



Long-term ecological footprints of a man-made freshwater discharge onto a sandy beach ecosystem



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ABSTRACT

Sandy shores comprise one of the coastal ecosystems most vulnerable to human impacts, and they are increasingly affected by a variety of stressors. Local-scale drivers such as man-made freshwater discharges have changed the salinity, temperature and nutrient regimes, leading to the degradation of sandy beaches. However, there is still little understanding about the effects of salinity changes on the structure and functioning of sandy shores at the ecosystem level of ecological organization. This study seeks to identify the main spatial and long-term variations in a sandy beach ecosystem due to salinity changes induced by a freshwater discharge using a trophic network approach and thus linking anthropogenic pressures with functional and structural ecosystem changes. The trophic networks of nine scenarios involving three sampling sites representing different salinity stress regimes and three study phases established between 1987 and 2015 were modelled and compared. The results showed important space-time variations that were reflected at the community and ecosystem levels. A more complex trophic structure was developed with longer distances to the freshwater inflow, with higher biomass, species richness and number of predators. The highly disturbed and undisturbed sites occupied discrete, contrasting and clearly distinguishable states over time, whereas the moderately disturbed site showed a variable pattern over time. Recent trends in ecosystem indicators reflected a more fragile state, characterized by a greater organization (Ascendency) and a lower adaptive potential (Overhead) to address unexpected disturbances. Ecosystem indicators were sensitive enough to distinguish among sites and long-term phases in the ecosystem, where different organization states can persist over time. Future studies aimed at assessing press disturbances on sandy beach ecosystems should emphasize a longer time scale in order to assess the recovery capacity of these systems that are increasingly threatened by long-lasting stressors.

1. Introduction

Sandy beaches provide critical ecosystem services that are being threatened by the increasing demand for natural resources and leisure on the coast, intense coastal development and the accelerated loss of habitat resulting from coastal squeeze (Defeo et al., 2009; McLachlan et al., 2013). Human impacts on these ecosystems are predicted to intensify over the next few decades, and thus it has become increasingly critical to understand how these ecosystems will respond to environmental changes (Brown et al., 2018; McLachlan and Defeo, 2018).

Sandy shores are dynamic ecosystems inhabited by specialized biotic assemblages that are structured mainly by physical forces (Defeo and McLachlan, 2005; McLachlan and Defeo, 2018). In this context, salinity has been identified as a critical variable that can affect biodiversity patterns at multiple scales. At a mesoscale (e.g., a single beach),

freshwater discharges appear as strong modifiers of environmental quality, affecting the distribution and life-history traits of the resident macrofauna, as well as nutrient regimes and habitat features (Defeo and Lercari, 2004). At a macroscale, Lercari and Defeo (2015) showed strong environmental and macrofaunal variations in sandy beaches of the Uruguayan coast affected by the discharge of the widest estuary of the world (Rio de la Plata). This was particularly evident at inner estuarine beaches, characterized by strong salinity variations and a decrease in habitat suitability and availability (e.g., low swash and beach width). These comparable results, representing a range of spatial scales, highlight the role of environmental variability and habitat suitability as drivers affecting the structure of the macrofaunal community, thus supporting the notion of scale dependence in sandy beach ecology (McLachlan and Defeo, 2018). Under press disturbances, defined as chronic perturbations that lead to persistent changes in ecosystem

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components (Glasby and Underwood, 1996), beach habitats could become unsuitable for sandy beach macrofauna in the medium- or long-term. However, there is still little understanding of the effects of persistent salinity changes on sandy beach ecosystems, including effects on its structure (e.g., trophic levels) and functioning (e.g., energy flows).

On the Atlantic coast of Uruguay, the 22-km sandy beach fringe between La Coronilla and Barra del Chuy (LCBC) is affected by a man-made freshwater canal discharge (Andreoni Canal) from inland crops (Lercari and Defeo, 1999; Lercari et al., 2002). Studies showed that low salinity levels and high variability generated by short-term fluctuations in the amount of freshwater discharge negatively affected macrofaunal assemblages and their habitat quality and availability (Lercari et al., 2002; Bergamino et al., 2009). The decrease in abundance and biomass of benthic species towards the disturbance source could also affect the ecosystem functions, which could be substantially reorganized as a result of this disturbance, potentially triggering a range of cascading effects (Defeo and de Alava, 1995).

The aim of this study is to identify spatial and temporal variations in a sandy beach ecosystem (LCBC) affected by a man-made freshwater discharge using a trophic networks approach, and thus linking anthropogenic pressures with macrobenthic community and ecosystem changes. The research strategy combined three sampling sites with different degrees of disturbance (defined by reduced average salinity with the proximity to the freshwater discharge) and three phases of study established between 1987 and 2015. The main questions addressed were: To what extent does the chronic impact of a man-made freshwater discharge affect the community and ecosystem structure of a sandy beach? In particular, what is the spatial extent and temporal persistence of the impact as measured by ecosystem indicators?

2. Materials and methods

2.1. Study area

The study was performed along the 22 km of continuous exposed sandy beach between La Coronilla (33°50'S; 53°27'W) and Barra del Chuy (33°40'S; 53°20'W) on the Atlantic coast of Uruguay (Fig. 1). This beach has been described as the southernmost beach of a chain of exposed sandy beaches defined as semi-closed ecosystems on the Atlantic shore of South America. It is characterized by fine to very fine well-sorted sands, a gentle slope, heavy wave action, and a wide surf zone, and it supports the greatest richness, diversity, abundance and biomass of sandy intertidal macrofauna among all Uruguayan beaches (Lercari and Defeo, 2006, 2015). This microtidal dissipative beach is delimited by two freshwater discharges, a natural one in the NE (Chuy Stream)

and an artificial one in the SW (Andreoni Canal). The latter is a man-made structure 68 km in length which drains a wide basin ($\approx 270,000$ ha) used for agricultural activities. Its discharge on the SW extreme of the beach generally follows a SW–NE direction, producing a strong salinity gradient. The canal flow is highly variable depending on the rainfall and water management regimes of the crops, reaching up to $89 \text{ m}^3 \text{ s}^{-1}$ in winter (Lercari et al., 2002).

2.2. Research strategy

Nine scenarios were analysed through the representation of trophic networks by Ecopath models. Three sampling sites were defined a priori according to the increasing-salinity gradient as an explanatory variable of the observed trends (Table 1: Lercari et al., 2002): a *Highly Disturbed* site (HD), placed at the mouth of the Andreoni Canal; a *Moderately Disturbed* site (MD), located 1 km away from the artificial freshwater discharge; and an *Undisturbed* site (UD), placed 13 km away from the mouth of the Andreoni Canal. The HD site showed significantly lower values of salinity, slope and width of the swash zone (Lercari et al., 2002; Lozoya and Defeo, 2006). In particular, long-term salinity trends showed consistent patterns within sites, exhibiting significantly lower values and greater variability in the HD site (Table 1).

The yellow clam *Mesodesma mactroides* constitutes a major component of the total community biomass at LCBC beach. This species has been subject to a small-scale fishery since the 1960s (Ortega et al., 2012), and has undergone contrasting management phases (Gianelli et al., 2015). Because of its biologic and socioeconomic significance, three phases with contrasting abundance of the yellow clam population stock were selected for the study (Gianelli et al., 2018). The first phase (1987–1993) represented a high abundance of *M. mactroides*, a 32-month fishery closure (April 1987–November 1989), an active fishery with very low fishing intensity (1990–1993) and an informal co-management governance mode. The second phase (1994–2007) included mass mortality events that decimated *M. mactroides* populations across their entire distribution range. The scale and magnitude of the impact prompted a full fishery closure between 1994 and 2008 (Gianelli et al., 2015). The third phase (2008–2015) was characterized by the partial recovery of *M. mactroides* and the implementation of an ecosystem approach to fishing that included co-management as the institutionalized governance mode (Gianelli et al., 2018: Supplementary Materials A).

2.3. Food web modelling

2.3.1. Core routine

Nine trophic models corresponding to the selected sites and phases were built through Ecopath with Ecosim 6 (EwE6), which represents ecosystems as interconnected networks of trophic groups based on biomass and linked by diet information (Polovina, 1984; Christensen and Pauly, 1992). Ecopath is a mass-balanced model, structured by a system of linear equations which represent each functional group (species with similar life history traits and ecological role) in the ecosystem. The master equation describes how group production equals the sum of the entire group losses (Christensen and Pauly, 1998; Christensen and Walters, 2004; Christensen et al., 2005), as follows:

$$B_i(P/B)_i - \sum_{j=1}^n B_j(Q/B)_j DC_{ji} - Y_i - B_i(P/B)_i(1-EE_i) = 0$$

where B_i and B_j are, respectively, the biomasses of prey and predators; $(P/B)_i$ is the production/biomass ratio equivalent to the total mortality rate (Z); $(Q/B)_j$ is the consumption/biomass ratio for predator j , DC_{ji} is the fraction of the prey i in the diet of the predator j ; Y_i is the total fishery catch rate (manual harvesting of *M. mactroides* was carried out only in the UD site during Phases 1 and 3, see Lercari et al., 2018); and, EE_i is the ecotrophic efficiency, defined as the proportion of the

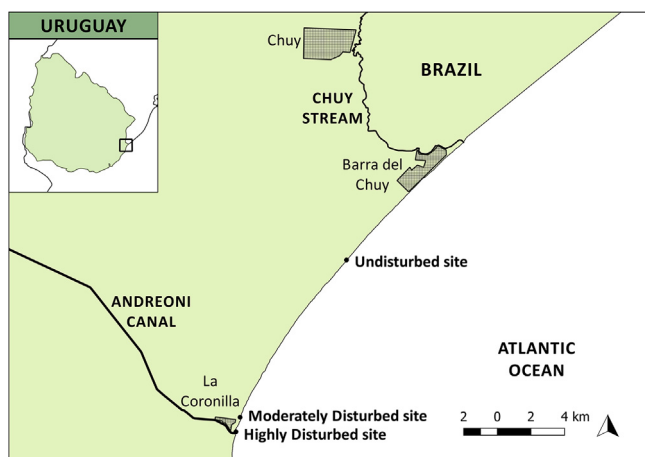


Fig. 1. Study area, showing the location of La Coronilla – Barra del Chuy beach (LCBC) along the eastern coast of Uruguay, the freshwater discharge of the Andreoni Canal and the three sampling sites.

Table 1

Mean and SE of the abiotic variables for the sites and phases under study (Lercari et al. 2002 and unpublished data). See text for a detailed description of Phases 1, 2 and 3, characterized by contrasting abundance of the yellow clam population.

	Highly Disturbed site			Moderately Disturbed site			Undisturbed site		
	Phase 1	Phase 2	Phase 3	Phase 1	Phase 2	Phase 3	Phase 1	Phase 2	Phase 3
Salinity	4.8 ± 2.5	5.7 ± 1.4	4.9 ± 2.6	22.9 ± 2.0	21.3 ± 1.6	27.6 ± 2.2	26.8 ± 0.3	25.4 ± 1.3	28.9 ± 1.5
Beach width (m)	61.3 ± 6.7	52.0 ± 6.4	60.4 ± 9.3	74.7 ± 1.3	46.9 ± 3.7	65.1 ± 7.7	71.7 ± 6.7	75.0 ± 4.8	78.7 ± 18.5
Swash width (m)	6.2 ± 2.6	6.5 ± 1.4	4.0 ± 4.0	15.6 ± 1.8	9.8 ± 0.8	11.0 ± 1.0	12.7 ± 1.5	12.7 ± 1.0	17.3 ± 5.3
Slope (cm·m ⁻¹)	2.3 ± 0.3	2.9 ± 0.2	4.5 ± 2.5	4.8 ± 0.2	5.1 ± 0.3	3.5 ± 0.7	3.3 ± 0.1	4.5 ± 0.6	3.2 ± 0.4
Temperature (°C)	17.2 ± 1.8	18.1 ± 1.3	19.4 ± 3.3	17.3 ± 1.5	16.5 ± 1.4	18.7 ± 2.9	17.3 ± 1.4	18.7 ± 1.5	18.6 ± 3.1
Mean grain size (ϕ)	2.2 ± 0.1	2.1 ± 0.1	2.1 ± 0.1	2.2 ± 0.1	2.1 ± 0.1	1.9 ± 0.1	2.2 ± 0.1	2.0 ± 0.1	1.9 ± 0.1

production of *i* that is consumed. The set of linear equations can be solved even if one of the four parameters of each group (B, P/B, Q/B or EE) is unknown, which is estimated by the model.

2.3.2. Data source and parameterization

Input data comes from a variety of sources, including field surveys, values gathered from published and unpublished data for the study area, and empirical relationships (Supplementary Materials B). In this work, six models corresponding to HD and MD sites were developed, and complemented with three models previously settled for the UD site (Lercari et al., 2018), which were re-evaluated.

Input data were compiled for each site and phase; otherwise the best available data were used, considering their spatial and/or temporal proximity. Functional groups were defined, whenever possible, at the species level. They included detritus, phytoplankton, zooplankton, the macrobenthic community, insects, fishes and birds, totalling 23 functional groups used in the nine models. Differences in the number of groups between models mainly reflected changes in the richness of benthic species.

Biomass estimates were mainly obtained from intensive field sampling. Detritus biomass was estimated in situ from total suspended solids, considering fractions of living (phytoplankton) and inorganic materials (Lercari et al., 2010). Phytoplankton biomass for each model was calculated from chlorophyll *a* assessments or cell counts (unpublished data) and converted to wet biomass (Odebrecht et al., 1995). Zooplankton biomass was obtained from Lercari et al. (2010). Macrofaunal and entomofaunal biomass estimates were obtained for each model through a systematic sampling from the sand dunes to the subtidal zone (see Defeo et al., 1992 for methodological details) performed at least seasonally for each phase. Bird biomass was estimated based on abundance and richness surveys (unpublished data; Lercari et al., 2010, 2018). Fish biomass was estimated based on trawl samples parallel to the coast, carried out in the UD site during Phase 3 (Lercari et al., 2018).

P/B and Q/B ratios were taken from previous studies made on the same system, from published information or empirical relationships (Brey, 2012) and corrected for local sea surface temperature (Opitz, 1996). DC estimates were mainly compiled from published information, qualitative records, and general knowledge of the trophic ecology of the groups. Input data for the balanced models is provided in Supplementary Materials C while diet information is provided in Supplementary Materials D.

The Ecopath Pedigree routine (Funtowicz and Ravetz, 1990) was used to assign a quality index to each input data source. An overall 'pedigree index' was calculated as the average of the pedigree indices for each input parameter and compared between different models (Pauly et al., 2000, Christensen and Walters, 2004). Pedigree takes values from 0 (low precision information) to 1 (local data), being classified into four categories according to quality: (1) low: < 0.2, (2) average: 0.2–0.399, (3) high: 0.4–0.599, and, (4) very high: > 0.6 (Lassalle et al., 2014). The theoretical and practical rigor of the models were validated through the pre-balance diagnoses (PREBAL: Link,

2010), which graphically identified issues of model structure and data quality, ensuring confidence and quality in model design, parameterization and implementation (Supplementary Materials E). To accomplish model consistency and coherence with physiological system constraints, it was ensured that for all groups $EE_i < 1$; $R/A < 1$; $P/R < 1$; and $0.1 < P/Q < 0.3$, where R is respiration and A is assimilation (Christensen et al., 2008; Heymans et al., 2016). According to the general strategy used to attain mass balance, only slight modifications of diet input data were needed.

2.3.3. Ecosystem indicators

Based on the Ulanowicz theory (1986), several ecosystem attributes were assessed to characterize the system in terms of its structure and functioning (Christensen et al., 2005): (1) Total system throughput (TST), an index of the ecosystem size in terms of biomass flows. It is defined as the sum of all flows (consumption, respiration, exports, imports and detritus) in the system. (2) Finn's cycling index (FCI), the fraction of TST that is recycled in the system. (3) System omnivory index (SOI), the extent to which an ecosystem exhibits web-like features. (4) Connectance index (CI), the ratio of effective trophic links to possible links in the food web. (5) Ascendency (A), a measure of average mutual information (a magnitude which captures the organization of the flow structure) in a system, scaled by TST. It characterizes the degree of development and organization of the system. (6) Capacity (C), the upper limit for the size of the A and represents the maximum potential of ecosystem development. (7) Overhead (O), the difference between the C and A, representing the ecosystem potential for recovery or innovative restructuring (e.g., resilience). (8) Primary production/total respiration (PP/R), the fate of the assimilated food. (9) Primary production/total biomass (PP/B), a measure of ecosystem maturity *sensu* Odum (1969).

Ecosystem sustainability was analysed through the Robustness index (Ulanowicz, 2014, Fath, 2015), an indicator aimed to quantify ecosystem growth (e.g., TST) and development (e.g., information or connectivity). The modelled sites discriminated by phase were positioned in a hypothetical curve of "ecosystem fitness for evolution" or Robustness (defined as $(-A/C) \ln(A/C)$) vs. "degree of order" (defined as $a = A/C$ ($1 > a > 0$)) to assess the compromise between efficiency and resilience.

2.4. Statistical analysis

Biomass differences between sites and phases were tested for the ecosystem (all functional groups) and macroinvertebrates (benthos + insects) using a generalized linear model (GLM) with an identity link function. When significant differences were found, a Holm multiple-comparison post hoc test was performed. The biomass was log-transformed to comply with statistical assumptions. A non-metric multidimensional scaling (NMDS) analysis was used to obtain a two-dimensional (2D) ordination of the nine models, according to the biomass of functional groups. For this purpose, only those groups that contributed to the ordination were considered, which resulted in an

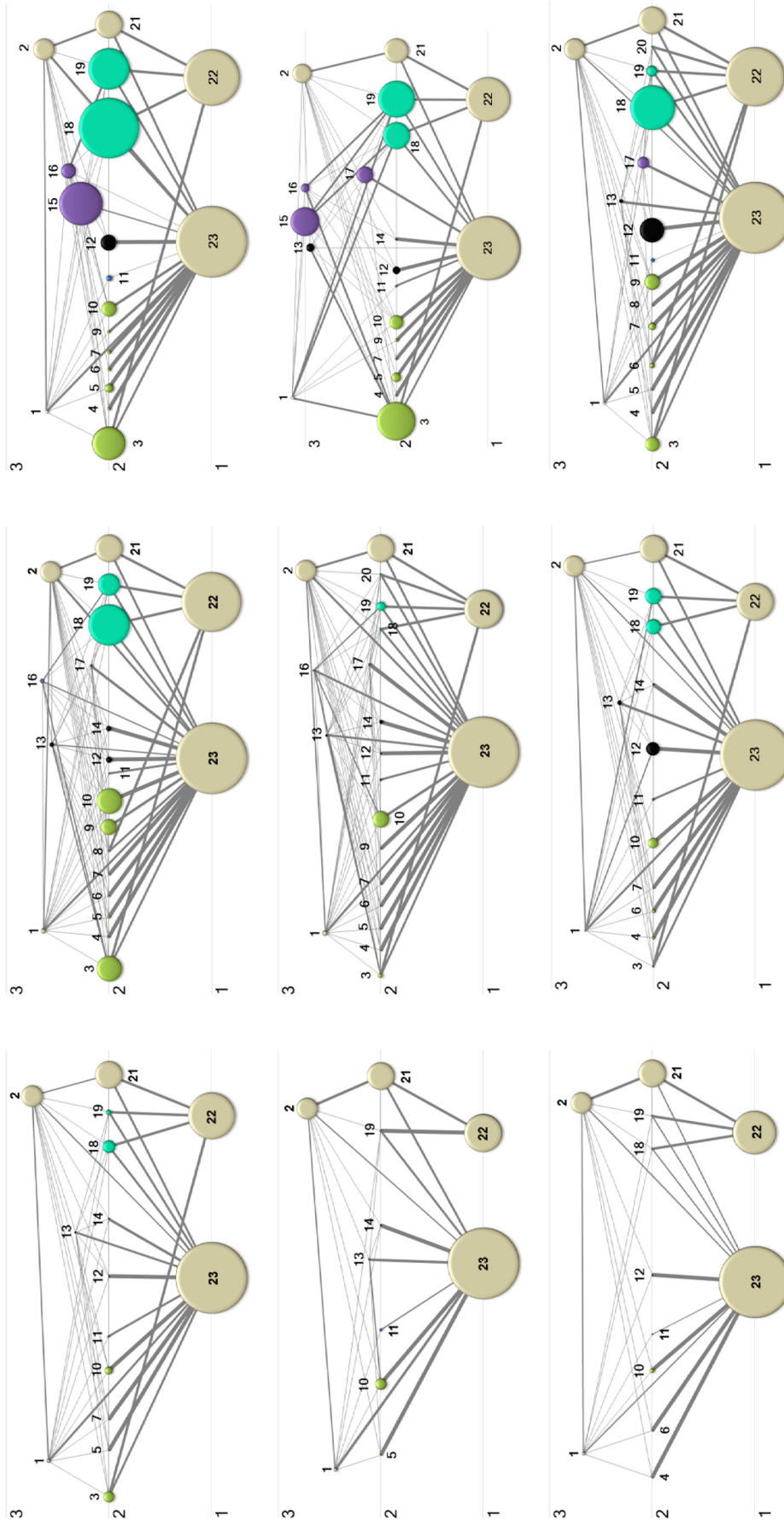


Fig. 2. Trophic networks and trophic levels (y-axes) of the Highly Disturbed (left), Moderately Disturbed (middle) and Undisturbed (right) sites during Phase 1 (top), Phase 2 (centre) and Phase 3 (bottom). Circles represent the groups and their relative biomass. Macroinvertebrates are grouped: crustaceans (green), insects (blue), polychaetes (black), gastropods (violet), bivalves (cyan). The remaining groups appear in light brown. Lines represent the trophic connections and their intensity. 1: birds, 2: fishes, 3: *Emerita brasiliensis*, 4: *Phoxocephalopsis* sp., 5: *Atlantorchestoidea brasiliensis*, 6: *Bathyporeia ruffoi*, 7: *Macrochiridiotea gambiata*, 8: *Macrochiridiotea liliana*, 9: *Excitrolana brasiliensis*, 10: *Excitrolana armata*, 11: insects, 12: *Euzonus furciferus*, 13: *Hemipodus olivieri*, 14: *Scolecopsis gaucha*, 15: *Olivancillaria auricularia*, 16: *Olivella formicacorsii*, 17: *Buccinanops duartei*, 18: *Mesodesma macrotoides*, 19: *Donax hanleyanus*, 20: *Donax gemmula*, 21: zooplankton, 22: phytoplankton, 23: detritus. Phases are defined following Section 2.2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

NMDS of Bray-Curtis dissimilarity performed on log-transformed ($\ln X + 1$) macroinvertebrate biomass. An analysis of similarities (ANOSIM) based on the Bray-Curtis dissimilarity matrix was applied to assess biomass differences among groups, sites and phases. The covariance of ecosystem attributes was analysed according to the Pearson correlation coefficient. An NMDS of Bray-Curtis dissimilarity was used to obtain a 2D ordination of the ecosystem attributes for the nine scenarios analysed.

Statistical analyses were performed using the computing environment R (R Development Core Team, 2008) (<http://www.R-project.org>).

3. Results

PREBAL diagnoses suggested the consistency of the input data (Supplementary Materials E). The overall pedigree index of the models indicated an average to high quality level (P between 0.312 and 0.465: Lassalle et al., 2014).

The flow diagrams corresponding to the nine analysed scenarios showed a clear simplification of the system structure towards the freshwater discharge and over time (Fig. 2). A lower number of functional groups were found in the HD site, without large differences between MD and UD sites. As a general trend, there was a decrease in the number of groups over time for HD and MD sites, while the UD site showed minor long-term changes. There were no species with exclusive presence in the HD site. *M. mactroides* occurred in eight of the nine scenarios, being absent in the HD site during Phase 2. The most common trophic levels corresponded to primary producers and consumers (1–2). Birds, fishes and the gastropod *Olivella formicacorsii* were the main top predators, while the polychaete *Hemipodus olivieri* and the gastropods *Buccinanops duartei* and *Olivancillaria auricularia* acted as intermediate predators (Supplementary Materials F). With the exception of *H. olivieri*, an increase in the trophic level of predators was observed with longer distances to the freshwater discharge and during Phase 2.

The highest biomass was placed in lower trophic levels (detritus and phytoplankton, Fig. 2). The macrobenthic community structure in terms of biomass clearly differed among sites and phases. During Phase 1, *M. mactroides* was dominant in all three sites (HD: 44%, MD: 70% and UD: 79% of the total community biomass). In Phase 2, *M. mactroides* and the entire benthic community biomass decreased sharply in all sites, being dominant the isopod *Excirrolana armata* in HD (99%) and MD (68%) sites, while the filter feeders *Emerita brasiliensis* (42%) and *Donax hanleyanus* (33%) dominated in the UD site. In Phase 3, *M. mactroides* recovered its dominance in the UD site (87%), but was far from reaching pre-mortality levels (< 20% of the initial value). During this phase, *D. hanleyanus* dominated the community in the MD sites (33%) and, to a lesser extent, the partial recovery of the dominance of *M. mactroides* was observed (28%: 3.5% of the initial value). *Excirrolana armata* dominated the community in the HD site (92%). The ecosystem structure in terms of biomass (except detritus) also differed among sites and phases, reaching the highest values at the UD site during Phase 1 (291 g/m²) and Phase 3 (165 g/m²), followed by the MD in Phase 1 (161 g/m²). The lowest ecosystem biomass values were recorded at the HD site during Phase 2 (14 g/m²) and the MD site during Phase 3 (15 g/m²) and 2 (16 g/m²).

A decrease in biomass was observed with the proximity to the freshwater discharge, and this tendency was more pronounced for macroinvertebrates than for the ecosystem as a whole (Fig. 3). The GLM showed that the ecosystem biomass was significantly higher in the UD site, with no differences between HD and MD sites. Macroinvertebrate biomass differed significantly among sites (Table 2), and non-significant differences in ecosystem biomass were observed among phases. Macroinvertebrate biomass significantly differed between Phases 1 and 2 and marginally differed between Phases 1 and 3. As a general trend, for both the whole ecosystem and macroinvertebrates, a higher biomass was recorded in Phase 1, decreasing towards Phase 2. During Phase 3,

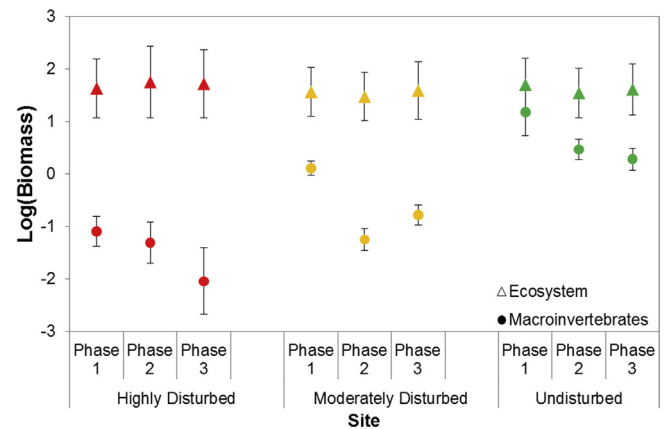


Fig. 3. Ecosystem and macroinvertebrate biomass (mean \pm SE) for the sites and phases under study. Note the logarithmic scale along the y-axis. Highly Disturbed (red), Moderately Disturbed (orange) and Undisturbed (green) sites. Phases are defined following Section 2.2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the ecosystem biomass increased, while the macroinvertebrate biomass decreased in the HD and UD sites and increased in the MD site (Fig. 3). These consistent trends were reflected in the GLM analyses, which always showed that interactions between sites and phases were not significant (Table 2), indicating independence between these factors.

NMDS ordination of the nine models for macroinvertebrate biomass (Fig. 4) identified two groups at a dissimilarity level of 85% (stress = 6.4e-4). UD site models were grouped with the MD site model in Phase 1, while the HD site models were grouped with MD site models in Phases 2 and 3. The presence of *M. mactroides* was related to the grouping of UD sites, while *E. armata* clustered HD and MD sites.

ANOSIM showed clear differences in the macroinvertebrate community structure between sites and phases (Table 2).

NMDS ordination (Fig. 4) according to ecosystem attributes (Table 3) clearly identified two groups at the dissimilarity level of 60% (stress = 6.9e-5). The models corresponding to HD and UD sites were arranged in two groups, whereas the MD site models were spread between them.

The TST decreased in proximity to the freshwater discharge and in Phase 2. The higher values were observed in the UD site in Phases 1 and 3 and in the MD site during Phase 1. Flow-partitioning estimates showed similar fractions for the nine models, with most flows assigned to detritus (40–49% of TST) and exports (37–48%), and only a minor proportion assigned to consumption (2–17%) and respiration (1–6%) in the food web. CI and SOI increased with the proximity to the freshwater discharge in all phases. CI values indicated that only 17–29% of possible connections occurred in the food webs, and the highest value was reached in the HD site during Phase 2. FCI did not show a clear trend, although the lowest values were observed in the UD site. The proportion of the production that is consumed (measured by the EE) highlighted a consistently low utilization of detritus, phytoplankton, zooplankton and insects in all models.

Ascendency increased over time in the UD site and decreased in the MD site, whereas Overhead followed the opposite trends in these sites (Fig. 5). The UD site showed an increase in efficiency over time, indicative of a greater vulnerability of the system to disturbances. The MD site displayed the opposite trend, showing an increase in resilience over time. The HD site showed an increase in resilience in Phase 2 and a subsequent increase in efficiency in Phase 3 (Fig. 6).

As a general trend, the different ecosystem attributes showed that MD and UD sites had opposing behaviour. P/B, P/R and Ascendency decreased over time in the MD site and increased over time in the UD site, whereas O and Robustness showed the opposite pattern. The

Table 2

GLM (upper part) results and Holm post hoc test comparisons between sites and phases for ecosystem and macroinvertebrate biomass. ANOSIM (lower part) results and pairwise comparisons using macroinvertebrate biomass as a response variable. HD: Highly Disturbed, MD: Moderately Disturbed and UD: Undisturbed sites. Phases are defined following Section 2.2. p-significant values are in bold.

		Site				Phase			
		Global	HD-MD	HD-UD	MD-UD	Global	1–2	1–3	2–3
GLM									
p-value	Ecosystem	–	0.641	0.006	0.019	–	0.220	0.563	1.000
	Macroinvertebrates	–	0.009	2.6e–8	4.0e–4	–	0.013	0.099	0.630
ANOSIM									
R	Macroinvertebrates	0.514	0.259	0.960	0.259	-0.128	0	-0.111	-0.222
p-value		2.2e–4	0.002	0.001	0.002	0.007	0.003	0.007	0.008

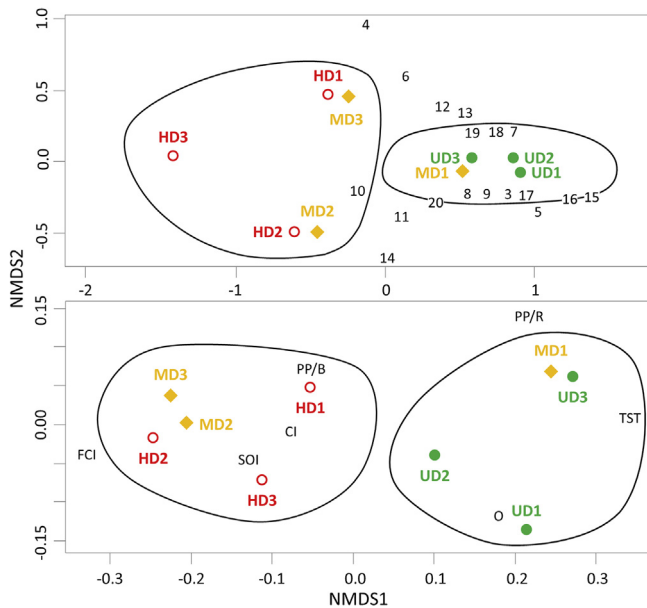


Fig. 4. NMDS ordination of the nine models according to macroinvertebrate biomass (top). Clusters at a dissimilarity level of 85%. NMDS ordination of the nine models according to ecosystem attributes (bottom). Clusters at a dissimilarity level of 60%. HD: Highly Disturbed (red, ○), MD: Moderately Disturbed (orange, ◆), UD: Undisturbed (green, ●) sites. Numbers beside each abbreviated site refer to the corresponding Phases 1, 2 and 3 defined in Section 2.2. Species are numbered following Fig. 2. TST: Total system throughput, PP/R: Production/respiration ratio, PP/B: Production/biomass ratio, IC: Connectance index, SOI: System omnivory index, O: Overhead and FCI: Finn's cycling index. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

patterns followed by the HD site with respect to the P/B, P/R, CI and Robustness indices could not be matched with those exhibited by the MD and UD sites, highlighting the importance of environmental stress in the structuring of trophic networks at impacted sites.

4. Discussion

4.1. Main trends

The salinity gradient induced by the freshwater discharge altered ecosystem function and organization, showing a simpler trophic structure at higher stress levels over time, which were reflected in terms of number of functional groups, predators and total biomass. Temporal fluctuations in *M. mactroides* biomass had an impact on the overall community and therefore on ecosystem biomass, inducing changes in trophic network attributes over time. The HD and UD sites occupied discrete, contrasting and clearly distinguishable states over time,

whereas the MD site showed a changing pattern over time. The recent Phase reflected a more fragile ecosystem state: particularly in the UD site, Ascendency, Overhead and Robustness evidenced a lower resilience of the sandy beach system due to the persistent changes imposed by the freshwater discharge and highlight the need for effective management measures.

4.2. Ecosystem structure

The lower number of functional groups found near the freshwater discharge could result from a loss of environmental quality and a decrease in habitat suitability as a result of the salinity gradient and the alteration of natural morphodynamics (Lercari and Defeo, 1999, 2015). Direct evidence of habitat loss for benthic species towards the freshwater discharge, given by the decrease in the beach and swash width, has been reported (Lercari et al., 2002). The absence of *M. mactroides* in the HD site during Phase 2 and its inability to recover biomass levels during Phase 3 indicated a more hostile environment for the recolonization of the site. The coastal current caused by the freshwater discharge acts as a hydrodynamic barrier that modifies sediment texture, affecting larval settlement (Defeo, 1996). Moreover, the observed decrease in the number of predators towards the freshwater discharge could be attributed to a lower food quality and availability, reflected in the lower biomass documented for the HD site (Lercari et al., 2002, Lercari and Defeo, 2003) or to a greater susceptibility to habitat changes by predatory species (Baum and Worm, 2009) such as gastropods and polychaetes. On the other hand, studies at the population level highlighted the role of salinity as an explanatory variable of the observed trends, showing a reduction in individual growth, fecundity, biomass and survival (reviewed in Defeo and Lercari, 2004). Due to the use of the canal for rice crops, the contribution of fertilizers and pesticides could add complexity to the impacts driven by salinity. Sauco et al. (2010) detected a major propanil metabolite in the HD site that was undetectable in the UD site, and their microcosm toxicity bioassays performed in *E. brasiliensis* suggested an increasing susceptibility to the herbicide with smaller body sizes. Thus, the decrease in salinity and concentration of herbicides could be acting as cumulative variables that lead to synergistic negative effects, increasing mortality and reducing larval settlement rates in *E. brasiliensis* near the HD site.

The decline in biomass of *M. mactroides* promoted an increase in the relative representation of two filter-feeders with warm-water affinity (*E. brasiliensis* and *D. hanleyanus*) in the UD site, after mass mortalities of the cool-water yellow clam (Phase 2). These results showed a trend for the tropicalization of this filter feeding guild (Celentano and Defeo, 2016; McLachlan and Defeo, 2018), which has been mainly attributed to a systematic increase in sea surface temperature (Ortega et al., 2016; Lercari et al., 2018). Under a climate-change scenario, the overall decline in species richness towards Phase 3 suggests an adverse environment that could be intensified by the simultaneous action of external drivers (e.g., the decrease in primary productivity that affects food availability and quality) acting at multiple temporal and spatial scales,

Table 3
Ecosystem attributes of the nine analysed models, including flow and organization indicators. Phases and sites are defined following Section 2.2.

Parameter	Highly Disturbed site			Moderately Disturbed site			Undisturbed site			Units
	Phase 1	Phase 2	Phase 3	Phase 1	Phase 2	Phase 3	Phase 1	Phase 2	Phase 3	
Sum of all consumption	652	650	642	897	666	668	2239	1134	924	g/m ² /year
Sum of all exports	4913	1455	2956	23,353	1661	1425	15,385	6979	22,849	g/m ² /year
Sum of all respiratory flows	219	219	213	387	230	230	1236	519	410	g/m ² /year
Sum of all flows into detritus	5047	1592	3086	23,612	1811	1574	15,958	7256	23,101	g/m ² /year
Total system throughput	10,832	3915	6898	48,249	4368	3898	34,818	15,887	47,284	g/m ² /year
Sum of all production	5432	1971	3467	24,066	2189	1956	17,163	7889	23,584	g/m ² /year
Calculated total net primary production	5129	1669	3166	23,736	1887	1652	16,607	7501	23,255	g/m ² /year
Total primary production/total respiration	23	8	15	61	8	7	13	14	57	
Finn's cycling index	0.9	3.1	1.5	0.3	2.8	3.2	0.7	0.9	0.3	
Net system production	4910	1450	2953	23,349	1656	1422	15,371	6982	22,845	g/m ² /year
Total primary production/total biomass	150	121	143	147	120	109	57	83	141	
Total biomass/total throughput	0.003	0.004	0.003	0.003	0.004	0.004	0.008	0.006	0.003	/year
Total biomass (excluding detritus)	34	14	22	161	16	15	291	91	165	g/m ²
Connectance Index	0.25	0.29	0.26	0.22	0.22	0.24	0.19	0.17	0.18	
System Omnivory Index	0.109	0.167	0.203	0.082	0.122	0.086	0.081	0.055	0.071	
Ascendency (A)	11,195	4047	7125	49,795	4550	4034	37,826	17,017	48,879	
Ascendency (A%)	62	46	55	78	46	44	58	55	78	
Overhead (O)	6797	4805	5781	13,680	5272	5148	27,419	14,171	13,705	
Overhead (O%)	38	54	45	22	54	56	42	45	22	
Capacity (C)	17,992	8852	12,906	63,476	9822	9182	65,246	31,187	62,585	
Ecopath pedigree index	0.389	0.395	0.357	0.423	0.423	0.431	0.312	0.316	0.465	
Measure of fit, t*	1.462	1.215	1.147	1.981	1.981	1.722	0.841	0.913	2.100	

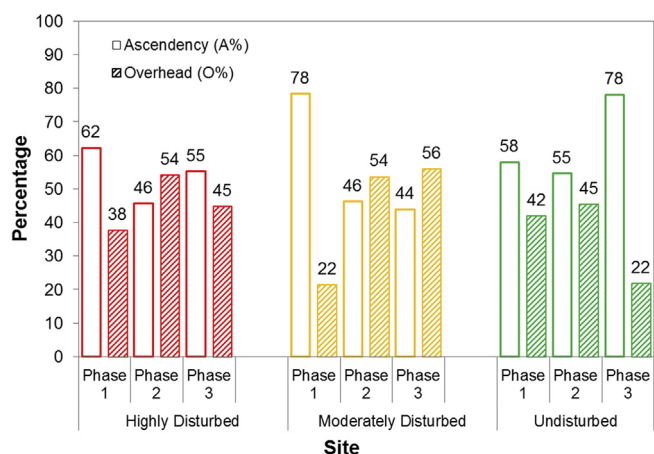


Fig. 5. Tendencies of Ascendency and Overhead (%) of the nine analysed models. Highly Disturbed (red), Moderately Disturbed (orange) and Undisturbed (green) sites. Phases are defined following Section 2.2 (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

thus adding dimensionality and higher uncertainty levels to sandy beach systems (McLachlan and Defeo, 2018).

Marked differences in macroinvertebrate biomass were observed between sites and time phases. The community in HD and UD sites occupied discrete and clearly distinguishable states over time, whereas the MD site showed a variable pattern according to the studied phase. A similar behaviour of the MD site was recorded by Defeo and Lercari (2004) on a shorter time scale, showing that during spring and summer the MD site was grouped with the UD site while during the autumn and winter it was grouped with the HD site. This changing pattern of the MD site was associated with the seasonal variation of the canal flow. The present analysis could be reflecting a similar variation pattern but at an interannual scale. These results support the idea that sandy beaches are highly dynamic environments, where press and pulse disturbances can dissimilarly affect different areas of a single stretch of beach (McLachlan and Defeo, 2018).

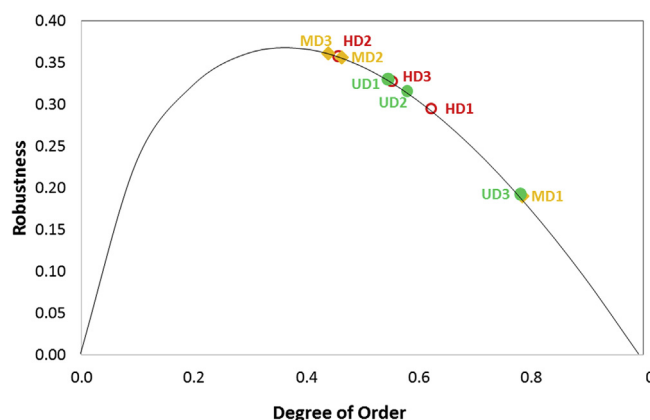


Fig. 6. Observed vitality window of LCBC beach. Robustness vs. Degree of Order is shown for the nine analysed models. HD: Highly Disturbed (red, ○), MD: Moderately Disturbed (orange, ◆) and UD: Undisturbed (green, ●) sites. Numbers beside each abbreviated site refer to the corresponding Phases 1, 2 and 3 defined in Section 2.2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.3. Ecosystem indicators

The nine models presented an analogous distribution of flow-partitioning that reflects an internal stability of the LCBC beach system, suggesting a high resilience to changes. CI was consistently low among scenarios, but the increase in the number of connections towards the freshwater discharge could be interpreted as the systems attempt to enhance stability against external disturbances, since species with several connections are less prone to secondary extinction (Saint-Béat et al., 2015). In relation to this, SOI and FCI have been described as indicators of stress, which have the potential to act as buffers of change and thus reduce the magnitude of environmental impacts (Odum, 1985; Saint-Béat et al., 2015). The observed increase in SOI towards the freshwater discharge could reflect the environmental impact driven by the canal. A similar pattern was observed in the Bay of Seine (English Channel) where the impacts of muddy fine-grained sandy dredged material were assessed before and after being dumped (Perzy et al., 2017). On the other hand, the greater cycling activity shown by the

disturbed sites could be seen as an increase in system resistance to changes imposed by the freshwater discharge (Christensen and Pauly, 1992).

Ascendency has shown to be a sensitive index to environmental changes (Saint-Béat et al., 2015). The UD site developed a more complex trophic structure and showed higher values of Ascendency and Capacity than the HD site, while the MD site showed an intermediate situation, reporting the highest value of Ascendency and Capacity during Phase 1. Analogous results were observed by Reyes-Martínez et al. (2015), who analysed the implications of anthropogenic pressure in the functioning of two beaches located in the Bay of Cádiz (Spain) with different stress levels due to urbanization and tourism.

The most organized scenarios were the MD site in Phase 1 and the UD site in Phase 3. Considering Overhead as an indicator of resilience (Ulanowicz, 2004), the low values obtained by these models could suggest a fragile ecosystem due to anthropogenic and environmental pressures acting simultaneously. This index represents the degrees of freedom available in the system and implicitly represents the potential to adapt to new circumstances. A state with high Ascendency and insufficient Overhead, as those observed in the MD site in Phase 1 and the UD site in Phase 3, may not be able to respond effectively to changing environmental demands (Ulanowicz, 2004). According to Robustness, the UD site showed an increase in efficiency over time, indicative of a low sustainability of the system in the recent phase, and therefore highly vulnerable to unexpected natural or anthropogenic disturbances, which could disrupt the internal cycling. Heymans and McLachlan (1996) also showed a high ecosystem order (A/C) for an exposed sandy beach in South Africa, denoting a well-organized and stable system.

5. Conclusion

Results highlight the dynamic and complex response of a sandy beach ecosystem under the influence of a press disturbance provided by a man-made freshwater canal discharge. Evident spatial and temporal changes in the ecosystem structure and functioning and in important ecosystem attributes were detected. The effect of salinity as a proximate driver of the system reduced ecosystem stability and threatened marine biodiversity. Biodiversity loss heavily affected the functioning of the sandy beach ecosystem, whereas the turnover of dominant species along phases in the UD site provided a compensatory response to maintain ecosystem functionality in response to environmental changes (Isbell et al., 2018). The consequences of biodiversity loss quantified by ecosystem indicators were not constant across sites and over time, emphasizing the role of environmental context (Kardol et al., 2018). Thus, the growing necessity for solutions to complex environmental problems highlights the need for science-based management to assess the health status of sandy beach ecosystems (Borja et al., 2016). The analysis of trophic networks is presented as a useful tool with which to derive reliable ecological indicators, providing quantitative evidence that allows the detection of significant variations in response to environmental changes. Future studies directed to assessing press disturbances on sandy beach ecosystems should emphasize a long-term timescale in order to assess the recovery capacity of these systems that are increasingly threatened by long-lasting stressors acting at different spatial scales.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2018.09.024>.

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