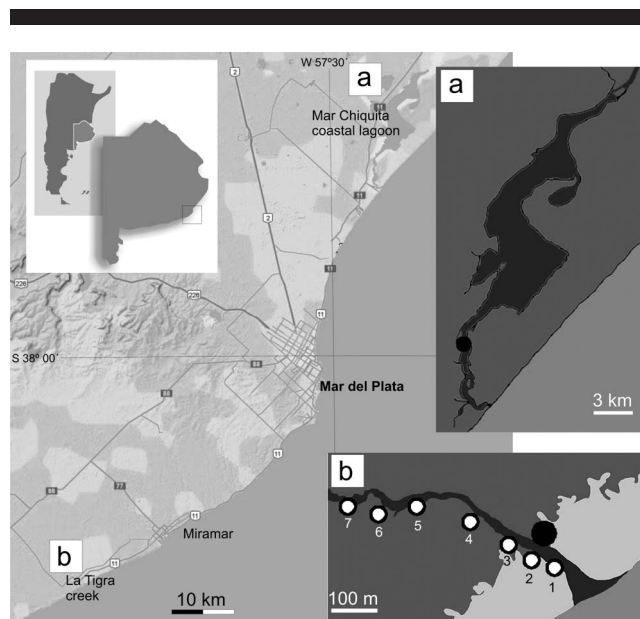


Figure 1. Study sites location in coastal Buenos Aires Province, Argentina. (a) Map of Mar Chiquita coastal lagoon (37°43' S, 57°24' W), showing the location (solid black dot) where grazing experiments were performed. (b) Map of La Tigra creek (38°19' S, 57°56' W), showing the location of grazing experiments (solid black dot), and the seven stations considered for the baseline transect (white dots).

The lagoon is fringed by salt marshes characterized by a halophytic community dominated by *Spartina densiflora*, accompanied by the mudflat colonist *Salicornia perennis* and other brackish macrophytes, such as *Isolepis cernua* (Stutz and Prieto, 2003).

La Tigra (Arroyo Potrerillo de la Tigra, in Spanish) is a second-order stream (length, ~33 km; catchment area, ~80 km²) located on the Atlantic coast of Buenos Aires Province (38°19' S, 57°56' W; Figure 1b). Like other Pampean lotic systems, it presents a gentle slope (1.6 m km⁻¹) and is relatively shallow (0.3–2.5 m) with a hydrological regime controlled by rainfall and underground seepage. This area has experienced marine intrusions due to sea level change during the past 7,000 years (Isla, 1989), with the resultant feature of numerous coastal creeks carved into upper Cenozoic loessic silts (Espinoza, De Francesco, and Isla, 2003). These coastal creeks are mixohaline in their terminal stretches, where they show vertical and horizontal salinity gradients in relation to ocean proximity. However, they are not subject to periodic tidal wave excursions from the adjacent ocean because of low mean tidal amplitudes (0.8 m; Martos, Reta, and Guerrero, 2004) and sandy beaches acting as buffers; but sporadic storm events can increase the tidal amplitude to 2.5 m and generate saltwater intrusions (Olivier *et al.*, 1972) with extensive residence time in the deeper portions of creek basins (~2.5 m). This creates mixohaline conditions and explains the presence of brackish animals (*e.g.*, juveniles of the crab *Cyrtograpsus angulatus*) and macrophytes (*e.g.*, *Scirpus americanus*).

Experimental Design and Sampling

Short-term (~1.5 h), microcosm-grazing experiments were conducted using cylindrical (inner diameter = 22.5 cm; height = 28.5 cm), opaque, polyvinyl chloride (PVC) tanks; filled with 9 L of ambient seawater. The experiments were carried out *in situ* at both locations on consecutive dates (*i.e.* on 12 January 2007 in MC and on 13 January 2007 in LT). In each case, intact clumps of *F. enigmaticus* (~2,500 cm³ each, oblong shape) were collected during a flood tide from wild populations at the experimental sites (the area known as Recreo Galán in Mar Chiquita, located at the boundary between the marine- and inland-influenced subsystems, *sensu* De Marco *et al.*, 2005; and the NE margin of La Tigra creek at its terminal stretches). The clumps of polychaetes were carefully placed into tanks filled with ambient seawater and allowed to acclimate for ~30 minutes; after acclimation, they were gently transferred to new experimental tanks, representing the start of the grazing experiment. Three experimental and three control (without polychaetes) replicate tanks were considered *per* experimental run. At this point, nutrients were added to all tanks to achieve the following concentrations: 2 µM nitrogen as NH₄Cl, and 0.12 µM phosphorus as NaH₂PO₄ (based on ammonia excretion budgets for polychaetes by Haberfield, Haas, and Hammen, 1975; Hult, 1969; and O'Malley and Terwilliger, 1975, and phosphate excretion budgets for invertebrates by Propp *et al.*, 1983). The addition of nutrients serves the purpose of compensating for the lack of annelid excretion in control tanks devoid of macrozoobenthos. All tanks were covered with 1 cm-thick polystyrene lids fitted to the rim of the container, to keep temperature close to ambient and to reduce light intensity (after Lonsdale *et al.*, 2009). Empirical measurements of light attenuation, made with a standard photosynthetically active radiation (PAR) quantum sensor (Skye Instruments Ltd., model SKP 200), showed that the polystyrene lids cut PAR by ~98%. The tanks remained *in situ*, semisubmerged in the water (~70% of tank height), and resting on the bottom to prevent rocking, which might create an experimental artifact. The water in the tanks was gently agitated midway through the grazing experiments.

Water samples were taken at the beginning and end of each experimental run to characterize the plankton assemblage and those changes in biomass and structure resulting from polychaete grazing. Total and size-fractionated chlorophyll *a* content was calculated from duplicate 30-mL water samples taken with opaque containers, kept in ice in a cooler, and processed immediately upon arrival at the laboratory. Water was concentrated onto Whatman GF/F filters for whole water and the <20-µm (partitioned by gravity filtration on a Nitex mesh) and <5-µm fractions (partitioned using a polycarbonate membrane filter). Chlorophyll *a* was extracted in absolute methanol for at least 12 hours (Holm-Hansen and Riemann, 1978), and concentration determinations were made with a scanning spectrophotometer (Hewlett Packard, model 8452A; wavelengths 250–750 nm) and calculated using the equation published by Porra, Thompson, and Kriedemann (1989).

Water samples (100 mL) were collected for characterization of microplankton (>20 µm) and preserved in 10% acidic Lugol's iodine solution, in amber jars stored in the dark (Stoecker, Gifford, and Putt, 1994). Microplankton samples were pro-

cessed following standard settling techniques (Edler and Elbrächter, 2010; Utermöhl, 1958) and counted using an inverted light microscope (Olympus, model CK2). Organisms were classified into the following taxonomic groups: centric and pennate diatoms and aloricate (oligotrich) and tintinnid ciliates; some tychopelagic or benthic species usually found within the water column of well-mixed environments were included in the counts. Other groups found within the microplanktonic size range included euglenoids, dinoflagellates, silicoflagellates, and colonial cyanobacteria and rhizopods. In most cases, individual cells were counted; for colonial or filamentous organisms, cells were counted only if the colony was >20 µm. Taxa were identified to the lowest taxonomic level possible (Frenguelli, 1925; Maeda, 1986; Maeda and Carey, 1985; Tomas, 1997). Standard measurements of cell dimensions were performed for biovolume estimations (Sun and Liu, 2003), and conversion factors were applied to yield biomass estimates (Menden-Deuer and Lessard, 2000; Putt and Stoecker, 1989; Strathmann, 1967; Verity and Langdon, 1984).

Water samples (5 mL) were preserved in 1% formaldehyde for the enumeration of nanoplankton (2–20 µm) and stored in the dark at 4°C until processed. The densities of nanoplanktonic size-range particles were estimated with a Coulter Multisizer 3 (Hewes, Reid, and Holm-Hansen, 1984; Parsons, 1969), fitted with a 100-µm aperture, and a counting duration of 26 seconds. Samples were previously strained by gravity filtration through a 40-µm Nitex mesh, to prevent clogging of the equipment with larger particles. A microscopy checkup, using a 1000× immersion objective, revealed the nanoplanktonic assemblage to be mostly composed of 2–7-µm nano-eukaryotes (*e.g.*, cryptophytes). Using biovolume estimates from the automated counts, biomass was estimated through conversion factors for flagellates by Menden-Deuer and Lessard (2000).

Clearance rates were calculated following the Coughlan (1969) indirect method and equation, based on the rate of removal of particles from a known volume of suspension. Biomass, rather than cell densities, was preferred to base our calculations of clearance rates because it was thought to better represent trophic interactions, given the range of particle sizes that serpulids can process. At the end of the experiments, all clumps of polychaetes were collected and brought to the laboratory, where individual worms were counted to estimate densities and were later separated from the calcareous tube and dried at 60°C for ~72 hours to estimate soft tissue dry weight. Averaged dry tissue weight *per* clump ± SE = 3.35 ± 0.59 g, and 3.67 ± 0.20 g for the Mar Chiquita and La Tigra experiments, respectively. Clearance rates are expressed in units of dry tissue weight.

Environmental parameters (temperature, salinity) were recorded in the ambient and in the tanks, at the beginning, midpoint, and end of each experiment, with a handheld water-quality checker (HORIBA, model U-10).

Additionally, benthic samples of *F. enigmaticus* clumps and their accompanying benthos (~450 g whole-clump weight, including exoskeletons and sediments) were taken at both locations, fixed in 4% buffered formaldehyde, and later transferred to 97% ethanol. Macroinvertebrates were sorted using a dissecting microscope (Wild Heerbrugg, model M3).

Baseline Transect for La Tigra Creek

A baseline for the terminal mixohaline stretches of La Tigra creek, for physical parameters, plankton assemblage, and polychaete–reef structures, was established, providing a firsthand characterization of the system. Seven stations along a 680-m transect from the low tide sea-surf, running upstream to the limnetic portion of the creek were considered. Percentage of cover area by *F. enigmaticus* was estimated for La Tigra Creek, with a 0.04-m² quadrat, placed randomly at six sites on both margins, within each sampling station. Water temperature, salinity, and pH were monitored along the transect at 1 m depth (*i.e.* the “stagnant” saltwater lens underneath the freshwater course) with a handheld water quality checker (HORIBA, model U-10). In addition, subsurface water samples were taken for total chlorophyll *a* ($n = 2$ at each station), microplankton ($n = 2$ at each station), and nanoplankton ($n = 1$ at each station) and were analyzed as previously described to characterize the planktonic community structure.

Statistical Analysis

Differences in planktonic structure, in terms of chlorophyll *a* size fractions across and within experimental sites were analyzed with a two-way analysis of variance (ANOVA), with chlorophyll fraction and site as factors. The same test was performed on nanoplanktonic and microplanktonic biomass estimates across and within experimental sites. Differences in chlorophyll/biomass-based clearance rates were analyzed with a two-way ANOVA, with repeated measures on one factor (Zar, 1999), with size-fraction/group-specific biomass and site as factors. If significant, *post hoc*, pairwise, multiple comparisons were performed with a Tukey honestly significant difference (HSD) test (Zar, 1999). Differences in the distribution along a transect and area cover of serpulid reefs at both margins of La Tigra creek were analyzed with a two-way ANOVA. Statistical tests were carried out using the program SigmaStat 3.5. All values in figures are reported as means \pm SE.

RESULTS

Experimental Plankton Assemblage Characterization

The two locations considered in this study showed significant differences in the structure of phytoplankton (as evidenced by chlorophyll *a* data, Figure 2), and in terms of nanoplanktonic and microplanktonic biomass and composition (Figure 3) for the dates of sampling in January 2007.

Chlorophyll *a* contents in ambient whole seawater for Mar Chiquita averaged (\pm SE) $12.01 \pm 1.75 \mu\text{g L}^{-1}$, whereas it was ~ 4.4 -fold higher at La Tigra, with $52.57 \pm 4.26 \mu\text{g L}^{-1}$. Phytoplankton $>20 \mu\text{m}$ dominated the autotrophic biomass in Mar Chiquita (Figure 2a), whereas phytoplankton in the 20–5- μm size range were dominant in La Tigra (Figure 2b). Thus, the experiments were run under different conditions at the two locations, with a dominance of microplanktonic autotrophs in Mar Chiquita and of nanoplanktonic components in La Tigra. The autotrophic biomass structure of the environments (related to chlorophyll *a* concentration) was significantly different in terms of size fractions and between locations (two-way ANOVA, size-fraction: $F(2,35) = 35.2$, $p < 0.001$; location: $F(1,35) = 219.0$, $p < 0.001$).

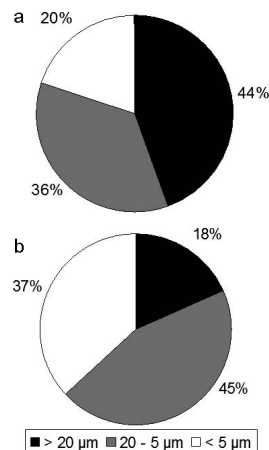


Figure 2. Percent composition of autotrophic plankton based on chlorophyll *a* fractions ($>20 \mu\text{m}$, 20–5 μm , $<5 \mu\text{m}$), for (a) Mar Chiquita (mean total \pm SE = $12.01 \pm 1.75 \mu\text{g L}^{-1}$), in January 2007. (b) La Tigra ($52.57 \pm 4.26 \mu\text{g L}^{-1}$), in January 2007.

In terms of C-content, the biomass at La Tigra was 2.8-fold larger than at Mar Chiquita (with total values of $2602 \pm 318 \text{ mg C m}^{-3}$ in the former, and $942 \pm 124 \text{ mg C m}^{-3}$ in the latter). The automated analysis of the planktonic assemblage evidenced that a group of 2–7- μm nanoeukaryotes (*e.g.*, cryptophytes) dominated the biomass at both locations (Figures 3a and b). On average, La Tigra ($\sim 4.36 \times 10^5 \text{ cells mL}^{-1}$) presented almost threefold the cell concentration of nanoeukaryotes found in Mar Chiquita ($\sim 1.53 \times 10^5 \text{ cells mL}^{-1}$). Planktonic biomass and composition varied significantly with location (two-way ANOVA, $F(1,107) = 18.67$, $p < 0.01$) and among plankton components (two-way ANOVA, $F(8,107) = 59.66$, $p < 0.01$). In Mar Chiquita, other abundant components of the microplankton were centric and pennate diatoms, with biomasses of $63 \pm 18 \text{ mg C m}^{-3}$ and $59 \pm 13 \text{ mg C m}^{-3}$, respectively (Figure 3a). Conversely, a heterotrophic component (*i.e.* oligotrichous ciliates) was the second most-abundant group at La Tigra, with $179 \pm 94 \text{ mg C m}^{-3}$, followed by pennate ($138 \pm 13 \text{ mg C m}^{-3}$) and centric diatoms ($51 \pm 13 \text{ mg C m}^{-3}$; Figure 3b). In Mar Chiquita, pennate diatoms were represented by eight frequently occurring genera (*Amphiprora*, *Amphora*, *Asterionellopsis*, *Cylindrotheca*, *Gomphonema*, *Navicula*, *Nitzschia*, and *Pleurosigma*), whereas there were five recurrent genera of centric diatoms (*Biddulphia*, *Chaetoceros*, *Coscinodiscus*, *Licmophora*, and *Thalassiosira*). Strombids (*e.g.*, *Strombidium*) were the dominant ciliates at La Tigra. With the exception of *Asterionellopsis* and *Cylindrotheca*, La Tigra presented the same representative genera of pennate diatoms, and four others (*Cymbella*, *Epithemia*, *Rhopalodia*, and *Surirella*). Also shared by both water bodies were the centric genera *Coscinodiscus* and *Thalassiosira*, whereas La Tigra also presented representatives of the genera *Melosira* and *Terpsinoe*. In general, the diatom assemblages at both locations were made up by cosmopolitan planktonic and tychopelagic species. It is worth mentioning the presence of

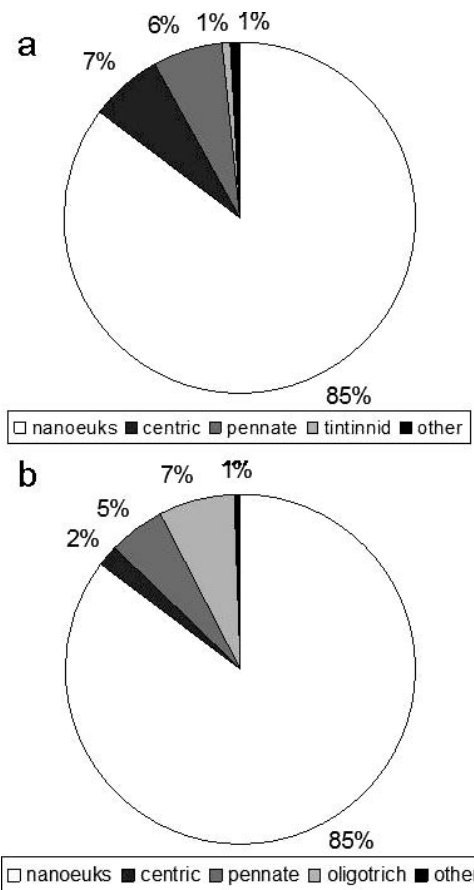


Figure 3. Percent composition of the dominant nanoplanktonic and microplanktonic groups, based on biomass estimates, for (a) Mar Chiquita (mean total \pm SE = 942 ± 124 mg C m⁻³), and (b) La Tigra (2602 ± 318 mg C m⁻³), January 2007. Nanoeuks: 2–7 μ m nanoeukaryotes; microplanktonic components (>20 μ m) include centric and pennate diatoms, tintinnid and oligotrichous ciliates, and other groups of microplankton with minor abundances.

colonial chlorophytes characteristic of freshwater systems, such as *Ankistrodesmus* and *Scenedesmus*, at both locations, as well as naked forms of dinoflagellates (namely, gymnodinoids in Mar Chiquita, and amphidinoids in La Tigra).

Microcosm-Grazing Experiments

Subsurface ambient water temperature (mean \pm SE; $n = 6$) on experimental dates was $20^\circ\text{C} \pm 0.55$ at Mar Chiquita and $18^\circ\text{C} \pm 0.02$ at La Tigra. On average, water temperature on the experimental tanks (both control tanks and treatment tanks with serpulids) increased 1°C throughout the course of the experiment in Mar Chiquita, whereas it remained constant in La Tigra. Subsurface salinity was 32 for Mar Chiquita and 25 for La Tigra, and there were no variations in this parameter throughout the experiments.

Averaged chlorophyll-based clearance rates for whole seawater ranged between 4.34 ± 0.18 l h⁻¹ g DW⁻¹ and 1.87 ± 0.06 l h⁻¹ g DW⁻¹ for Mar Chiquita and La Tigra, respectively

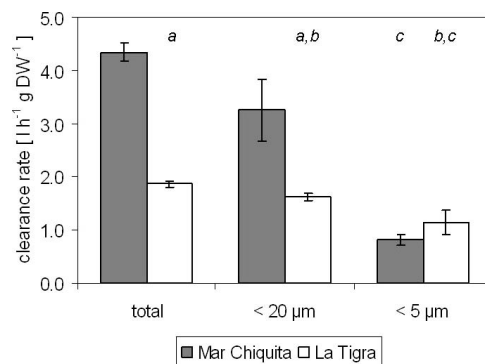


Figure 4. Weight-specific clearance rates [l h⁻¹ g DW⁻¹] of *Ficopomatus enigmaticus*, based on total and fractionated chlorophyll *a*, for Mar Chiquita and La Tigra, January 2007. Error bars are SE.

(Figure 4). Except for the <5- μ m fraction, there were significant differences in clearance rate across experimental sites (two-way repeated measures ANOVA, location: $F(1,17) = 39.72$, $p < 0.001$). Additionally, there were significant differences in clearance rate in relation to size-fraction (two-way repeated measures ANOVA, size-fraction: $F(2,17) = 29.42$, $p < 0.001$); these differences were more marked in Mar Chiquita, where there was a ~ 5.3 -fold difference in clearance rates between the whole and the <5- μ m chlorophyll fraction, and the same was true for La Tigra (albeit with a ~ 1.6 -fold difference in clearance rates). On average, the suspension-feeding activity of *F. enigmaticus* removed 83% of the initial total standing stock and 80% of the <20- μ m fraction in Mar Chiquita during the experimental time, whereas phytoplankton biomass removal amounted to 64% of the total and 62% of the <20- μ m chlorophyll fraction in La Tigra. Removal of the <5- μ m chlorophyll fraction was 60 and 57% of the initial standing stock, for Mar Chiquita and La Tigra, respectively.

A two-way repeated measures ANOVA evidenced that clearance rates differed for individual components of the plankton assemblage (planktonic prey: $F(3,23) = 4.16$, $p < 0.05$; Figure 5). Clearance rates for pennate diatoms were significantly higher than those of any other component, with values of 2.39 ± 0.18 l h⁻¹ g DW⁻¹ and 2.37 ± 0.77 l h⁻¹ g DW⁻¹ for La Tigra and Mar Chiquita, respectively, a result that is in accordance with the highest clearance rates registered for the whole chlorophyll fraction (Figure 4) at both experimental sites. Clearance rate values for other planktonic prey, were > 1 l h⁻¹ g DW⁻¹ in all cases. It is noteworthy the elevated clearance rates (~ 1.5 l h⁻¹ g DW⁻¹) that *F. enigmaticus* presented for a heterotrophic component of the plankton assemblage (*i.e.* oligotrich ciliates), and which were comparable to those for autotrophic prey. On the other hand, there were no differences in prey-specific clearance rates between locations (locations: $F(1,23) = 1.48$, $p = 0.29$). On average, suspension-feeding by *F. enigmaticus* removed 76% of the initial centric diatom biomass at Mar Chiquita and 52% at La Tigra during the experimental run. The initial biomass of pennate diatoms was reduced 88% at La Tigra and 58% in Mar Chiquita, whereas the biomass of

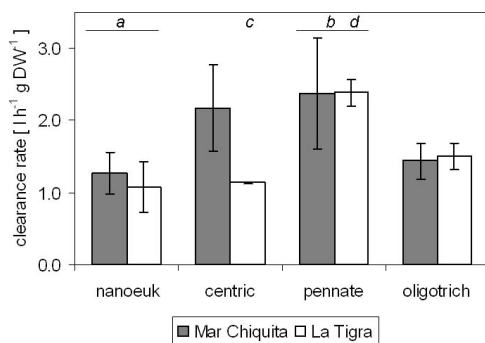


Figure 5. Weight-specific clearance rates [$\text{l h}^{-1} \text{g DW}^{-1}$] of *Ficopomatus enigmaticus*, based on the biomass of specific components of the nano-planktonic and microplankton community of Mar Chiquita and La Tigua, January 2007. Error bars are SE.

nanoeukaryotes was reduced 64% and 56% in the Mar Chiquita and La Tigua experiments, respectively. Averaged biomass removal by *F. enigmaticus* suspension feeding amounted to 79% in La Tigua.

Benthic Macrofauna Associated with *Ficopomatus enigmaticus* Reefs

The faunistic analysis of the accompanying macrofauna in clumps of *F. enigmaticus* revealed that clumps from Mar Chiquita had 13 different benthic taxa, whereas those from La Tigua had only six taxa (all of which were also present at Mar Chiquita). The taxonomic groups found comprised hydrozoans, turbellarians, oligochaetes and polychaete annelids, crustaceans (ostracods, cirripedes, amphipods, and decapods), gastropods and bivalves, and bryozoans. Suspension feeders were absent from the assemblage at La Tigua, whereas they were the second most-abundant trophic guild, after the detritivores, at Mar Chiquita. Although no biomass estimations were made, the suspension-feeder biomass (other than that of *F. enigmaticus*) was minimal in comparison to that of the serpulid.

Baseline Transect for La Tigua Creek

Only the first five stations along the upstream transect starting from the low tide surfzone presented serpulid reefs and incrustations growing on hard substrates (mostly the carved loessic walls that channel the stream course, but also bridge pilings and submerged objects, such as discarded tires, glass bottles, and submerged logs). The first ~70 m upstream (*i.e.* coinciding with a sandy beach) were devoid of serpulids, despite the presence of a wave breaker of granitic rock built to prevent course changes in the stream. There were significant differences in the marginal area covered by serpulid reefs between the sampling stations (two-way ANOVA, stations: $F(4,59) = 214.14$, $p < 0.001$). Even when *F. enigmaticus* did not create a continuous cover along the margins of La Tigua creek, there was a gradual increment in area cover from the 80-m sampling station (salinity = 25), peaking at the 188-m station (with 0.048 and 0.039 m^{-2} at the SW and NE margins, respectively; salinity = 18). From the latter station upstream,

area cover decreased gradually, with the last aggregations of serpulids being recorded at 450 m upstream from the low-tide surfzone (salinity = 15).

Even when all samples of the upstream transect were taken within 1 hour, there were marked and statistically significant differences in total chlorophyll *a* between the stations (one-way ANOVA, $p < 0.001$; Figure 6a). Chlorophyll *a* concentrations ranged from a minimum of $9.12 \pm 2.36 \mu\text{g L}^{-1}$ at the station located 600 m upstream from the surfzone (salinity = 1), to a maximum of $40.48 \pm 1.28 \mu\text{g L}^{-1}$ at the station 333 m upstream (salinity = 15). Likewise, the concentration of nanoplankton (2–7 μm cryptophyte population) had a marked peak at the 600 m upstream station (Figure 6a), with cell concentration reaching $8.7 \times 10^5 \text{ cells mL}^{-1}$ (biomass values provided in Figure 6a), and coinciding with a brisk change in salinity (from 15 to 1) and pH (from 7.5 to 7.0). On average, the rest of the stations presented nanoplankton concentrations that were intermediate to those where the experiments were performed at Mar Chiquita and La Tigua ($\sim 3.0 \times 10^5 \text{ cells mL}^{-1}$). Mean particle size averaged 3.00 μm for the first five stations, whereas, at the two last upstream stations, mean particle sizes were bigger (3.52 and 3.26 μm , respectively). Subsurface water temperature did not vary much along the 681 m transect, presenting a mean of $23.1 \pm 0.3^\circ\text{C}$.

Microplankton biomass was roughly an order or magnitude lower than that of nanoplankton at La Tigua creek (see Figures 6a b); however, it presented a pattern of horizontal variation similar to total chlorophyll *a* and nanoplankton. Figure 6b presents biomass values for the three most-abundant groups of microplankters. Diatoms dominated the microplanktonic biomass throughout the transect, with pennate diatoms being consistently more abundant than centric species. Representative genera were the same as those described in a previous section. Flagellates (especially dinoflagellates and silicoflagellates) were most abundant at the station located 80 m upstream, where the coastal ocean influence was more marked (salinity = 25; pH = 8.0); peridinioid dinoflagellates were more common in upstream stations. Ciliates peaked in abundance at the 188 m upstream station, mostly because of an elevated tintinnid biomass (55 mg C m^{-3}); strombiids were the most common representatives among aloricate ciliates.

DISCUSSION

The two water bodies considered in this study showed significant differences in the summer plankton community structure. Nanoeukaryotes (*e.g.*, cryptophytes) dominated the planktonic biomass at both locations, but, on average, La Tigua presented an almost threefold greater cell concentration of nanoeukaryotes than those found in Mar Chiquita. Certain estuarine environments, such as coastal lagoons, are dominated by $< 5 \mu\text{m}$ plankton (also known as ultraplankton); for instance, a survey in Great South Bay, New York, found great variation in the densities of diatoms and dinoflagellates, whereas ultraplanktonic cryptomonads and chlorophytes were abundant throughout the year, contributing to approximately one-half of the total biomass (Lively, Kaufman, and Carpenter, 1983). As for the causes of ultraplankton dominance, Cloern and Dufford (2005) indi-

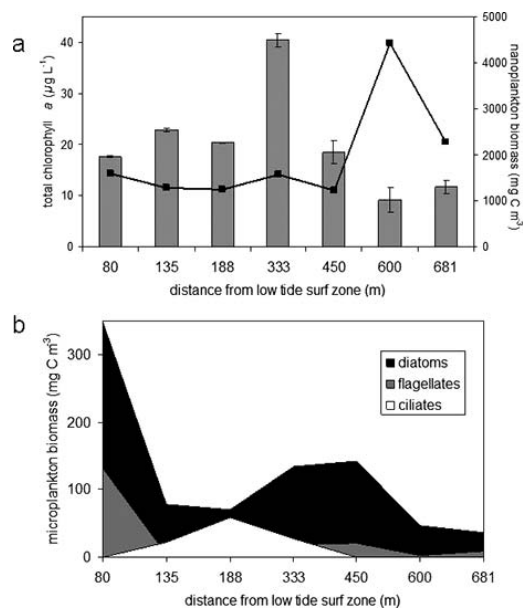


Figure 6. Characterization of the plankton of La Tigua creek, along a 681-m transect, upstream from the low-tide surfzone, January 2007. (a) Grey bars = averaged total chlorophyll *a* concentration \pm SE ($\mu\text{g L}^{-1}$); black squares = nanoplanktonic biomass (mg C m^{-3}) from a population of 2–7- μm cryptophytes. (b) Microplanktonic community composition and biomass estimates (mg C m^{-3}); diatoms include centric and pennate species, flagellates include dinoflagellates and silicoflagellates, and ciliates include tintinnids and oligotrichs.

cate that cell size in estuarine phytoplankton communities is determined both by nutrient supply and by selective grazing. Small size (high surface to volume ratio) provides a competitive advantage in nutrient-impoverted systems (Falkowski, 1981), but this advantage disappears in systems in which high nutrient concentrations promote selective growth of large cells (Marcoval, Villafaña, and Helbling, 2008). Although there are virtually no published studies on nutrient dynamics for La Tigua or other creeks in the area, De Marco *et al.* (2005) carried out a year-round study at Mar Chiquita and concluded that the system profits from unusual nutrient inputs from agricultural runoff, resulting in a higher biological production within the coastal lagoon than in other coastal environments, which would not explain the dominance of ultraplankton from a bottom-up perspective. Therefore, the causes might lie in top-down effects (see below).

The microplanktonic assemblage in summer in both water bodies was dominated by diatoms (49% of the biomass at La Tigua, 88% at Mar Chiquita). This finding was in agreement with that of De Marco (2002) and De Marco *et al.* (2005), who found a similar pattern for the summer months at the same station in Mar Chiquita, where diatoms represented up to 90% of total cell counts. It is worth mentioning that at La Tigua, a heterotrophic component (*i.e.* oligotrichous ciliates) was the second most-abundant group. The relatively high densities of microheterotrophs might have been related to the abundant

nanoplanktonic biomass and the role of ciliates as grazers upon bacteria, picoautotrophs, and nanoautotrophs (Finlay and Fenchel, 1996).

Clearance rates calculated from our *in situ* grazing experiments fall within the range of published estimates for other serpulids (*e.g.*, *Ditrupa arietina*, *Hydroides norvegica*, *Pomatoceros triqueter*, *Salmacina dysteri*, *Spirorbis borealis*, compiled by Jordana *et al.*, 2001b). Davies, Stuart, and de Villiers (1989) provided the only other reference, to our knowledge, on specific clearance rates for *F. enigmaticus*, estimating filtration in laboratory experiments with natural seawater by automated counts of particles in the 2–16- μm size range. Their averaged clearance rate was $8.59 \text{ l h}^{-1} \text{ g DW}^{-1}$, which is within the same order of magnitude, but nearly twice as much as the highest clearance rate estimate from our study (*i.e.* $4.34 \text{ l h}^{-1} \text{ g DW}^{-1}$). However, Davies, Stuart, and de Villiers (1989) found their estimations to be “remarkably high” and, besides the clearance rates not being estimated for particles larger than nanoplankton, they did not provide complementary environmental data (such as the temperature and salinity at which the experiments were run) to provide a further basis for comparisons with our estimates.

The elevated phytoplankton biomass at La Tigua (*i.e.* ~4.4-fold difference with reference to Mar Chiquita) probably had an effect on the filtration activity of *F. enigmaticus*, resulting in significantly lower rates. The current literature does not provide much background for the interpretation of this finding. Jordana *et al.* (2001a) found that food intake increased linearly with food availability in the serpulid *Ditrupa arietina*, and Davies, Stuart, and de Villiers (1989) similarly stated that clearance rates for *F. enigmaticus* increased with particle concentration with no indication of a saturation point. Neither author referred to limitation in the serpulid’s capacity to process food, which seemed to be the case in our experiment at La Tigua. Additionally, our estimation of clearance rates might have been differentially influenced by intrinsic characteristics of either populations of the polychaete, such as age (Jordana *et al.*, 2000). On the other hand, we rule out differences in filtration being attributable to environmental conditions because the experiments were carried out at comparable water temperatures (20°C for Mar Chiquita, 18°C for La Tigua), and Jordana *et al.* (2000) found that there was no correlation between temperature and the activity of the filtration apparatus in *Ditrupa arietina*.

Clearance rates were significantly different between chlorophyll fractions, indicating that *F. enigmaticus* was preferentially removing phytoplankton of larger sizes at both locations. The filtration apparatus of suspension-feeding polychaetes, consisting of ciliated radioles, can retain a broad range of particle sizes down to 1–2 μm (Jordana *et al.*, 2001b; Phillips Dales, 1957). On the other hand, food quality has generally been assumed to correlate directly with carbon content and, thus, also with cell size (Dame, 1996), and it would seem reasonable to assume that an organism like *F. enigmaticus*, capable of feeding on a vast array of particle sizes, would tend to maximize its carbon ingestion by selecting bigger prey items. Additionally, we found that clearance rates were higher for centric and pennate diatoms compared with other components of the microphytoplankton assemblage. Studies on the mech-

anisms of prey selection by suspension-feeding polychaetes are almost nonexistent, but nonetheless, it should be considered that there are chemical cues in phytoplankton that elicit prey selection. For example, Beninger and Decottignies (2005) demonstrated that centric diatoms possess an organic coating (the perifrutular envelope) that renders the cells more palatable for scallops, independent of the carbon content of the cell. Contrary to our finding, Davies, Stuart, and de Villiers (1989) reported that all particles within the 2–12- μm size range were filtered with similar efficiency by *F. enigmaticus*, suggesting that there was no particle selectivity by the serpulid. Our study incorporated automated and microscopic techniques of particle classification and counting and, thus, is more comprehensive than that of Davies, Stuart, and de Villiers (1989), which was based solely on automated counts of particles within a limited size range.

According to the high percentages of biomass removal by the grazing activity of *F. enigmaticus* at both water bodies (removal of >50% of the initial standing stocks for all components, considering a ~1.5-h experimental run), it becomes apparent that this species is capable of regulating planktonic biomass (also found by Bruschetti *et al.*, 2008; and Davies, Stuart, and de Villiers, 1989) and diverting water column production to the benthos. The elevated clearance rates *F. enigmaticus* presented for a heterotrophic component of the plankton assemblage (*i.e.* 1.5 l h⁻¹ g DW⁻¹ for oligotrich ciliates) were comparable to those for autotrophic prey. That finding implies more-complex trophic interactions of *F. enigmaticus*, not only as a primary consumer/detritivore but also as a predator upon planktonic primary consumers. Considering *F. enigmaticus* as a model suspension feeder, further studies should incorporate the filtration of other components of the planktonic assemblage (*e.g.*, picoplankton and bacterioplankton), which might contribute significantly to the biomass of the systems considered here or analogous ones.

Benthic suspension-feeding metazoans are known to provide positive effects to coastal ecosystems (most notably established for bivalve molluscs, see reviews by Lonsdale *et al.*, 2009; Newell, 2004; Prins, Smaal, and Dame, 1998). Surprisingly few studies in benthic ecology incorporate plankton community composition and abundance as a key habitat component for benthic metazoans; however, its importance becomes apparent in studies that contrast coastal systems that have experienced dramatic changes in abundances of suspension-feeding benthos (*e.g.*, see the case studies referred to in the “Introduction”). Within that framework, this study provided a firsthand indication that *F. enigmaticus* has the potential to promote changes in the plankton community of shallow estuarine systems with limited flushing and restricted circulation patterns. The lack of historical data on plankton community structure for either one of the coastal systems covered in this study limits the interpretation on the effects that *F. enigmaticus* has had on plankton and water quality and on how the invasion of the polychaete, started ~70 years ago, might have altered plankton dynamics. Nevertheless, this study provides evidence that *F. enigmaticus* has the potential to drive compositional and biomass changes in the plankton community which translate in water quality.

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