

## High abundance and diversity of consumers associated with eutrophic areas in a semi-desert macrotidal coastal ecosystem in Patagonia, Argentina

Paulina Martinetto<sup>a,b,\*</sup>, Pedro Daleo<sup>a,b</sup>, Mauricio Escapa<sup>a,b</sup>, Juan Alberti<sup>a,b</sup>, Juan Pablo Isacch<sup>a,b</sup>, Eugenia Fanjul<sup>a,b</sup>, Florencia Botto<sup>a,b</sup>, Maria Luz Piriz<sup>b,c</sup>, Gabriela Ponce<sup>c</sup>, Graciela Casas<sup>b,c</sup>, Oscar Iribarne<sup>a,b</sup>

<sup>a</sup> Laboratorio de Ecología, Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, B7600WAG Mar del Plata, Argentina

<sup>b</sup> Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

<sup>c</sup> Centro Nacional Patagónico, Boulevard Brown s/n, (U9120ACV), Puerto Madryn, Chubut, Argentina

### ARTICLE INFO

#### Article history:

Received 19 November 2009

Accepted 14 April 2010

Available online 27 April 2010

#### Keywords:

Patagonia  
coastal eutrophication  
bottom-up  
algal bloom  
benthic invertebrates  
marine birds

### ABSTRACT

Here we evaluated the response to eutrophication in terms of abundance and diversity of flora and fauna in a semi-desert macrotidal coastal system (San Antonio bay, Patagonia, Argentina, 40° 48' S) where signs of eutrophication (high nutrient concentration, seaweed blooms, high growth rate of macroalgae) have been reported. We compared abundances and species composition of macroalgae, small infaunal and epifaunal invertebrates, and birds associated with tidal channels of the San Antonio Bay subject to contrasting anthropogenic influence. Macroalgae were more abundant and diverse in the channel closer to human activity where nutrient concentrations were also higher. In contrast to what others have observed in eutrophic sites, small invertebrates and birds were also more abundant and diverse in the channel with macroalgal blooms and high nutrient concentration. The large water flushing during the tidal cycle could prevent anoxic or hypoxic events, making the environment suitable for consumers. Thus, this could be a case in which eutrophication supports high densities of consumers by increasing food availability, rather than negatively affecting the survival of organisms.

© 2010 Elsevier Ltd. All rights reserved.

### 1. Introduction

Eutrophication is one of the most significant consequences of human alteration of coastal habitats (Valiela, 2006). Its broad geographic scope, impact on resources, widespread effects, and evident anthropogenic influence have made eutrophication a high priority as an agent of change in coastal environments (Bricker et al., 1999; Valiela, 2006; Smith and Schindler, 2009).

Eutrophication is typically triggered by the addition of nutrients, mainly land-derived (Nixon, 1995; Cloern, 2001; Valiela, 2006). As a consequence of high nutrient loads to coastal waters there is an increase in primary production followed by changes in composition and abundance of flora and fauna (e.g., Duarte, 1995). The initial increased growth of macroalgae can have beneficial effects, including short-term nutrient sequestration (Howarth et al., 1996; Boyer et al., 2002) and supply of more and better food particles for consumers (see Valiela, 2006). In the more advanced stages of

eutrophication, the macroalgae canopy may have detrimental effects (Smith and Schindler, 2009). For instance, the overgrowth of opportunistic seaweeds usually has deleterious effects on the previously dominant species (e.g., losses of eelgrass habitats), and can lead to decreases in shellfish and finfish populations, increases in frequency of harmful algal blooms, and hypoxic or anoxic events (e.g., Duarte, 1995; Short and Burdick, 1996; Valiela et al., 1997; Hauxwell et al., 1998). Negative effects, are not limited to the water. Seaweed wracks accumulated along shorelines can also negatively affect intertidal and terrestrial communities (e.g., Hauxwell et al., 2001; Pirtitz et al., 2003) by generating anoxic conditions in the sediment as algal material decays (e.g., Valiela et al., 1992; D'Avanzo and Kremer, 1994). Thus, macroalgal blooms can reorganize natural communities and ecosystem function (e.g., Duarte, 1995; Valiela et al., 1997; Raffaelli et al., 1998; Osterling and Pihl, 2001).

Stable isotopes have been broadly used to evaluate the source of nutrients to coastal systems (e.g., McClelland et al., 1997; Cole et al., 2004, 2005). Nitrogen in wastewater effluent is typically in the form of  $\text{NH}_4^+$  (Valiela et al., 1997), with a  $\delta^{15}\text{N}$  of 6‰. As ground-water moves through the aquifer,  $\text{NH}_4^+$  carried by it undergoes several transformations. Some  $\text{NH}_4^+$  volatilizes, leaving the residual

\* Corresponding author. Laboratorio de Ecología, Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, B7600WAG Mar del Plata, Argentina.

E-mail address: [pmartin@mdp.edu.ar](mailto:pmartin@mdp.edu.ar) (P. Martinetto).

$\text{NH}_4^+$  enriched in  $^{15}\text{N}$  (Aravena et al., 1993).  $\text{NH}_4^+$  may also be converted to  $\text{NO}_3^-$ , by the process of nitrification. Some of the  $\text{NO}_3^-$  produced in this way may then be denitrified, a process which also discriminates against the  $^{14}\text{N}$  bearing molecules, leaving the remaining  $\text{NO}_3^-$  with an even more elevated  $\delta^{15}\text{N}$  (Aravena et al., 1993). The  $\delta^{15}\text{N}$  of primary producers reflects N inputs from land to the water body (McClelland et al., 1997; Martinetto et al., 2006) and has been correlated to the percentage wastewater contribution (Cole et al., 2005). Thus,  $\text{NO}_3^-$  derived from wastewater typically carries a high  $\delta^{15}\text{N}$ , which can be traced into estuaries.

The SW Atlantic Patagonian coast, an almost pristine area (see Orensanz et al., 2002), is also receiving increasing nutrient loads (e.g., Teichberg et al., in press). Given the lack of agricultural activities, nutrients inputs from fertilization are negligible in this region, but the wastewater produced by human coastal populations may become an important nutrient source. Wastewater treatment plants are uncommon in this area, thus domestic wastewater enters the groundwater via on-site septic systems and moves to the aquifer. For this reason, events of eutrophication near human settlements are expected (see Johannes, 1990). In addition, given the unconsolidated sandy sediments that underlay several Patagonian cities, percolation of wastewater and rainwater through the sediment and into the aquifer is expected to be fast (see LeBlanc, 1984).

The San Antonio Bay ( $40^\circ 48' \text{ S}$ , Fig. 1) is located at the northern Argentinean Patagonia and is an important biological conservation site. The area is a Western Hemisphere Shorebird Reserve Network International site (WHSRN) given its importance as stopover site for Neotropical migratory shorebirds (González et al., 1996). High nutrient concentrations, macroalgae blooms, and high growth rates of *Ulva lactuca* have been reported near the town of San Antonio Oeste (Teichberg et al., in press). The most likely nutrient source driving this eutrophication is the discharge of wastewater from the coastal town of San Antonio Oeste (~25,000 inhabitants). As in other Patagonian towns, wastewater passes through septic tanks into the groundwater and then into the bay without further treatments, likely delivering nutrients to the bay and thus changing the ecosystem.

Most eutrophic coastal sites are estuaries, bays or semi-closed areas subject to low water exchange that retains nutrients in the system (Livingston, 2001). If tidal exchange is high, nutrients may be swept to the sea quickly (Howarth et al., 1996) and the residence time of nutrients within the system might be insufficient to allow assimilation by primary producers (Monbet, 1992; Pace et al., 1992; Cloern, 2001). In San Antonio Bay, the tidal amplitude is up to 9 m, generating a large water exchange twice a day. In spite of this high tidal amplitude, DIN concentrations reported during low tide are 2-fold the concentrations found in Venice Lagoon ( $88.6 \pm 5.6 \mu\text{M}$  in San Antonio Bay and  $43.5 \pm 6.2 \mu\text{M}$  in Venice Lagoon, Carrer et al., 2000; Teichberg et al., in press), which is a recognized highly eutrophic site. In addition, the net growth of *U. lactuca* in this site is 2- to 5-fold higher than in other sites around the world (Teichberg et al., in press). Thus, despite the large water exchange, nutrients seem to remain at high concentrations long enough to promote macroalgal blooms.

The influence that the large land-derived nutrient input has on the composition and abundance of flora and fauna in this system is unknown. We hypothesize that the ecosystem response to eutrophication under this unusual condition of high water exchange and high nutrient concentrations might be different compared to other eutrophic sites. Based on this, in this study we evaluated the response to eutrophication in terms of abundance and diversity of flora and fauna in a macrotidal coastal system in an arid, semi-desert region. To do this, we first measured  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations in the water column and determined the  $\delta^{15}\text{N}$  signature in fronds of *U. lactuca*, and then we compared abundances and diversity of macroalgae, small infaunal and epifaunal invertebrates, and birds associated to tidal channels of the San Antonio Bay subject to contrasting anthropogenic influence.

## 2. Materials and methods

### 2.1. Study area

The bay is an  $80 \text{ km}^2$  body of marine water affected by a semi-diurnal symmetrical macrotidal regime (up to 9 m tidal amplitude)

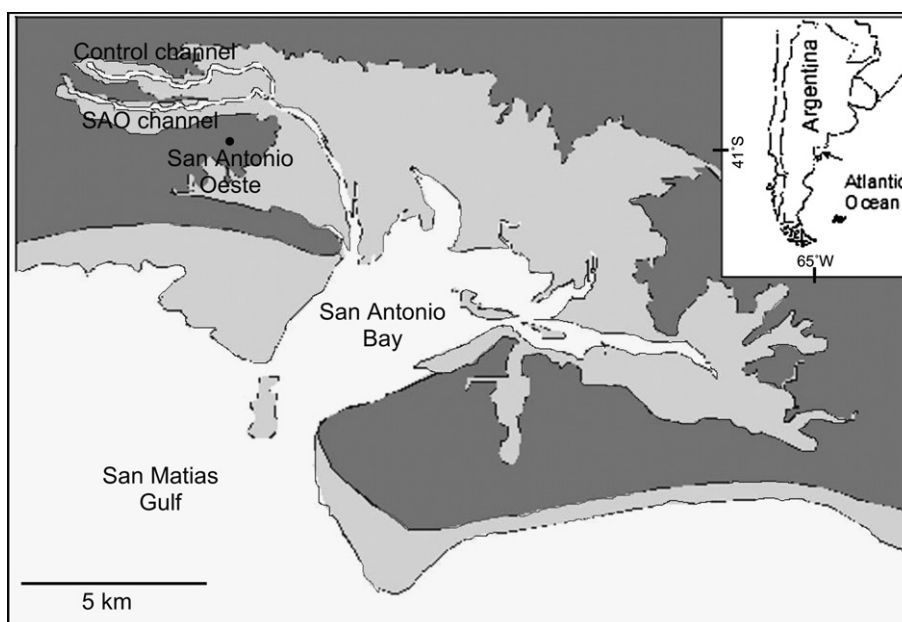


Fig. 1. Map of San Antonio Bay showing the flooded area during high tide (light grey) and the area under water during low tide (white). The SAO channel passes through the town of San Antonio Oeste and the control channel located further from human activities.

and is characterized by an extensive intertidal (mainly sand/pebble flats) surrounded by salt marshes (mainly *Spartina alterniflora*; Isacch et al., 2006). Sampling was performed year round (2003) in two tidal channels of San Antonio Bay: one that runs along the town of San Antonio Oeste (hereafter SAO channel) and another that runs parallel to the first, but is separated by a long bar breaking contact to populated areas (hereafter control channel, Fig. 1). Given the low average rainfall ( $\sim 250$  mm year<sup>-1</sup>; see Isacch et al., 2006), there is almost no freshwater input via precipitation and as a result, the bay is generally hypersaline (see Pascual et al., 2001). The main freshwater input is groundwater introduced via septic systems. This freshwater input is nitrogen-rich and affects the SAO channel, where high DIN concentrations and canopies of opportunistic fast-growing seaweeds had been reported (Teichberg et al., in press). Dense canopies of seaweeds have never been reported in the control channel suggesting that the nutrients derived from town do not affect this channel. Truly independent site replication is virtually impossible to find in nature, but this sampling design in the San Antonio Bay offers an opportunity to examine the effect of anthropogenic N inputs on receiving waters by comparing the biological and chemical characteristics of these two well matched sites (e.g., size, depth, water time residence). Other investigators have used a similar sampling design, using natural, but imperfect replicates to draw comparison (e.g., Pickett, 1989; Geertz-Hansen et al., 1993; McClelland and Valiela, 1998; Hauxwell et al., 2003, 2006). This is a limitation imposed by the nature of the system that we cannot solve, so we assume limitations on the inference to other systems.

## 2.2. Freshwater contribution, nitrogen concentrations, and <sup>15</sup>N labeling of *Ulva lactuca*

Groundwater travels through the aquifer and drains into the bay along a narrow band (i.e., seepage face). This water may have two origins: (a) seawater forced into the ground by the high tide and/or (b) freshwater coming from the groundwater (mainly from household consumption given the low precipitation). Water from the first source is expected to be nitrogen-poor, whereas water from the second is expected to be freshwater and have high N load because of its septic origin. To evaluate these possibilities samples from the water surfacing at the intertidal from the seepage face were taken to determine the salinity. With this aim, 10 samples of groundwater were obtained from the high intertidal during a complete tidal cycle at both channels at the same time. Sample salinity was measured *in situ* with a refractometer. In addition, we measured ammonium (NH<sub>4</sub><sup>+</sup>) and nitrate (NO<sub>3</sub><sup>-</sup>) concentration at the two channels during low tide. Ten samples of water from each channel were filtered (Whatman GF/F) and frozen immediately for later standard colorimetric analyses. To evaluate differences in salinity between channels we used *t*-tests for each tidal level and a one way ANOVA to evaluate differences in salinity along the tidal cycle in each channel. Differences in NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> concentrations between channels were evaluated with *t*-tests. Here and thereafter, when a *t*-test was used, a Welch correction was applied to fix for heterogeneity of variances (Zar, 1999).

To evaluate if algae growing in different channels incorporate N in the tissue from different sources we used stable isotopes analysis. Five samples of *U. lactuca* fronds were obtained from the SAO and the control channel. The fronds were rinsed with distilled water to remove any attached organisms or detritus, then dried in oven (60 °C) and ground to a fine powder. All samples were weighed and loaded into tin capsules and  $\delta^{15}\text{N}$  signatures were determined with a mass spectrometer by the University of California-Davis Stable Isotope Facility (see Lajtha and Michener, 1994 for details). The stable isotopes ratios were expressed as:

$\delta^{15}\text{N} (\text{‰}) = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}] \times 10^{-3}$ , where *R* is the ratio <sup>15</sup>N/<sup>14</sup>N. The standard was N<sub>2</sub> in air. A *t*-test was used to test the null hypothesis of no differences in the  $\delta^{15}\text{N}$  signature of *U. lactuca* between channels.

## 2.3. Diversity and abundance of macroalgae

To evaluate differences in macroalgae diversity between channels, we collected algae from 8 randomly sampled quadrates (30 cm side) at both the SAO and the control channels during the period of higher algal cover (October 2003). Algae was carefully removed and transported to the laboratory. Species were identified under microscope (to the lowest taxonomic level possible) and then the dry weight (dried at 60 °C for 48 h) for each species was obtained. The null hypothesis of no differences in total algal biomass between channels was evaluated using *t*-test. Diversity was analyzed using Shannon diversity index (*H'*; see Wilhm, 1968) and *t*-test was used to evaluate the null hypothesis of no differences in species diversity between channels.

To evaluate changes in the algal coverage throughout the year, algal cover was visually estimated in 10 squares (1 m<sup>2</sup> area) in each channel bi-monthly between January and December 2003. Differences in algal cover between channels for each sampled month were evaluated with *t*-tests. Changes in algal cover throughout the year were evaluated for each channel using one way ANOVA.

## 2.4. Diversity and abundance of small invertebrates

To evaluate if the diversity and abundance of small infaunal and epifaunal invertebrates was different between channels and throughout the year, we sampled bi-monthly in each channel from January to December 2003. On each sampling date, 10 sediment samples (10 cm diameter and 15 cm depth) were obtained from the low intertidal at each channel and sieved through a 500- $\mu\text{m}$  mesh. The retained organisms were preserved in 70% ethanol, identified, and counted using a 20 $\times$  binocular microscope. Diversity was analyzed using the Shannon diversity index and *t*-test was used to evaluate the null hypothesis of no differences in diversity between channels. Differences in abundance of invertebrates between channels for each sampled month were analyzed using a *t*-test, and differences throughout the year were evaluated using one way ANOVA for each channel.

## 2.5. Diversity and abundances of birds

To evaluate if the abundance and diversity of birds differed in tidal channels subjected to contrasting anthropogenic influence, we carried out a sampling in the SAO and the control channel. The sampling were done bi-monthly between January and December 2003, and consisted of 11 transects (100 m long and using 8  $\times$  40 binoculars) following a line along the tidal channels and walking at an approximate rate of 5 min per transect (following Conner and Dickson, 1980). Each transect included both sides of the channel (width 15 m from each side; covering a total area of 0.003 km<sup>-2</sup> per transect). Numbers of individuals per species were recorded during the 2 h around the time of low tide. For the analysis, the most abundant species were grouped by taxonomic group and trophic habits as: gulls (*Larus dominicanus*, *Larus atlanticus*, *Larus maculipennis*), oystercatchers (*Haematopus palliatus*), migratory shorebirds (plovers, godwits, yellowlegs and sandpipers; see scientific names in Table 3), and ducks (dominated by *Anas specularoides*). For each bird species, density was expressed as birds per transect. The null hypothesis of no difference between channels in species richness and abundance of each group for each date was evaluated

with a *t*-test. Data transformation ( $\log_{10}[Y + 1]$ ) was used when needed to meet homocedasticity (Zar, 1999).

### 3. Results

#### 3.1. Freshwater contribution, nitrogen concentrations, and $^{15}\text{N}$ labeling of *Ulva lactuca*

Salinity in the water from the seepage face in the control channel was stable through the tidal cycle ( $F_{5,54} = 3.689$ ,  $p = 0.056$ ) and higher than in the SAO channel (Fig. 2). Salinity values in the SAO channel decreased during the ebbing tide ( $F_{5,54} = 22.626$ ,  $p < 0.001$ ; Fig. 2).

Concentration of both  $\text{NH}_4^+$  and  $\text{NO}_3^-$  were higher in the SAO channel than in the control channel (Table 1;  $t = 2.087$ ,  $p = 0.045$  and  $t = 3.120$ ,  $p = 0.011$  for  $\text{NH}_4^+$  and  $\text{NO}_3^-$  respectively). The  $\delta^{15}\text{N}$  signature of *U. lactuca* was enriched by 10‰ in fronds from the SAO channel compared to those from the control channel (Table 1;  $t = 5.5$ ,  $df = 8$ ,  $p < 0.05$ ).

#### 3.2. Abundance and diversity of macroalgae

A total of 13 macroalgae taxa were recorded. Eight taxa were present only in the SAO channel, while only one species, *Blidingia minima*, was found exclusively in the control channel (Table 2). Algal biomass (SAO channel =  $125.333 \text{ g m}^{-2}$ ,  $se = 1.623$ ; control channel =  $62.515 \text{ g m}^{-2}$ ,  $se = 1.009$ ;  $t = 4.41$ ,  $df = 15$ ,  $p < 0.01$ ) as well as species diversity ( $H_{SAO}' = 0.48$ ,  $H_{control}' = 0.22$ ;  $t = 5.3$ ;  $df = 92$ ;  $p < 0.01$ ) was higher in the SAO channel compared to the control channel. In addition, the algal cover was higher in the SAO than in the control channel during all sampled months except September when there was no difference (Fig. 3). Algal cover also changed through the year at both the control ( $F_{4,45} = 18.980$ ,  $p < 0.001$ ) and the SAO channel ( $F_{4,45} = 77.687$ ,  $p < 0.001$ ). In both channels, the algal coverage was similar in January and April and different between all other comparisons with higher values during September and December (Fig. 3).

#### 3.3. Abundance and diversity of small invertebrates

Twelve main invertebrate taxa were identified (Table 3). Polychaetes from the families syllidae and sipunculidae were more abundant in the SAO channel, while all other polychaetes did not show differences between channels (Table 3). The mud crabs *Cyrtograpsus altimanus* and *Cyrtograpsus angulatus*, the amphipods *Corophium* sp. and *Mellita palmata* and the snail *Buccinanops*

**Table 1**

Ammonium and nitrate concentrations (mean  $\pm$  SE) measured in two channels of San Antonio Bay (Argentina), and  $\delta^{15}\text{N}$  signature of *Ulva lactuca* fronds collected in the same channels. The SAO channel is located close to the town of San Antonio Oeste and the control is farther from town.

	$\text{NH}_4^+$ ( $\mu\text{M}$ )	$\text{NO}_3^-$ ( $\mu\text{M}$ )	$\delta^{15}\text{N}$ (‰)
SAO	$15.2 \pm 14.4$	$70.7 \pm 14.1$	$15.4 \pm 1.8$
Control	$1.7 \pm 1.5$	$40.6 \pm 16.3$	$5.2 \pm 0.7$

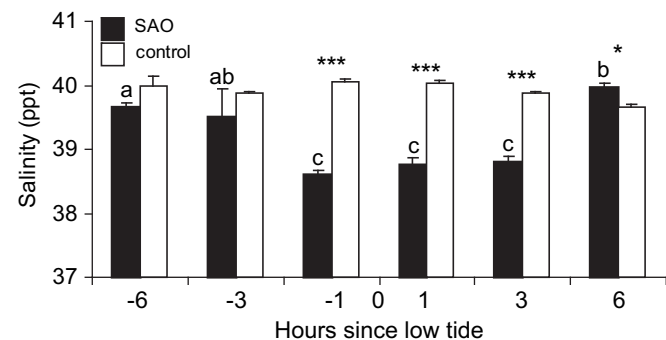
*globosum* were also more abundant in the SAO channel (Table 3), while the snail *Heleobia australis* was more abundant in the control channel. The abundance of the mussel *Brachidontes rodriguezii* did not show difference between channels, but in December it was more abundant in the control channel (Table 3). Diversity of invertebrates in April and September was higher in the SAO channel (Table 4), while in all other months there were no differences.

#### 3.4. Diversity and abundance of birds

A total of 20 bird species were recorded (Table 5). The Neotropic cormorant and the White-rumped Sandpiper were seen on a few occasions exclusively in the control channel (Table 5). In contrast, 11 species were observed exclusively in the SAO channel (Table 5). Species richness peaked in April and June with higher values in the SAO channel (Fig. 4; April:  $t = 3.50$ ,  $df = 20$ ,  $p = 0.02$ ; June:  $t = 6.90$ ,  $df = 20$ ,  $p < 0.001$ ). Duck and gull abundance was higher in the SAO channel than in the control channel during April and June (Fig. 5; Ducks: April:  $t = 2.47$ ,  $df = 20$ ,  $p = 0.002$ ; June:  $t = 3.51$ ,  $df = 20$ ,  $p = 0.002$ ; Gulls: April:  $t = 2.20$ ,  $df = 11$ ,  $p = 0.049$ ; June:  $t = 4.74$ ,  $df = 12$ ,  $p = 0.001$ ) while no difference was observed in the other sampled months (Fig. 5). Migratory shorebird abundance was not different between channels (Fig. 5), while Oystercatchers *H. palliatus* were more abundant during January and December in the control channel (Fig. 5; January:  $t = 3.22$ ,  $df = 20$ ,  $p = 0.004$ ; December:  $t = 3.19$ ,  $df = 20$ ,  $p = 0.005$ ) and during April in the SAO channel (Fig. 5; April:  $t = 2.57$ ,  $df = 20$ ,  $p = 0.018$ ).

## 4. Discussion

Our results show evident signs of eutrophication in the SAO channel. The changes in salinity in the water from the seepage face in this channel indicate delivery of freshwater from groundwater. Groundwater in this arid system is typically derived from domestic use and is expected to carry high nitrogen loads associated with

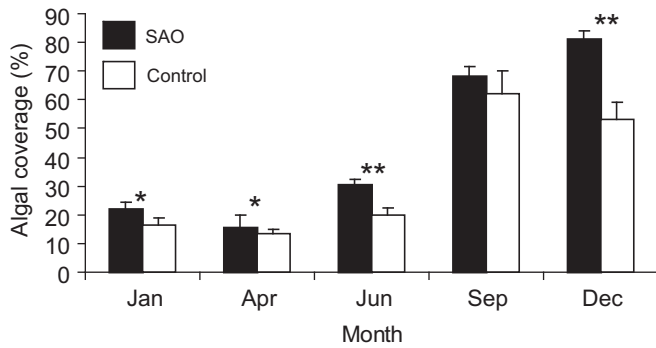


**Fig. 2.** Salinity (mean  $\pm$  SE) of water surfacing at the seepage face throughout a tidal cycle in the SAO and control channel of San Antonio Bay. Different letters indicate differences in salinity in the SAO channel along the tidal cycle (Tukey test). Asterisks indicate difference in salinity between channels (*t*-test; \*,  $p < 0.050$ , \*\*,  $p < 0.010$ , \*\*\*,  $p < 0.001$ ).

**Table 2**

Biomass ( $\text{g m}^{-2}$ , means  $\pm$  SE) of algal species recorded in two channels of San Antonio Bay (Argentina), one of them close to the town of San Antonio Oeste (SAO Channel) and the other farther from town (Control Channel). Group *Blidingia-Enteromorpha* includes undistinguished species within these genera.

Algal species	SAO	Control
<i>Blidingia minima</i>	0	$42.74 \pm 1.05$
Group <i>Blidingia</i> – <i>Enteromorpha</i>	$52.51 \pm 1.85$	0
<i>Chaetomorpha aerea</i>	$0.56 \pm 0.05$	0
<i>Enteromorpha</i> spp.	$46.76 \pm 1.89$	0
<i>Gymnogongrus</i> sp.	$3.42 \pm 0.15$	0
<i>Hincksia granulosa</i>	$1.91 \pm 0.11$	0
<i>Monostroma</i> sp.	$0.51 \pm 0.04$	$10.88 \pm 0.40$
<i>Polysiphonia abscissa</i>	$0.34 \pm 0.02$	$0.81 \pm 0.07$
<i>Polysiphonia argentinica</i>	$1.18 \pm 0.08$	$0.66 \pm 0.06$
<i>Polysiphonia hassleri</i>	$0.26 \pm 0.02$	0
<i>Punctaria</i> sp.	$0.74 \pm 0.04$	$1.21 \pm 0.11$
<i>Streblocadia comptoclada</i>	$0.42 \pm 0.04$	0
<i>Ulva lactuca</i>	$16.86 \pm 0.35$	0



**Fig. 3.** Algal coverage (%) in two channels of San Antonio Bay (Argentina), the first passes through the town of San Antonio Oeste (SAO) and the second is further from human activities (control). Asterisks indicate difference in the algal cover between channels (*t*-test; \*:  $p < 0.050$ , \*\*:  $p < 0.010$ , \*\*\*:  $p < 0.001$ ).

wastewater plumes. Thus, the high nutrient concentration found near the town of San Antonio Oeste is most likely land-derived and related to human population. The land-derived nitrogen was assimilated by macroalgae, as was evident by the high stable

**Table 3**

Abundances (individuals per sample) of small invertebrates (mean (SE)) in two channels of San Antonio Bay (Argentina), the first passes through the town of San Antonio Oeste (SAO) and the second is further from human activities (Control). Asterisks indicate difference between channels (*t*-test; \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ ). (p): Polychaeta, (c): Crustacea, (m): Mollusca.

	January	April	June	September	December
<b>Syllidae (p)</b>					
SAO	15.9 (7.6)	13.5 (5.9)	17.9 (8.5)	12.7 (16.9)	10.2 (9.6)
Control	6.9 (5.7)***	9.4 (2.9)*	6.6 (6.2)***	9.6 (5.0)	12.1 (4.2)
<b>Maldanidae (p)</b>					
SAO	0.5 (0.2)	0.3 (0.1)	0.6 (0.2)	0.8 (0.2)	0.4 (0.1)
Control	0.1 (0.03)	0	0.2 (0.1)	0.2 (0.1)	0.7 (0.1)
<b>Orbinidae (p)</b>					
SAO	5.1 (2.5)	5.2 (3.6)	4.3 (2.3)	4.2 (3.2)	4.1 (3.9)
Control	3.4 (0.9)	4.0 (2.5)	3.6 (1.9)	4.1 (1.6)	2.8 (2.3)
<b>Lumbrinidae (p)</b>					
SAO	0.4 (0.2)	0.5 (0.2)	0.6 (0.2)	0.5 (0.1)	0.9 (0.2)
Control	0.1 (0.03)	0.1 (0.03)	0.2 (0.1)	0.2 (0.1)	0.4 (0.2)
<b>Sipunculidae (p)</b>					
SAO	1.1 (1.0)	1.8 (0.4)	1.7 (0.4)	1.9 (0.5)	1.5 (0.4)
Control	0.3 (0.2)*	0.2 (0.1)**	0.4 (0.1)**	0.6 (0.1)**	0.8 (0.2)
<b>Cyrtograpsus altimanus (c)</b>					
SAO	0.7 (0.1)	0.5 (0.2)	0.2 (0.1)	1.4 (0)	2.1 (0.3)
Control	0.1 (0.03)*	0.1 (0.03)	0.2 (0.1)	0.3 (0.1)*	0.3 (0.1)***
<b>Cyrtograpsus angulatus (c)</b>					
SAO	0.8 (0.2)	0.2 (0.1)	0.6 (0.4)	1.0 (0.2)	1.5 (0.3)
Control	0.1 (0.03)*	0.1 (0.03)	0.3 (0.1)	0.1 (0.03)**	0.1 (0.03)**
<b>Corophium sp. (c)</b>					
SAO	8.6 (6.5)	8.5 (0.8)	8.1 (11.4)	11.2 (14.2)	15.5 (47.6)
Control	1.3 (0.2)***	0.7 (0.2)**	1.2 (0.2)**	0.8 (0.1)***	1.2 (0.3)**
<b>Mellita palmata (c)</b>					
SAO	1.1 (0.2)	1.1 (0.8)	1.0 (0.2)	1.1 (0.3)	1.4 (0.5)
Control	0.4 (0.1)*	0.1 (0.03)	0.2 (0.1)*	0.6 (0.2)	0.5 (0.2)
<b>Heleobia australis (m)</b>					
SAO	1.4 (0.2)	1.2 (0.1)	0.6 (0.2)	1.2 (0.2)	0.4 (0.2)
Control	1.1 (0.2)	0.7 (0.2)	2.3 (1.7)*	4.3 (2.1)**	4.2 (1.9)***
<b>Brachidontes rodriguezii (m)</b>					
SAO	0.5 (0.4)	2.2 (1.2)	1.7 (1.3)	1.1 (0.5)	0.2 (0.1)
Control	0.7 (0.4)	1.8 (1.4)	1.7 (1.3)	0.8 (0.3)	1.0 (0.3)*
<b>Buccinanops globosum (m)</b>					
SAO	1.9 (1.5)	2.1 (1.8)	2.9 (2.1)	1.4 (0.8)	0.8 (0.7)
Control	1.7 (1.0)	1.7 (0.7)	0.6 (0.1)*	1.5 (0.7)	1.0 (0.5)

**Table 4**

Shannon diversity indices for small invertebrates from two channels of San Antonio Bay (Argentina), the first passes through the town of San Antonio Oeste (SAO) and the second is further from human activities (control). Asterisks indicate difference in diversity between channels (*t*-test, \* $<0.050$ , \*\* $<0.010$ ).

	SAO	Control
January	0.68	0.63
April	0.68	0.51**
June	0.67	0.62
September	0.72	0.65*
December	0.67	0.64

isotopic signature of *U. lactuca* fronds. The abundance and diversity of macroalgae were higher in the channel with higher nutrient concentration, dominated by opportunistic green algae species (i.e., *Enteromorpha* sp., *U. lactuca*). In contrast to what others have observed, higher abundance of small infaunal and epifaunal invertebrates was associated with high nutrient concentrations and large macroalgal canopies, as well as higher abundance and diversity of birds.

Nutrient concentrations in the SAO channel were among the higher values in a record of more than one hundred estuaries in the US (Holmes, 2008) and were higher than the concentrations found in other eutrophic coastal areas such as Venice lagoon in Italy, Mondego River in Portugal, and Urias estuary in Mexico (Teichberg et al., in press). Nitrogen in wastewater effluent is typically in the form of  $\text{NH}_4^+$ , but DIN in the SAO channel was mostly  $\text{NO}_3^-$ . Although  $\text{NH}_4^+$  may be the physiologically preferred form of N (Thomas and Harrison, 1987), macroalgal blooms have been observed in estuaries that received nitrate-rich wastewater, and macroalgae in enriched estuaries often bear the  $\delta^{15}\text{N}$  of  $\text{NO}_3^-$  entering the estuary (McClelland et al., 1997; McClelland and Valiela, 1998; Cole et al., 2006). Our results show that in this system there is a high availability of N in terms of  $\text{NO}_3^-$ . This  $\text{NO}_3^-$  can be used by macroalgae under low supply of  $\text{NH}_4^+$  and supports blooms. The high  $\delta^{15}\text{N}$  signature of macroalgae fronds supports the idea that macroalgae are using land-derived  $\text{NO}_3^-$  as an N source.

**Table 5**

Bird species (common and scientific names) observed in two channels of San Antonio Bay (Argentina), the first passes through the town of San Antonio Oeste (SAO) and the second is further from human activities (Control). +: presence, -: absence.

	SAO	Control
<b>Ducks</b>		
Speckled teal- <i>Anas flavirostris</i>	+	-
Crested duck- <i>Anas specularioides</i>	+	+
Oystercatcher		
American oystercatcher- <i>Haematopus palliatus palliatus</i>	+	+
<b>Migratory shorebirds</b>		
Two-banded plover- <i>Charadrius falklandicus</i>	+	+
Hudsonian godwit- <i>Limosa haemastica</i>	+	-
Greater yellowlegs- <i>Tringa melanoleuca</i>	+	+
Lesser yellowlegs- <i>Tringa flavipes</i>	+	-
White-rumped sandpiper- <i>Calidris fuscicollis</i>	-	+
<b>Gulls</b>		
Olrog's gull- <i>Larus atlanticus</i>	+	-
Kelp gull- <i>Larus dominicanus</i>	+	+
Brown-hooded gull- <i>Larus maculipennis</i>	+	+
Trudeau's tern- <i>Sterna trudeaui</i>	+	-
<b>Others</b>		
Pale-faced sheathbill- <i>Chionis alba</i>	+	-
Chilean skua- <i>Catharacta chilensis</i>	+	-
Chimango caracara- <i>Milvago chimango</i>	+	-
Great grebe- <i>Podiceps major</i>	+	+
Imperial shag- <i>Phalacrocorax atriceps</i>	+	-
Neotropical cormorant- <i>Phalacrocorax olivaceus</i>	-	+
Great white egret- <i>Egretta alba</i>	+	-
Chilean flamingo- <i>Phoenicopterus chilensis</i>	+	-

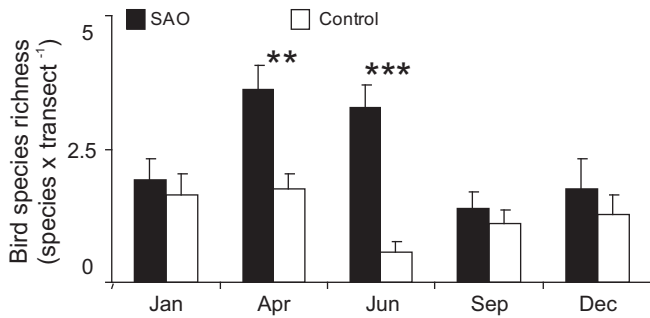


Fig. 4. Bird species richness in the SAO and the control channel of San Antonio Bay throughout the year. Asterisks indicate difference in bird abundance between channels ( $t$ -test; \*,  $p < 0.050$ , \*\*,  $p < 0.010$ , \*\*\*,  $p < 0.001$ ).

Macroalgal respiration consumes oxygen at night driving hypoxic/anoxic events. During the day, this can be reversed by production of oxygen during photosynthesis. Several cloudy days, may decrease photosynthesis resulting in greater consumption of oxygen than production, and turn the system anoxic (D'Avanzo and Kremer, 1994). These events of hypoxia and anoxia affect the survival of many organisms such as fishes, shellfishes, and other consumers, including macroalgal grazers (D'Avanzo and Kremer, 1994; Fox et al., 2009). Thus, highly eutrophic sites are characterized by high nutrient loads, dominance of fast-growing seaweeds, and consequently lower abundance and diversity of organisms. It seems that in San Antonio in spite of high nutrient availability, high macroalgal biomass and the high growth rate of *U. lactuca* (Teichberg et al., in press), the system remains as in initial state of eutrophication where there is abundant high quality food for herbivores, but the system does not shift towards the anoxia typical of advanced eutrophication. This is also evidenced by the higher density of invertebrates found in the SAO channel. Dissolved oxygen values recorded in the SAO channel (2 years survey, Martinetto unpublished data) have never been low enough to turn the system anoxic (considering  $4.6 \text{ mg O}_2 \text{ l}^{-1}$  as the limit to maintain most taxa (Vaquer-Sunyer and Duarte, 2008)). One possible explanation is that pronounced tidal flushing provides a continuous input of oxygen-rich water that limits anoxic or

hypoxic events. Thus, this could be a case in which eutrophication supports high densities of herbivores by increasing food availability (Nixon and Buckley, 2002), rather than negatively affecting the survival of organisms.

Negative effects of macroalgae on habitat use by shorebirds and seabirds have also been reported. For instance, macroalgae can cover the foraging area and affect sediment penetrability (see Bryant, 1979; Quammen, 1984; Mouritsen and Jensen, 1992). The SW Atlantic intertidals are important stopover sites for migratory shorebirds that breed in the northern hemisphere and spend their winter in the southern hemisphere (Morrison and Ross, 1989; Botto et al., 1998). In particular, San Antonio Bay, which was designated as a Western Hemisphere Shorebird Reserve Network International Site (WHSRN; González et al., 1996), is an important stopover site for Nearctic migratory shorebirds. Thus, alteration of these habitats may have strong effect on migratory shorebirds and other endangered seabirds such as *L. atlanticus* (Birdlife, 2004). However, bird species richness and abundance was higher in the areas with higher algae biomass. This pattern may be due to higher densities of epibenthic organisms that birds use for food (see Soulsby et al., 1982; Raffaelli et al., 1998; Cabral et al., 1999; Raffaelli, 1999; Lopes et al., 2000).

In spite of significant tidal flushing, nutrients seem to remain in the system long enough to be assimilated by macroalgae and to support blooms. The system also allows a high abundance of consumers including herbivores. The implication of these results is that, in contrast to other eutrophic coastal areas that are clearly controlled by nutrients from the bottom-up, top-down forces could be also strong in this system. Indeed, herbivores in the SAO channel reduce the growth rate of *U. lactuca* by 65% (Martinetto unpublished data). This reduction is quite high compared to other eutrophic systems (e.g., 29.3% in Maasholm Bay, Baltic Sea (Lotze and Worm, 2000), negligible in the eutrophic inner part of the Roskilde Fjord estuary in Denmark (Geertz-Hansen et al., 1993) and in Childs River, Waquoit Bay, USA (Morgan et al., 2003)). Thus, high land-derived nutrients in this system support macroalgal blooms as is typical in eutrophic systems. However, the process of eutrophication seems to remain in an initial state, resulting in beneficial effects, such as sequestering of nutrients by macroalgae and furnishing better food particles, but not reducing abundances of

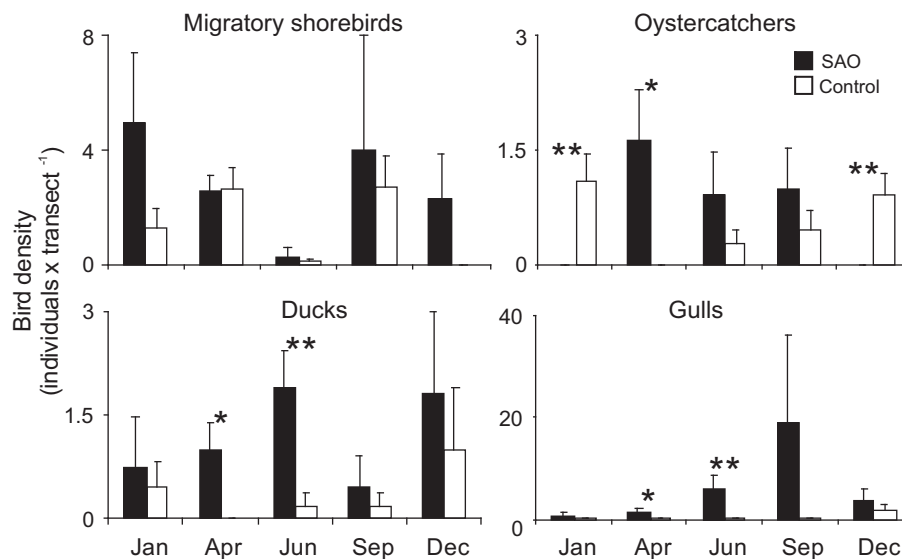


Fig. 5. Bird abundances grouped by migratory shorebirds, oystercatchers, ducks, and gulls in the SAO and the control channel of San Antonio Bay throughout the year. Asterisks indicate difference in bird abundances between channels ( $t$ -test; \*,  $p < 0.050$ , \*\*,  $p < 0.010$ , \*\*\*,  $p < 0.001$ ).

consumers due hypoxic or anoxic events. In consequence, the competing controls by bottom-up and top-down forces appear to be in balance in San Antonio Bay.

## Acknowledgements

This work was supported by grants from: Universidad Nacional de Mar del Plata, Fundación Antorchas, CONICET, Agencia Nacional de Promoción Científica y Tecnológica to O. Iribarne. M. Narvarte and R. González (from Instituto de Biología Marina y Pesquera “Alte. Storni”) provided insights and logistic assistance. J. York provides valuable insight on the ms. We thank I. Valiela for important inputs at the beginning of this project.

## References

- Aravena, R., Evans, M.L., Cherry, J.A., 1993. Stable isotopes of oxygen and nitrogen in source identification of nitrate from septic systems. *Ground Water* 31, 180–186.
- Birdlife, 2004. Threatened Birds of the World. Birdlife International, Lynx Editions, Barcelona, Spain.
- Botto, F., Iribarne, O., Martinez, M., Delhey, K., Carrete, M., 1998. The effect of migratory shorebirds on the benthic fauna of three SW Atlantic estuaries. *Estuaries* 21, 700–709.
- Boyer, E.W., Goodale, C.L., Jaworski, N.A., Howarth, R.W., 2002. Anthropogenic nitrogen sources and relationship to riverine nitrogen export in the north-eastern USA. *Biogeochemistry* 57/58, 137–169.
- Bricker, S.B., Clement, C.G., Pirhalla, D.E., Orlando, S.P., Farrow, D.R.G., 1999. National Estuarine Eutrophication Assessment: Effects of Nutrient Enrichment in the Nation's Estuaries. NOAA, National Ocean Service, Special Projects Office and National Centers For Coastal Ocean Science, Silver Spring, MD.
- Bryant, D.M., 1979. Effects of prey density and site character on estuary usage by overwintering waders (Charadrii). *Estuarine, Coastal and Marine Science* 9, 369–384.
- Cabral, J.A., Á. M., PardalLopes, R.J., Múrias, T., Marques, J.C., 1999. The impact of macroalgal blooms on the use of the intertidal area and feeding behavior of waders (Charadrii) in the Mondego estuary (west Portugal). *Acta Oecologica* 20, 417–427.
- Carrer, G.M., Todesco, G., Bocci, M., 2000. Environmental monitoring in the Palude della Rosa, lagoon of Venice. In: Lasserre, P., Marzollo, A. (Eds.), *The Venice Lagoon Ecosystem: Inputs and Interactions Between Land and Sea*. UNESCO and Parthenon Publishing Group, Paris.
- Cloern, J.E., 2001. Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series* 210, 223–253.
- Cole, M.L., Valiela, I., Kroeger, K.D., Tomasky, G.L., Cebrían, J., Wigand, C., McKinney, R.A., Grady, S.P., Carvalho da Silva, M.H., 2004. Assessment of a  $\delta^{15}\text{N}$  isotopic method to indicate anthropogenic eutrophication in aquatic ecosystems. *Journal of Environmental Quality* 33, 124–132.
- Cole, M.L., Kroeger, K.D., McClelland, J.W., Valiela, I., 2005. Macrophytes as indicators of land-derived wastewater: application of a  $\delta^{15}\text{N}$  method in aquatic systems. *Water Resources Research* 41, W01014. doi:10.1029/2004WR003269.
- Cole, M.L., Kroeger, K.D., McClelland, J.W., Valiela, I., 2006. Effects of watershed land use on nitrogen concentration and  $\delta^{15}\text{N}$  nitrogen in groundwater. *Biogeochemistry* 77, 199–215.
- Conner, R.N., Dickson, J.G., 1980. Strip transects sampling and analysis for avian habitat studies. *Wildlife Society Bulletin* 8, 4–10.
- D'Avanzo, C., Kremer, J.N., 1994. Diel oxygen dynamics and anoxic events in a eutrophic estuary of Waquoit Bay, Massachusetts. *Estuaries* 17, 131–139.
- Duarte, C., 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41, 87–112.
- Fox, S.E., Teichberg, M., Olsen, Y.S., Heffner, L.E., Valiela, I., 2009. Restructuring of benthic communities in eutrophic estuaries: lower abundance of prey leads to trophic shifts from omnivory to grazing. *Marine Ecology Progress Series* 380, 43–57.
- Geertz-Hansen, O., Sand-Jensen, K., Hansen, D.F., Christiansen, A., 1993. Growth and grazing control of abundance of the marine macroalga, *Ulva lactuca* L. in a eutrophic Danish estuary. *Aquatic Botany* 46, 101–109.
- González, P.M., Piersma, T., Verkuil, Y., 1996. Food, feeding and refueling of Red Knots during Northward migration at San Antonio Oeste, Río Negro, Argentina. *Journal of Field Ornithology* 67, 575–591.
- Hauxwell, J., Cebrían, J., Furlong, C., Valiela, I., 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuaries ecosystems. *Ecology* 82, 1007–1022.
- Hauxwell, J., Cebrían, J., Valiela, I., 2003. Eelgrass *Zostera marina* loss in temperate estuaries: relationship to land-derived nitrogen loads and effect of light limitation imposed by algae. *Marine Ecology Progress Series* 247, 59–73.
- Hauxwell, J., Cebrían, J., Valiela, I., 2006. Light dependence of *Zostera marina* annual growth dynamics in estuaries subject to different degrees of eutrophication. *Aquatic Botany* 84, 17–25.
- Hauxwell, J., McClelland, J., Behr, P.J., Valiela, I., 1998. Relative importance of grazing and nutrient controls of macroalgae in three temperate shallow estuaries. *Estuaries* 21, 347–360.
- Holmes, G.T., 2008. Nutrient Supply, Water Residence Time, Temperature, and Grazing as Controls of Size-Fractionated Phytoplankton Biomass in Shallow Temperate Estuarine Ecosystems. Ph.D. Dissertation, Boston University, MA.
- Howarth, R.W., Billen, G., Swaney, D., Townsend, A., Jaworski, N., Lajtha, K., Downing, J.A., Elmgren, R., Caraco, N., Jordan, T., Berendse, F., Freney, J., Kudeyarov, V., Murdoch, P., Zhao-Liang, Z., 1996. Regional nitrogen budget and riverine N and P fluxes for the drainages to the Atlantic Ocean: natural and human influences. *Biogeochemistry* 35, 181–226.
- Isacch, J.P., Costa, C.S., Rodríguez-Gallego, L., Conde, D., Escapa, M., Gagliardini, D.A., Iribarne, O., 2006. Distribution of saltmarsh plant communities associated with environmental factors along a latitudinal gradient on the SW Atlantic coast. *Journal of Biogeography* 33, 888–900.
- Johannes, R.E., 1990. The ecological significance of the submarine discharge of groundwater. *Marine Ecology Progress Series* 3, 365–373.
- Lajtha, K., Michener, R.H., 1994. *Stable Isotopes in Ecology and Environmental Science*. Blackwell Scientific Publishers, Oxford.
- LeBlanc, D.R., 1984. Sewage Plume in a Sand and Gravel Aquifer, Cape Cod, Massachusetts. US Geological Survey. Water Supply Paper 2218.
- Livingston, R.J., 2001. Eutrophication Processes in Coastal Systems. CRC Press, Boca Raton, FL, 327 pp.
- Lopes, R.J., Pardal, M.A., Marques, J.C., 2000. Impact of macroalgal blooms and wader predation on intertidal macroinvertebrates: experimental evidence from the Mondego estuary (Portugal). *Journal of Experimental Marine Biology and Ecology* 249, 165–179.
- Lotze, H.K., Worm, B., 2000. Variable and complementary effects of herbivores on different life stages of bloom-forming macroalgae. *Marine Ecology Progress Series* 200, 167–175.
- Martinetto, P., Teichberg, M., Valiela, I., 2006. Coupling of benthic and pelagic food webs to land-derived nitrogen sources in Waquoit Bay, Massachusetts, USA. *Marine Ecology Progress Series* 307, 37–48.
- Mombet, Y., 1992. Control of phytoplankton biomass in estuaries: a comparative analysis of macrotidal and microtidal estuaries. *Estuaries* 15, 563–571.
- Morgan, J.A., Aguiar, A.B., Fox, S., Teichberg, M., Valiela, I., 2003. Relative influence of grazing and nutrient supply on growth of the green macroalgae *Ulva lactuca* in estuaries of Waquoit Bay, Massachusetts. *Biological Bulletin* 205, 252–253.
- Morrison, R.I.G., Ross, R.K., 1989. Atlas of Nearctic shorebirds on the coast of South America. Canadian Wildlife Service Special Publications 2, 131–323.
- Mouritsen, K.N., Jensen, K.T., 1992. Choice of microhabitat in tactile foraging dunlins *Calidris alpina*: the importance of sediment penetrability. *Marine Ecology Progress Series* 85, 1–8.
- McClelland, J.W., Valiela, I., 1998. Linking nitrogen in estuarine producers to land-derived sources. *Limnology & Oceanography* 43, 577–585.
- McClelland, K.J., Krause-Jensen, D., Rysgaard, S., Christensen, P.B., 1997. Patterns of ammonium within dens mats of the filamentous algae *Chaetomorpha linum*. *Aquatic Botany* 59, 99–115.
- Nixon, S.W., 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia* 41, 199–219.
- Nixon, S.W., Buckley, B.A., 2002. “A strikingly rich zone”: nutrient enrichment and secondary production in coastal marine ecosystems. *Estuaries* 25, 782–796.
- Orensanz, J.M., Schwindt, E., Pastorino, G., Bortolus, A., Casas, G., Darrigran, G., Elías, R., López Gappa, J.J., Obenat, S., Pascual, M., Penchaszadeh, P., Piriz, M.L., Scarabino, F., Spivak, E.D., Vallarino, E.A., 2002. No longer a pristine confine of the world ocean: a survey of exotic marine species in the southwestern Atlantic. *Biological Invasions* 4, 115–143.
- Osterling, M., Pihl, L., 2001. Effects of filamentous green algal mats on benthic macrofaunal functional feeding groups. *Journal of Experimental Marine Biology and Ecology* 263, 159–183.
- Pace, M.L., Findlay, S.E.G., Lints, D., 1992. Zooplankton in advective environments: the Hudson River community and a comparative analysis. *Canadian Journal of Fisheries and Aquatic Science* 49, 1060–1069.
- Pascual, M.S., Zampatti, E.A., Iribarne, O., 2001. Population structure and demography of the Puelche Oyster (*Ostrea puelchana*, D'Orbigny) grounds in northern Patagonia, Argentina. *Journal of Shellfish Research* 20, 1003–1010.
- Pickett, S.T.A., 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (Ed.), *Long-term Studies in Ecology: Approaches and Alternatives*. Springer-Verlag, New York.
- Piriz, M.L., Eyra, M.C., Rostagno, C.M., 2003. Changes in biomass and botanical composition of beach-cast seaweeds in a disturbed coastal area from Argentine Patagonia. *Journal of Applied Phycology* 15, 67–74.
- Quammen, M.L., 1984. Predation by shorebirds, fish and crabs on invertebrates on intertidal mudflats: an experimental test. *Ecology* 65, 529–537.
- Raffaelli, D., 1999. Nutrient enrichment and trophic organization in an estuarine food web. *Acta Oecologica* 20, 449–461.
- Raffaelli, D.G., Raven, J.A., Poole, L.J., 1998. Ecological impact of green macroalgal blooms. *Oceanography and Marine Biology Annual Review* 36, 97–125.
- Short, F.T., Burdick, D.M., 1996. Quantifying eelgrass habitat loss in relation to housing development and nitrogen loading in Waquoit Bay, MA. *Estuaries* 19, 730–739.
- Smith, V.H., Schindler, D.W., 2009. Eutrophication science: where do we go from here? *Trends in Ecology and Evolution* 24, 201–207.

- Soulsby, P.G., Lowthion, D., Houston, M., 1982. Effects of macroalgal mats on the ecology of intertidal mudflats. *Marine Pollution Bulletin* 13, 162–166.
- Teichberg, M., Fox, S.E., Olsen, Y.S., Valiela, I., Martinetto, P., Iribarne, O., Muto, E.Y., Petti, M.A.V., Corbisier, T.N., Soto-Jiménez, M., Páez-Osuna, F., Castro, P., Freitas, H., Zitelli, A., Cardinaletti, M., Tagliapietra, D. Eutrophication and macroalgal blooms in temperate and tropical coastal waters: nutrient enrichment experiments with *Ulva* spp. *Global Change Biology*, in press. doi:10.1111/j.1365-2486.2009.02108.x.
- Thomas, T.E., Harrison, P.J., 1987. Rapid ammonium uptake and nitrogen interactions in five intertidal seaweeds grown under field conditions. *Journal of Experimental Marine Biology and Ecology* 107, 1–8.
- Valiela, I., 2006. *Global Coastal Change*. Blackwell Publishing, Malden, MA, 368 pp.
- Valiela, I., Collins, G., Kremer, J., Lajta, K., Geist, M., Seely, B., Brawley, J., Sham, C.-H., 1997. Nitrogen loading from coastal watersheds to receiving estuaries: new methods and applications. *Ecological Applications* 7, 358–380.
- Valiela, I., Foreman, K., LaMontagne, M., Hersh, D., Costa, J., Peckol, P., DeMeo-Anderson, B., D'Avanzo, C., Babione, M., Sham, C.-H., Brawley, J., Lajta, K., 1992. Couplings of watersheds and coastal waters: sources and consequences of nutrient enrichment in Waquoit Bay, Massachusetts. *Estuaries* 15, 443–457.
- Vaquier-Sunyer, R., Duarte, C.M., 2008. Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of Science USA* 105, 15452–15457.
- Wilhm, J.L., 1968. Use of biomass units in Shannon's formula. *Ecology* 49, 53–56.
- Zar, J.H., 1999. *Biostatistical Analysis*. Prentice-Hall, Inc., Englewood Cliff.