



Effect of increased inundation time on intertidal ecosystem functions of South West Atlantic soft-bottom environments

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ABSTRACT: Soft-bottom intertidal systems are valuable due to the ecosystem services they provide. Although these systems are normally subjected to highly variable environmental conditions, disturbances have become more frequent due to increases in anthropogenic pressure. Sea level rise (SLR) may generate changes in the ecosystem functioning of intertidal systems and in the ecosystem services they provide. In the Argentinean coast (SW Atlantic), SLR analysis shows trends similar to the global ones. It is not known how disturbances may affect the activity of benthic communities and the associated ecosystem functions. Therefore, through a field experiment at the marsh–mudflat edge in northeastern Argentina, we evaluated the effect of increased inundation time on bioturbation intensity, detritus decomposition and microphytobenthic primary production. Sediment physicochemical parameters (pH, temperature, water content and organic matter) were also measured. The results showed that increased inundation time had no effect on microphytobenthic primary production or bioturbation intensity in summer. Nevertheless, inundation time increased the burrowing activity of the intertidal crab *Neohelice granulata* in winter and spring and greatly decreased the variability in *Spartina densiflora* decomposition and organic matter content. In the context of a changing world due to global climate change, reduced variability in ecosystem functioning could indicate a decline in ecosystem resilience. As a consequence, vital ecosystem functions could be altered or lost, thus impacting the ecosystem services they deliver.

KEY WORDS: Intertidal systems · Sea level rise · Bioturbation · Primary production · Detritus decomposition

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1. INTRODUCTION

Intertidal systems are transition ecosystems between land and sea that have characteristics of both terrestrial and aquatic communities as well as their own intrinsic features (e.g. Bertness 1999). In protected coastal areas, sediments often accumulate, generating soft bottoms characterized by the presence of halophytic vegetation, forming marshes in temperate zones and mangroves in tropical areas

(Adam 1990). These environments are highly valuable due to the ecosystem services they provide (Costanza et al. 2014). For example, high rates of primary and secondary production provide various services such as erosion control and shoreline protection, carbon sequestration, food supply and shelter for wildlife, nutrient cycling and water filtration (Adam et al. 2008). These ecosystems are naturally subjected to extremely variable environmental conditions (Helmuth et al. 2006, Cabrerizo et al. 2017)

that have created systems that are resilient to natural changes (Villnäs et al. 2013, Griffiths et al. 2017). In other words, these ecosystems are capable of withstanding a certain amount of disturbance before shifting to an alternative state (Holling 1973). However, the effects of global climate change (GCC), intensified by growing anthropogenic pressure (IPCC 2013), makes natural disturbances increasingly frequent and widespread in marine and coastal systems (Cloern et al. 2016), affecting their vulnerability. In the last few decades, this has become evident; for example, the direct effect of accelerated sea level rise (SLR) (Simas et al. 2001, Craft et al. 2009) alters inundation regimes in coastal systems, affecting ecosystem functioning (Hewitt & Thrush 2009, Griffiths et al. 2017) and the provided ecosystem services (Craft et al. 2009).

Ecosystem services are regulated by ecosystem functions as a byproduct of ecological attributes, properties and processes that mediate the transformations of matter and energy within an ecosystem (Reiss et al. 2009). Biomass production, organic matter (OM) processing (hereafter detritus) and nutrient recycling are among the most notable functions in soft-bottom intertidal environments (Levin et al. 2001). Benthic communities regulate some of these ecosystem functions through the interaction between abiotic factors and biological processes such as ingestion, digestion and excretion (Reiss et al. 2009) as well as bioturbation and bioirrigation of sediments (Escapa et al. 2004). Particularly, faunal bioturbation (i.e. the mixture of sediment particles by animal activity; Kristensen et al. 2012) is a key ecological process in these systems (Meysman et al. 2006). Bioturbation increases sediment mixing depth (Fanjul et al. 2007), the burial rate of detritus (Botto et al. 2006), nutrient cycling and oxygen supply to the sediment (Fanjul et al. 2007). All of these factors can stimulate aerobic respiration and thus increase OM mineralization rates (i.e. the decomposition of OM into more available nutrients; Fanjul et al. 2015). Bioturbation also affects macrofaunal community structure and composition (Alvarez et al. 2013). In turn, bioturbation intensity (understood as the ecosystem function) is regulated by a set of abiotic variables, e.g. temperature (Ouellette et al. 2004), inundation (Szura et al. 2017), amount and nutritional quality of OM (Fanjul et al. 2015), substrate hardness and geochemical profile (Maire et al. 2007), which interact with biological variables such as population and behavioral dynamics (e.g. abundance, Gilbert et al. 2007; size and level of activity of bioturbators, Hollertz & Duchêne 2001, among others).

Inundation frequency is crucial in determining population dynamics as well as the community composition of intertidal organisms, affecting species distribution and biological activity (Hanson 2014). Thus, if certain species modified their activities in response to changes in inundation frequency, it would be expected that the functions associated with those activities would also be affected. Furthermore, intertidal environments are extremely productive, with vascular plants, microphytobenthos and phytoplankton being responsible for regulating primary production in these systems (Heip et al. 1995). In the first millimeters of sediments, microphytobenthos contribute significantly to primary production by generating OM that is rapidly transferred to higher trophic levels (Underwood et al. 2005). The achieved productivity rates can vary according to species composition (Yallop et al. 1994), biological interactions (e.g. herbivory, Hicks et al. 2011; bioturbation, Giorgini et al. 2019) and abiotic environmental context (e.g. temperature, Hicks et al. 2011; inundation, Migné et al. 2009; turbidity, Pratt et al. 2014). Moreover, as mentioned before, coastal systems are highly variable over short time scales (e.g. tidal cycles and sudden weather events, Helmuth et al. 2006), and microphytobenthic communities are adapted to this type of change. Nevertheless, long-term alterations in abiotic conditions (e.g. increased inundation) as a result of SLR can exert strong influences on their functions (e.g. decline in primary production, O'Meara et al. 2017). Furthermore, the high production rates achieved in these systems promote the production of large amounts of dead plant material (i.e. detritus). Detritus decomposition enhances benthic metabolism and nutrient cycling, which is mainly regulated by tidal regimes (Langhans & Tockner 2006). Specifically, inundation period (Montemayor et al. 2011) and sediment characteristics (e.g. sediment-water content, Langhans & Tockner 2006; oxygen availability, Neckles & Neill 1994) are factors that directly affect detritus decomposition and primary production. Since these factors may be modified as a result of the disturbance generated by SLR (Lewis et al. 2014), the naturally occurring decomposition rates could also be modified. In this regard, field and model estimations have suggested accelerated detritus decomposition under rising temperatures and increased salinity as a function of changes in mean sea level and GCC (Wu et al. 2016).

The global mean sea level is rising at a relatively high rate ($3.3 \pm 0.3 \text{ mm yr}^{-1}$) in response to ocean warming and melting glaciers (Chen et al. 2017). This constitutes a threat to natural environments

close to the coast, such as coastal wetland systems. In marshes, for example, SLR increases erosion rates, contributing to the loss of valuable coastal habitats (Simas et al. 2001, Schuerch et al. 2018). In this sense, changes in vegetation cover, distribution and composition could affect the systems' productivity and trigger internal erosion processes (Janousek et al. 2016). In addition, long periods of inundation can generate changes in the sediment oxygen concentration and salinity, among others, resulting in stressful conditions for local communities (e.g. Levin et al. 2001). However, the effects of SLR on ecosystem functioning remain poorly explored. Since most of the evidence involves factors that are directly related to ecosystem functions (e.g. changes in vegetation cover can modify detritus production; modification of sediment physicochemical parameters can impact microphytobenthic communities), it can be expected that increased inundation time and frequency could modify intertidal functioning.

On the SW Atlantic coasts, SLR trends follow global patterns (e.g. Dragani et al. 2014, Tomazin et al. 2020). Specifically, changes in wind intensity and direction (Reguero et al. 2019) increasing the intensity and frequency of extreme weather events (e.g. storm surges and precipitation, Alberti et al. 2017, Morales et al. 2020) can cause higher water levels (and thus higher tidal range; e.g. Alberti et al. 2007). Intertidal soft bottoms from this region have high bioturbation intensity (Fanjul et al. 2007), detritus processing (Botto et al. 2006, Fanjul et al. 2015) and microphytobenthic primary production (Giorgini et al. 2019) that make these systems highly valuable. However, GCC (i.e. SLR) may affect these functions. Thus, the objective of this study was to assess the effect of increased inundation time on multiple ecosystem functions (i.e. bioturbation intensity, detritus decomposition and microphytobenthic primary productivity) in soft-bottom intertidal mudflats in the Mar Chiquita coastal lagoon (Argentina, 37° 32' S, 57° 19' W; UNESCO MAB Reserve, see Fig. 1). In particular, our work aimed to answer the following questions: (1) Is bioturbation intensity affected by an increase in inundation time? (2) Does increased inundation time impact the decomposition of *Spartina densiflora* detritus? (3) Does microphytobenthic primary productivity vary due to prolonged inundation? Based on the body of knowledge, we expected that bioturbation intensity and microphytobenthic primary production would decrease with increased inundation time while detritus decomposition would increase.

2. MATERIALS AND METHODS

2.1. Study area

This study was carried out from December (austral summer) 2016 to August (austral winter) 2019, in intertidal soft-bottom zones of the Mar Chiquita coastal lagoon (Fig. 1), where 2 sub-environments are evident: salt-marshes, vegetated by halophytic species such as *Spartina densiflora* and *Sarcocornia perennis* (Isacch et al. 2006), and mudflats, unconsolidated sediments without vascular vegetation composed of fine sands, silt and clays (Spivak 1997). Due to its geographical latitude and environmental conditions, the study site is in an area characterized as a southern temperate zone 'with oceanic influence' (Reta et al. 2001), with summer (Dec–Jan–Feb) air temperatures ranging from 14 to 25°C, winter (Jun–Jul–Aug) temperatures ranging from 4 to 14°C and spring (Sep–Oct–Nov) and autumn (Mar–Apr–May) average annual air temperatures fluctuating around 14°C (Argentinean National Weather Service–Servicio Meteorológico Nacional, <https://www.smn.gob.ar>). This coastal lagoon shows a semidiurnal and microtidal regimen (tidal amplitude < 1 m). Storms affect the water level (i.e. inundation) because of their impact on hydrological conditions and the geomorphological dynamics of the lagoon (Reta et al. 2001).

Several groups of benthic animals coexist in these environments; however, in the marsh–mudflat edge, the dominant species (because of its biomass and the way it affects the sediment) is the intertidal burrowing crab *Neohelice granulata* (previously known as *Chasmagnathus granulata*, Crustacea, Varunidae; ≤40 mm carapace width, Iribarne et al. 1997). *N. granulata* is a deposit-feeding crab, distributed from southern Brazil (22° 57' S) to northern Patagonia in Argentina (42° 25' S) (Spivak 2010), that modifies the habitat to such an extent that the areas inhabited by this crab are commonly known as crab beds (see Fig. 1B,C). The crabs construct semi-permanent open burrows that are normally funnel-shaped with wide entrances (up to 16 cm in diameter). The burrows extend up to 0.4 m into the sediment in the mudflat, whereas in the marsh, the burrows are cylindrical and deeper (up to 1 m into the sediment). *N. granulata* is considered a key 'regenerative bioturbator' (sensu Solan & Wigham 2005, Kristensen et al. 2012) in this system, transporting large amounts of sediment from deep layers to the surface (up to 2.4 and 6 kg m⁻² d⁻¹ of sediment in the marsh and mudflat, respectively; Iribarne et al. 1997) while con-

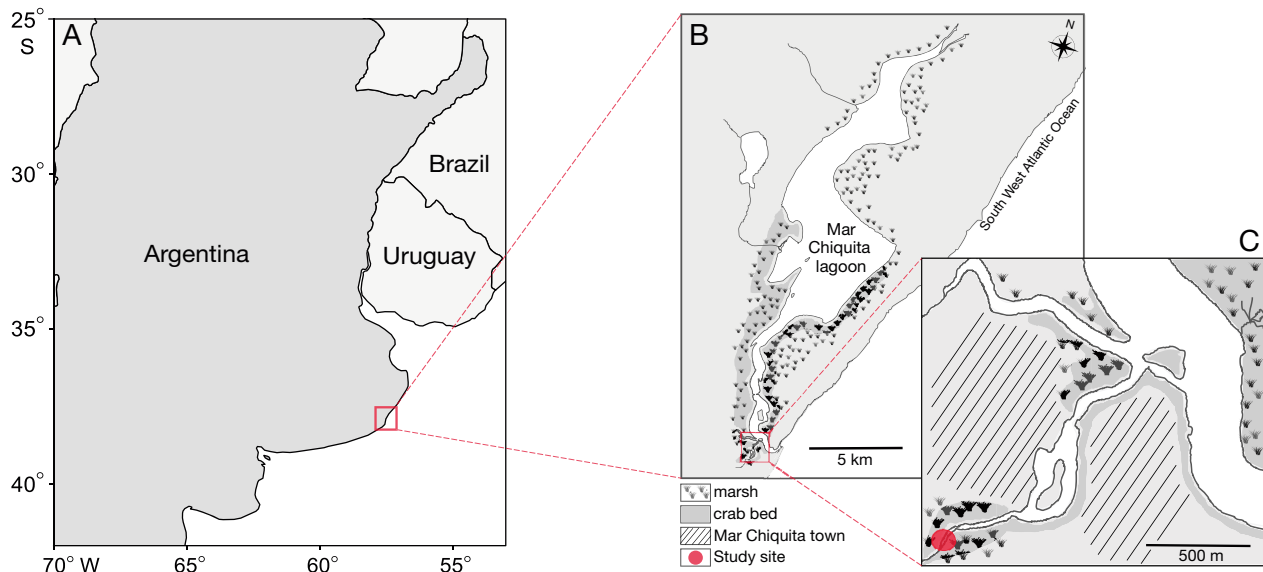


Fig. 1. (A) Study site location on the coast of Argentina: (B) Mar Chiquita coastal lagoon (37° 32' S, 57° 19' W), an estuary separated from the ocean by a wide chain of sand dunes, permanently connected to the southwest Atlantic Ocean through a channel approximately 6 km long and 200 m wide. (C) Study site, located in the marsh–mudflat edge, where the 2 study species (the halophytic plant *Spartina densiflora* and the burrowing crab *Neohelice granulata*) were found

structuring and maintaining its burrows. Because this crab shows the highest activity (i.e. sediment reworking, burrow maintenance, crab abundance) at the marsh–mudflat edge (Mendez Casariego et al. 2011) and the tide normally reaches this height (C. Diaz de Astarloa pers. obs.), we set up the inundation experiment in this zone.

2.2. Experimental setup

To evaluate the effect of increased inundation time on multiple ecosystem functions, a field experiment was carried out at the marsh–mudflat edge with 20 experimental units (EUs) designed to increase inundation time during low tide, adapting the methodology developed by Cherry et al. (2015). The EUs were constructed with 3 walls (high-impact polystyrene boxes, 1 m length and 0.45 m high, buried in the sediment to approximately 10 cm) in such a way that the 2 side walls were placed perpendicularly and a front wall was oriented parallel to the coastline (Fig. 2A). The size of the EUs (1 m²) was chosen in order to be able to perform each of the environmental measurements in different areas of the EU and so that the entire sediment surface would be undisturbed and thus the measurement of one response variable would not affect the other measurements. EU inundation occurred within minutes during high tide, when the water level reached the remaining open

side. Two treatments (n = 10) were randomly assigned to these EUs: natural inundation time (NIT; Fig. 2B) and increased inundation time (IIT; Fig. 2C), the former with the front wall ribbed to allow water flow into the EU during high and low tide. Within each EU, we randomly selected a 0.25 m² fixed area (hereafter plot) in order to quantify active burrows throughout the duration of the experiment. In addition, all EU were deployed at the same tidal height level. The functioning of the experiment was corroborated by direct observation: of all the times the tide rose (100%), the tide reached the EUs approximately 75% of the time and the IIT treatment remained covered with water (approximately 15 cm deep inside the EU) for more than 6 h after high tide.

2.3. Effect of increased inundation time on bioturbation intensity and burrow activity

Because the burrowing crab *N. granulata* shows high activity during summer (Luppi et al. 2013), bioturbation intensity (i.e. vertical particle displacement intensity) was evaluated within each EU from late January to early March 2017 (i.e. austral summer). Bioturbation intensity was estimated through the calculation of the bioturbation coefficient (D_b), using the non-radioactive tracer technique (Wheatcroft 1992), which consisted of the addition of 40 g of glass microspheres (20–70 μ m diameter) on the sediment

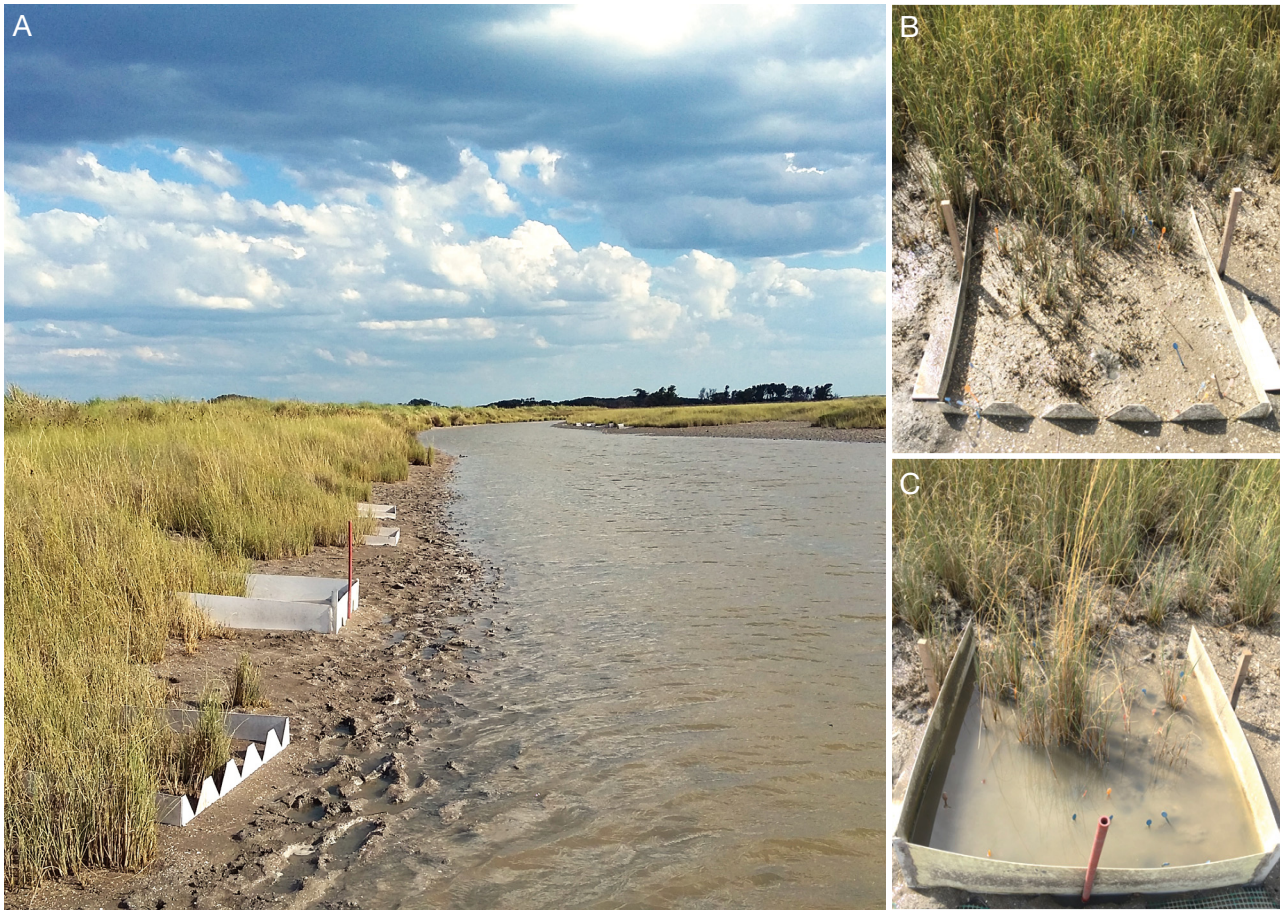


Fig. 2. (A) Intertidal zone of the Mar Chiquita coastal lagoon, where experimental units (1 m²) were arranged in the marsh–mudflat edge (note that 30% of each experimental unit was vegetated while 70% was bare sediment). Experimental units for (B) natural inundation time ($n = 10$) had ribbed walls that allowed water exchange during high and low tide while those for (C) increased inundation time ($n = 10$) had high walls that delayed water drainage during low tide

surface covering 100 cm² areas (following Fanjul et al. 2007). One month after the addition of the microspheres, a vertical sediment cylinder was extracted (5 cm diameter, 20 cm deep) from each EU and then frozen (−18°C) for further processing. Then, the sediment samples were cut at different depths (0.5 cm for the first layer, 1 cm for the following ones); subsamples were diluted with 10 and 15 ml of water, corresponding to the first and subsequent depths. Finally, an aliquot of 200 µl was taken from the subsample to determine the number of microspheres by counting under an optical microscope (40× magnification). These data allowed us to construct microsphere depth concentration profiles. Based on these profiles, the D_b was estimated, for each treatment, by means of the analysis of the observed gradients of microspheres following Wheatcroft (1992). Through inverse modeling, parameters derived from the general equation of the diffusion model were estimated,

which, in the absence of an advective transport, describes the decay curve in the concentration of a tracer over time:

$$\frac{\delta C}{\delta t} = D_b \frac{\delta^2 C}{\delta^2 x} \quad (1)$$

The solution to Eq. (1) is:

$$C(x, t) = \frac{1}{\sqrt{\pi D_b t}} \exp\left(\frac{-x^2}{4 D_b t}\right) \quad (2)$$

where D_b is measured in cm² d^{−1}, t is the time the microspheres remain in the sediment (days), x represents sediment depth and C refers to the concentration of microspheres (g cm^{−3}). Based on different D_b values obtained from Eq. (2), the experimental profiles of microspheres were simulated by repeatedly solving the theoretical curve (see Wheatcroft 1992) using different D_b values that were assumed constant for all depths. The values of D_b that generated the

lowest residual averages were used when comparing the theoretical and experimental profiles with microspheres.

Bioturbation in these systems is expected to depend largely on the burrowing activity of *N. granulata*, given its significant contribution to macrobenthic biomass (its density can reach up to 60 crabs m^{-2} , see Iribarne et al. 1997). To estimate the intensity of crab burrowing activity, which varies seasonally (Luppi et al. 2013), the number of active burrows (i.e. burrows with recently removed sediment, crab tracks or presence of crabs) was registered monthly. For this purpose, inside each EU, we selected fixed quadrants of 0.25 m^2 (plots, see Section 2.2) over 23 mo (from January [summer] 2017 to August [winter] 2019).

To evaluate if increased inundation time affected mean D_b , we performed a *t*-test (Zar 1999) after log-transforming the data because the assumption of normality was not met. Visual inspection of residual plots following transformation did not reveal any obvious deviations from homoscedasticity or normality.

To evaluate the relationship between increased inundation time and seasonality on the activity (i.e. number of active burrows) of *N. granulata*, we performed a generalized linear mixed-effect model (GLMM, Zuur et al. 2009). Within the global model, the fixed effects were treatment and season and their interaction, while the random factor was plot (i.e. fixed quadrants within the EUs where the number of active burrows was registered). Given that our data did not meet the assumptions of homoscedasticity and normality, we structured the variance by applying a power variance function structure ('varPower' function) and square-root-transformed the number of burrows data. We then visually accepted the assumptions of homoscedasticity and normality after the transformations. The random factor plot was significant in the model. The global model was then analyzed using the function 'lme' in the 'nlme' package (linear and non-linear mixed effects model, Pinheiro et al. 2021), which is a generic function that fits a GLMM. For selection of the model that best represented the data, a set of models was generated using the ' dredge ' function in the MuMIn R library (Barton 2020). The model with the smallest Akaike information criteria (AICc) and the highest Akaike weight (w_i) values was chosen to best represent the data. To perform the post hoc comparisons for the significant terms included in the best model, we used the 'lsmeans' function ('emmeans' package in R, Lenth 2021), which computes least-squares means for the factors or factor combinations included in the

selected model and contrasts them. All described analyses were performed with R software version 4.0.3 (R Core Team 2020).

To evaluate the effect of increased inundation time on the mean number of active burrows of *N. granulata* in March 2018, we performed a *t*-test (Zar 1999).

2.4. Effect of increased inundation time on *Spartina densiflora* decomposition rates

To evaluate whether inundation time modified detritus decomposition rate, we estimated these rates for *Spartina densiflora* detritus (which is the main source of OM in this system) in the sediment within the EUs (described in Section 2.2), using the litter-bag technique (see Harmon et al. 1999, Montemayor et al. 2011). Initially, healthy leaves and stems of *S. densiflora* were collected and dried in the oven (60°C) to a constant weight. Then, 10 g of the dry *S. densiflora* stems/leaves (weighed on analytical balance; accuracy 0.0001 g) were placed inside numbered fiberglass bags ($10 \times 10 \text{ cm}$, 1 mm mesh). Five *S. densiflora* bags were randomly placed in the surface sediment, held in place with galvanized metal stakes (between March and May 2017) within each EU. After 7, 15, 29, 50 and 154 d, the bags were collected, and once in the laboratory, the bags and remaining sediment material were carefully rinsed to remove excess sediment and dried in the stove (60°C) until constant weight for subsequent measurements. Finally, the degraded biomass was determined as the difference between the initial and remaining biomass for each incubation time (i.e. days). Using these data, decomposition rates (k) were estimated with a negative exponential model (Olson 1963):

$$X_t = X_0 \times e^{-kt} \quad (3)$$

where X_t corresponds to detritus mass (g dry weight) remaining at time t , X_0 is the initial detritus mass placed in each bag and t refers to debris exposure time (days) to degradation.

To evaluate the effect of inundation on detritus k , we performed an unequal variance corrected *t*-test (t_c -test; Welch approximation t_c , Zar 1999), given that the homoscedasticity assumption was not met even after transformations (Underwood 1996, Zuur et al. 2010). We then performed a *t*-test (Zar 1999) to evaluate the effect of inundation on the remaining percentage of *S. densiflora* detritus after 154 d.

2.5. Microphytobenthic primary production under increased inundation time

Benthic metabolism was determined *in situ* in March (early autumn) 2018 using benthic chambers, adapting the methodology of Fanjul et al. (2015). For this purpose, within the EUs ($n = 7$), paired acrylic chambers (4.5 cm diameter and 7 cm tall) corresponding to dark and light conditions were buried in the sediment (~4 cm deep) during low tide (in the IIT treatments, the remaining water in the chamber was extracted). The chambers had a perforation in the upper face to allow the addition and subsequent extraction of water. They were filled with water obtained from the nearest tidal channel, around solar noon and always during sunny conditions. We recorded dissolved oxygen concentration (initial oxygen) from the water that we used to fill the benthic chambers, using a portable oxygen sensor (Hach sension 6, precision: $0.01 \text{ mg O}_2 \text{ l}^{-1}$). Once the benthic chambers were filled with water, the upper face holes were closed with a silicone plug. The initial incubation time was set during high tide, when one of the 2 chambers was covered with aluminum foil (dark chambers), and the incubation time had an average duration of 1 h. Once the incubation time passed, a water sample was taken from each chamber with a syringe, and dissolved oxygen concentration (final oxygen) was measured immediately (by gently transferring the water to a flask). Through this test, net primary sediment productivity (NPP) and sediment respiration (R) were obtained from light and dark benthic chambers, respectively, applying the following equations:

$$\text{NPP} = \frac{(\text{O}_2 \text{ final} - \text{O}_2 \text{ initial}) \times V}{(t \text{ final} - t \text{ initial}) \times A} \quad (4)$$

$$R = \frac{(\text{O}_2 \text{ final} - \text{O}_2 \text{ initial}) \times V}{(t \text{ final} - t \text{ initial}) \times A} \quad (5)$$

where $\text{O}_2 \text{ final}$ and $\text{O}_2 \text{ initial}$ correspond to dissolved oxygen concentrations (mg l^{-2}) before and after incubation, V and A are the volume and area occupied by the water column (l and m^2 , respectively) inside the chamber and t is the incubation time (min). Microphytobenthic gross primary productivity (GPP) is obtained by subtracting the products of Eqs. (4) & (5):

$$\text{GPP} = \text{NPP} - R \quad (6)$$

In this way, the effect of inundation on NPP, sediment R and GPP were evaluated with a t -test (Zar 1999).

2.6. Sediment physico-chemical characteristics

Given that the physico-chemical characteristics of the sediment are related to the activities of the benthic organisms and, therefore, the ecosystem functions they regulate, we also analyzed the response of temperature, pH and sediment-water and OM content to experimental inundation. For this purpose, sediment temperature and pH were quantified *in situ* in February (summer)–July (winter) 2017 with glass electrodes and a bimetallic probe, respectively (with a ~15 d periodicity FC200, Hanna Instruments, precision: 0.1). For data registration, the glass electrodes and bimetallic probe were introduced into the first 3 cm of the sediment for a few seconds until stabilization of the sensors was reached. Unlike temperature and pH, sediment-water and OM content were measured only once at the end of the experiment. Sediment-water content was determined as wet and dry weight difference (after drying in the stove at 60°C until constant weight) from sediment samples obtained within each treatment (cylinders of 2 cm diameter and 3 cm depth, $n = 10$ for each treatment). OM content was determined from the dry sediment-water content samples as ash-free dry weight ($n = 10$ for each treatment), by incinerating the samples at 450°C for 6 h.

The effect of experimental inundation on pH and temperature at each time was evaluated with a t -test (Zar 1999) even if the data were not normally distributed after transformation (see Tables 2 & 3). The t -test is robust to violations of the assumption of normality with a large sample size (Underwood 1996) like the one used in this study. Moreover, the effect of sediment-water and OM content under increased inundation time was analyzed with a t -test and t_c -test, respectively, because in the latter only the assumption of homoscedasticity was not satisfied (Zar 1999).

3. RESULTS

3.1. Effect of increased inundation time on bioturbation intensity and burrow activity

Increased inundation time had no statistically significant effect on bioturbation intensity carried out by the burrowing crab *Neohelice granulata* ($t_{18} = -1.38$, $p = 0.183$). Mean (\pm SD) D_b were 23.91 ± 37.3 and $17.24 \pm 52.7 \text{ cm}^2 \text{ yr}^{-1}$ for the IIT and NIT treatments, respectively. Moreover, the number of active crab burrows was explained by the interaction of treatment and season (Table 1, Fig. 3). In particular, the

number of burrows was higher with increased inundation time than in the control conditions in winter and spring (16 and almost 3 times higher, respectively), especially during spring (IIT, mean: 103.6 ± 49.58 burrows m^{-2} ; NIT, mean: 39.2 ± 34.42 burrows m^{-2}), which was the season with the highest burrowing activity (Fig. 3). Increased inundation time also affected the variability in the number of active burrows, which was higher in autumn and winter for that treatment ($F_{1,186} = 4.07$, $p = 0.045$; $F_{1,118} = 58.36$, $p < 0.001$, respectively).

In March 2018, the number of active burrows was almost doubled in the IIT (mean: 71.43 ± 22.08 burrows m^{-2}) treatment compared to the NIT (mean: 41.14 ± 21 burrows m^{-2}) treatment ($t_{12} = -2.63$, $p = 0.022$).

3.2. Effect of increased inundation time on *Spartina densiflora* decomposition rate

The decomposition rate of *S. densiflora* showed a marked difference in the data variability between treatments, being 12 times higher in the NIT compared to the IIT treatment ($F_{18,20} = 5.39$, $p = 0.032$; Fig. 4A). However, there were no differences in mean decomposition rate between treatments ($t_{c11} =$

Table 1. Linear mixed-effect model selection. No. par_i: number of parameters; AICc: Akaike's information criterion; Δ_i : Akaike differences; w_i : normalized weights of AIC; T: treatment; S: season. The best model is shown in *italics*

Model	No. par _i	AICc	Δ_i	w_i
<i>T + S + T×S</i>	3	2688.6	0	1
T + S	2	2718.5	29.88	0
S	1	2736.3	47.75	0
T	1	3100.9	412.27	0
Null	0	3112.0	423.44	0

1.99 , $p = 0.073$). Moreover, after 154 d exposure of the litterbags to the sediment within the EUs, the remaining percentage of *S. densiflora* detritus was similar between treatments (IIT: $59.13 \pm 3.51\%$; NIT: $57.99 \pm 7.38\%$, $t_{16} = 1.85$, $p = 0.084$; Fig. 4B).

3.3. Microphytobenthic primary productivity under increased inundation time

None of the components of benthic metabolism (i.e. NPP, GPP and *R*) differed between IIT and NIT treatments (NPP: $t_{12} = 0.513$, $p = 0.617$; GPP: $t_{12} =$

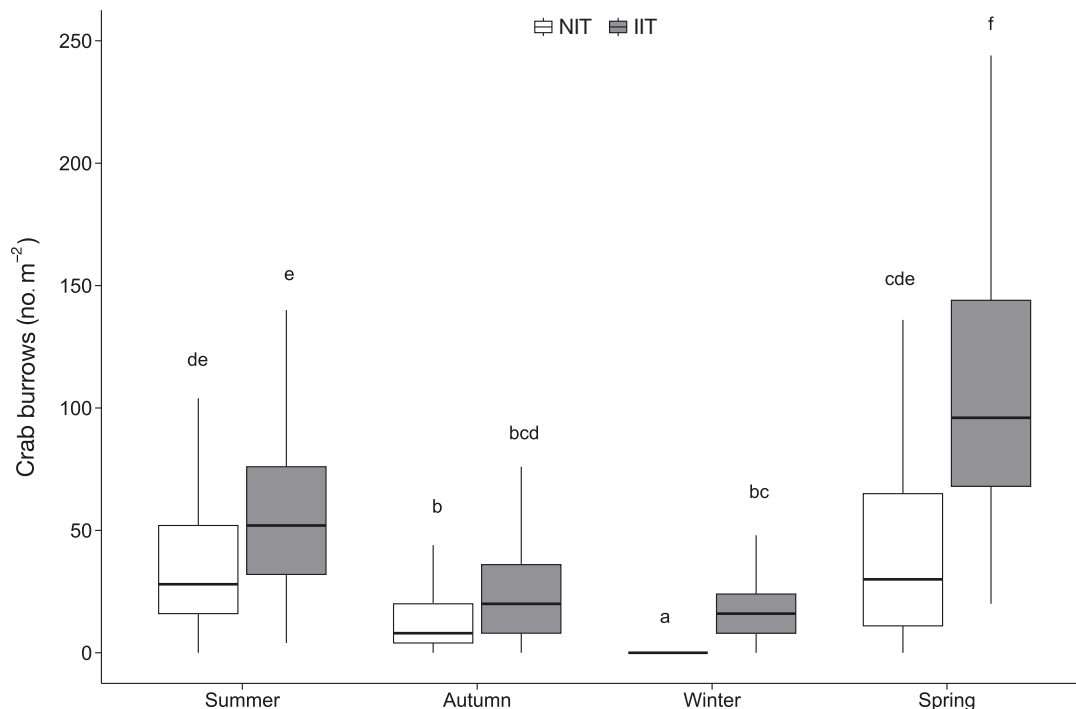


Fig. 3. Seasonal comparisons of the number of *Neohelice granulata* active burrows between treatments (IIT: increased inundation time; NIT: natural inundation time) were monitored between January (austral summer) 2017 and August (austral winter) 2019. Different letters above the boxes represent statistical differences (Tukey test after ANOVA, $p < 0.05$) between treatments and/or seasons. Boxes: 25th and 75th quartiles; dark horizontal line: median; whiskers: maximum and minimum values

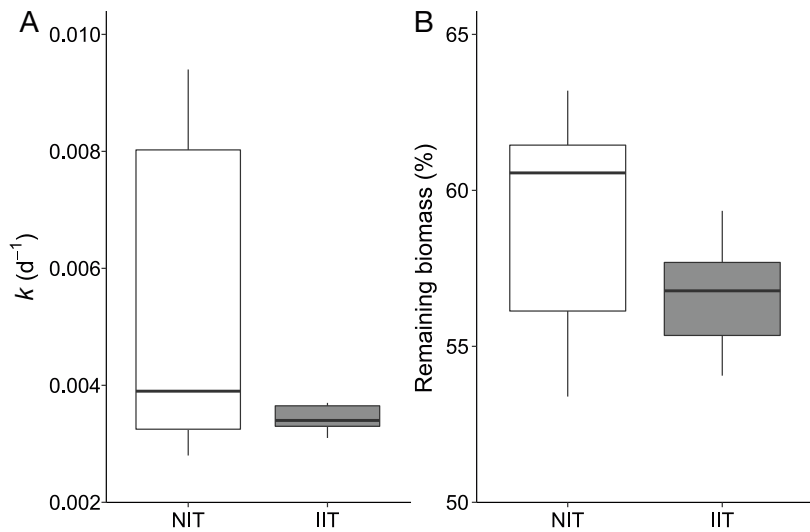


Fig. 4. (A) Median degradation rate (k) of *Spartina densiflora* and (B) percentage of *S. densiflora* detritus remaining in litterbags throughout the 154 d inundation experiment. Litterbags were placed on the sediment surface from March (end of summer) to May (autumn) 2017 within the experimental units. Boxplot parameters and experiment definitions as in Fig. 3

0.152, $p = 0.881$; R : $t_{12} = 0.713$, $p = 0.490$). The values hovered around 2.7 ± 0.54 , 3 ± 0.61 and -0.3 ± 0.26 $\text{mg O}_2 \text{ m}^{-2} \text{ min}^{-1}$ for NPP, GPP and R , respectively (Fig. 5).

3.4. Physico-chemical characteristics of sediments

Sediment temperatures in the NIT treatments were 1 and 2°C higher during April and May ($t_{c12.36} = 2.676$, $p = 0.019$, $t_{38} = 2.200$, $p = 0.034$, respectively) than in the IIT treatments (Table 2, Fig. 6A). Regarding pH, most months showed similar values between treatments, which were moderately acidic (mean: 6.5 ± 0.62). Only in May did the IIT treatment show higher values than the NIT treatment ($t_{38} = -5.835$, $p < 0.0001$; Table 3, Fig. 6C).

IIT treatments showed higher values of sediment-water content (mean: $25.24 \pm 1.47\%$, $t_{18} = 4.8$, $p < 0.0001$; Fig. 6B) and OM content (mean: $2.32 \pm 0.16\%$, $t_{13.36} = 4.02$, $p = 0.001$; Fig. 6D) than NIT treatments (sediment-water content, mean: $21.51 \pm 1.97\%$; OM content, mean: $1.88 \pm 0.31\%$). In addition, the values recorded for OM content in the NIT treatment were 2 times more variable than for IIT ($F_{1,18} = 5.87$, $p = 0.026$; Fig. 6D).

4. DISCUSSION

In this study, we showed that while the mean values of the estimated ecosystem functions were not affected by experimental inundation, the variability of some of the ecosystem functions in the NIT treatment was greatly reduced (e.g. detritus decomposition) or increased (number of active burrows in autumn and winter) under increased inundation time. Moreover, increased inundation time seems to favor *Neohelice granulata* activity in winter and especially in spring. In addition, OM and water content were higher under increased inundation time while sediment temperature and pH, in most cases, did not differ among treatments; therefore, we suggest that the design of the experiment was appropriate for the objectives set (i.e. manipulation of inundation time, for at least 6 h) even though it was a passive experiment in which barriers were only built to delay water drainage during low tide. It should be noted that an artefact effect (given by the plastic enclosures of the EU) could be present; however, the EUs were made sufficiently large (compared to mean sample size) and similar enough (the only difference between treatments was the ribbed front wall in the NIT treatment) to minimize those potential artefact effects.

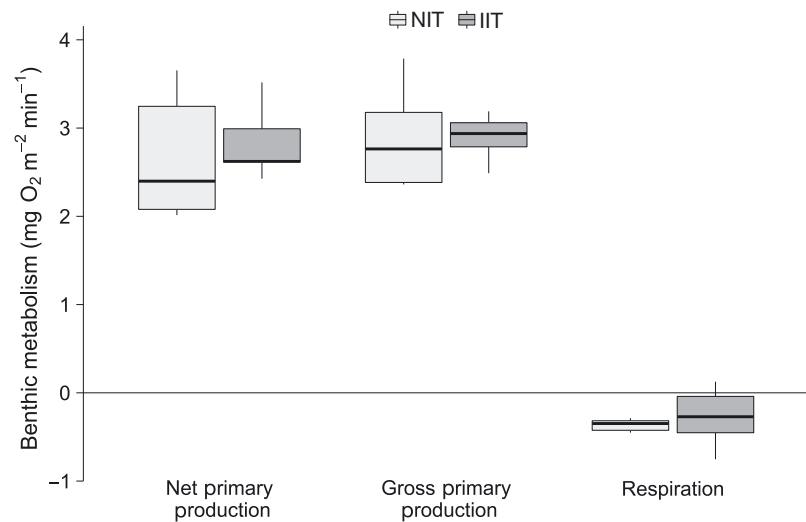


Fig. 5. Net primary production, gross primary production and respiration, estimated within the experimental units in March (summer) 2018. Boxplot parameters and experiment definitions as in Fig. 3

4.1. Bioturbation intensity response to increased inundation time

Changes in the disturbance regimes associated with GCC and anthropogenic pressure could affect benthic macrofauna and, in turn, impact the ecosystem functioning of coastal and estuarine systems (Hewitt & Thrush 2009, Snelgrove et al. 2014). For example, fiddler crabs *Uca annulipes* and *U. inversa* decreased their sediment bioturbation activities as a result of increased sewage loading exposure, resulting, in the long term, in degradations (given by an anoxic state) in the sediment health of the Tanzania manglar they inhabit (Bartolini et al. 2009). In contrast, the burrowing heart urchin *Brissopsis lyrifera* enhanced its bioturbation activity under slight decreases in pH, which could potentially lead to increased availability of macronutrients and a subsequent increase in pelagic primary production (Widdicombe et al. 2013). However, the nereid polychaete *Neanthes virens* did not present changes in its digging behavior under conditions similar to those mentioned in the previous example (i.e. acidification, Widdicombe & Needham 2007). In the first 2 examples, macrofaunal response to different environmental disturbances resulted in behavioral modifications; in the third example, it did not.

N. granulata is a semiterrestrial burrowing crab that, at our study site, is active from spring to most of

Table 2. Statistical summary of *t*-tests comparing mean sediment temperature (°C) values for the different months between treatments (IIT: increased inundation time; NIT: natural inundation time). If the data were not normally distributed even after transformation, a *t*-test was still used since this test is robust to the violation of this assumption with a high sample size and our data used satisfied this prerequisite. Where the assumption of homoscedasticity was not met, the Welch test was used. Feb and Mar: austral summer; Apr and May: autumn; Jun: winter. **p* < 0.05

Month	df	t_{obs}	p	Treatment	Mean (SD)
Feb	18	0.749	0.464	NIT	26.25 (1.36)
				IIT	25.86 (0.91)
Mar	18	0.776	0.448	NIT	20.9 (1.33)
				IIT	21.27 (0.72)
Apr ^a	12.364	2.676	0.019*	NIT	19.43 (1.04)
				IIT	18.47 (0.46)
May ^b	38	2.201	0.034*	NIT	18.15 (1.98)
				IIT	16.91 (1.56)
Jun ^b	38	1.243	0.222	NIT	8.66 (2.99)
				IIT	7.58 (2.48)

^aWelch test, ^bData not normally distributed

autumn (associated with reproductive strategies and feeding) but remains inside its burrows during winter (because of the low temperatures) (Spivak et al. 2012). At low tide in our study site, it behaves mostly as a *Spartina densiflora* grazer in the marsh and as a deposit feeder in the mudflat (Iribarne et al. 1997,

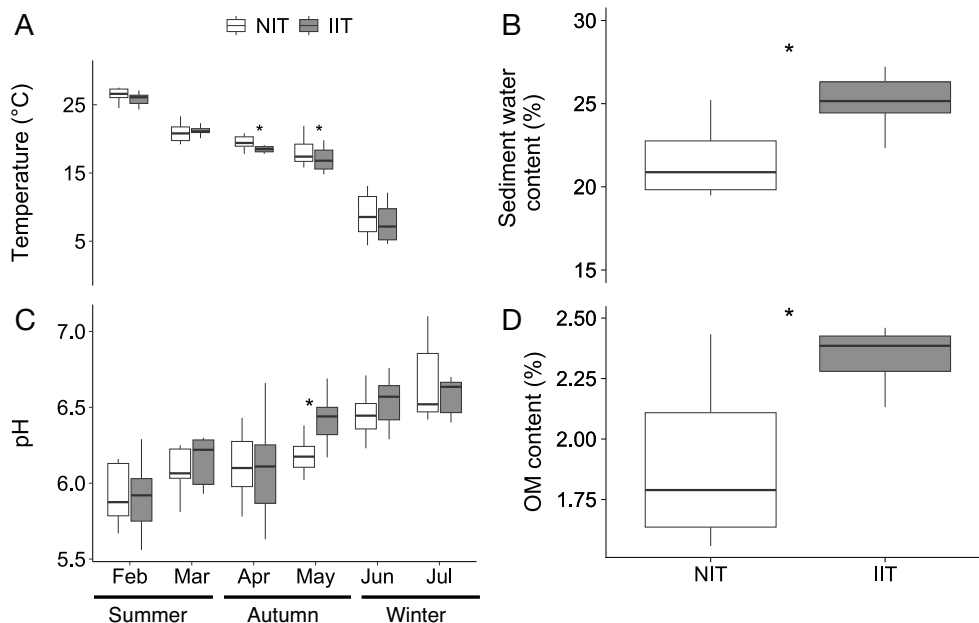


Fig. 6. (A) Sediment temperature, (B) sediment-water content percentage, (C) sediment pH and (D) organic matter (OM) percentage in the Mar Chiquita coastal lagoon. Asterisk indicates significant differences (*t*-test, *p* < 0.05) between treatments. Sediment-water content and OM content were measured only once at the end of the experiment. Boxplot parameters and experiment definitions as in Fig. 3

Table 3. Statistical summary of *t*-tests comparing mean pH values for the different months between treatments. See Table 2 for further details

Month	df	t_{obs}	p	Treatment	Mean (SD)
Feb	18	0.063	0.950	NIT	5.93 (0.2)
				IIT	5.92 (0.23)
Mar ^a	18	−0.987	0.336	NIT	6.09 (0.15)
				IIT	6.15 (0.15)
Apr	38	0.099	0.921	NIT	6.11 (0.2)
				IT	6.1 (0.3)
May	38	−5.835	< 0.0001*	NIT	6.18 (0.1)
				IIT	6.43 (0.17)
Jun	38	−1.607	0.116	NIT	6.46 (0.16)
				IIT	6.53 (0.15)
Jul	18	0.92	0.369	NIT	6.65 (0.24)
				IIT	6.58 (0.12)

^aData not normally distributed

Botto et al. 2006, Bas et al. 2014). When tides rise and the mudflat becomes inundated, this crab is seen climbing *S. densiflora* stems and eating its leaves (Alberti et al. 2007, Bas et al. 2014). In this context, we expected to obtain poor bioturbation activity of *N. granulata* within the IIT treatment, mainly due to a shift in its feeding preference (e.g. Alberti et al. 2007). However, its bioturbation intensity was not affected in summer (i.e. D_b between treatments, see Section 3.1). In addition, increased inundation time favored burrow construction (i.e. number of active burrows) during winter and spring, but not during summer, which was when D_b was estimated (Fig. 3). Although we did not estimate D_b during spring, all published evidence in the region has shown that the highest activity of *N. granulata* is in summer (e.g. Escapa et al. 2008, Mendez-Casariago et al. 2011, Luppi et al. 2013). Indeed, our results are consistent with other studies that have shown that during the cold months (when this crab shows very low activity) in high tides—but particularly during extraordinary ones—its movement activity is high (Mendez Casariago et al. 2011, Luppi et al. 2013). *N. granulata* is a crab that has a wide geographical distribution as well as a wide distribution within the intertidal system, so is adapted to contrasting physical (e.g. tidal amplitude, temperature, sediment type, salinity) and biological factors (e.g. predation, competition). This could explain the fact that increased inundation time did not negatively affect its burrowing activity (i.e. burrow construction) or its D_b .

Moreover, as mentioned before, the winter season is associated with dormancy in *N. granulata*, given the harsher climate conditions. The results obtained

in the NIT treatment (in winter) are consistent with this behavior. However, in the IIT treatment, we found the same burrowing activity as in autumn (in the IIT and NIT treatments) and spring (NIT treatment; see Fig. 3). This could indicate that the reproductive and feeding period of *N. granulata* may have been extended under increased inundation time. In this sense, reproductive and feeding time may vary along the species' geographic distribution, being longer in the northern part of its range (e.g. Jabaquara Beach, 23° 15' S; Gregati & Negreiros-Fransozo 2009), and shorter in the southern end (e.g. San Antonio, 40° 46' S; Ituarte et al. 2006). Indeed, at our study site, *N. granulata* shows a shorter reproductive and feeding strategy (from mid-spring to mid-autumn) than other burrowing crabs (from early spring to early winter) that are associated with the lower intertidal level (e.g. *Cyrtograpsus angulatus*). This difference is explained by better environmental conditions (i.e. higher temperatures under the water than in the open air), which enables more energy to be invested in reproduction (Spivak et al. 2012). Therefore, we can infer that increased inundation time did not have a negative influence on the burrowing activity of *N. granulata*; on the contrary, it had a positive effect. In addition, the greater degree of activity given by an increase in the number of active burrows in the IIT treatment in winter could be explained by softer sediments being produced by the greater inundation time (C. Diaz de Astarloa pers. obs.). Unconsolidated sediments probably facilitate systematic burrow collapse, promoting constant burrow maintenance by *N. granulata* and, thus, the results obtained here. Overall, it is important to continue studying seasonal patterns of bioturbation by benthic organisms such as *N. granulata* and the consequences on sediment characteristics and ecosystem functioning. Further work is still needed to understand the complex interplay between environmental factors and biotic processes and the implications of these interactions for the health and resilience of our ecosystems.

4.2. Decomposition rate of marsh plants under increased inundation time

Detritus decomposition is mainly performed by bacteria and fungi, and the rate of such processing is dependent on factors that may influence their activity rates (e.g. abiotic factors, litter quality, inundation time and chemical conditions under which decomposition occurs; Lillebø et al. 2007, Montemayor et al.

2011). These microorganisms are key catabolizers since, despite their decomposition activity, they enrich the nutritional quality and palatability of the detritus for macroinvertebrates (Hill & Perrotte 1995). In this study, we found that increased inundation time reduces the variability of *S. densiflora* decomposition rates compared to the control treatment (Fig. 4A). It might be thought that variable inundation conditions would favor detritus decomposition, but there are major inconsistencies with this relationship (inundation–decomposition). Detritus decomposition may be slowed down in standing water due to anoxic conditions (Neckles & Neill 1994, Battle & Golladay 2001), sediment deposition (Langhans & Tockner 2006) or even increased respiration rates of non-detritivorous microorganisms (Hietz 1992). However, it could be favored by physical (e.g. mechanical fragmentation, alternation between wet and dry cycles; Battle & Golladay 2001, Montemayor et al. 2011) and biological processes (e.g. microbial activity or invertebrate consumption; Battle & Golladay 2001, Lillebø et al. 2007). On the one hand, temporarily flooded systems generate microenvironments where physicochemical conditions are modified (e.g. pH, temperature, dissolved nutrient availability), positively affecting microbial and fungal activity, which, in turn, increases the palatability of the detritus for invertebrates during subsequent inundation events (Neckles & Neill 1994). On the other hand, detritus deprived of water slowly decomposes due to a decrease in microbial activity (Foote & Reynolds 1997). Thus, detritus that is permanently underwater also decomposes more slowly given the low oxygen concentrations in the system (e.g. Neckles & Neill 1994, Battle & Golladay 2001). In such cases, the recurrent alternation between wet and dry cycles would promote ideal conditions for detritus degradation (Battle & Golladay 2001, Pfaunder & Zimmer 2005). In the present study, the NIT treatment showed much higher decomposition rate variability than the IIT treatment; however, there were no differences between treatments in mean decomposition rate. This could indicate that, in this system, a longer inundation period may negatively affect the decomposing community due to an increase in sediment anoxia, making the activity of the facultative microorganisms an inefficient task (Altor 2000). This correlates with findings that immersion has a slight inhibitory effect on detritus decomposition (Halupa & Howes 1995). Moreover, it has been reported that in places where decomposition occurs under fundamentally oxic conditions, periodic inundation can increase soil moisture and microbial activity (Neckles & Neill 1994), whereas ex-

cessive inundation creates anoxic conditions that would limit decomposition. Therefore, it appears that over a longer time frame, the increment in inundation time might be following this direction and, eventually, negatively impact detritus decomposition.

4.3. Microphytobenthic primary productivity response to increased inundation time

Microphytobenthic primary production in intertidal environments constitutes an important source of labile OM, enhancing benthic food webs and playing a key role in nutrient cycling and sediment stabilization (Underwood & Kromkamp 1999). Microphytobenthos also contribute significantly to the total production of intertidal systems (Underwood et al. 2005); therefore, estimating the primary production rate is important since it allows the estimation of how much energy is available for the food webs (Kromkamp & Forster 2006). In these systems, microphytobenthic assemblages are susceptible to disturbances such as eutrophication (Tsikopoulou et al. 2020), desiccation (Bento et al. 2017) and flooding (Migné et al. 2009), among others. However, our results showed that increased inundation time had no appreciable effect on microphytobenthic primary production since both treatments presented the same productivity values (see Section 3.3, Fig. 5). The results obtained are surprising because it is known that these organisms live close to their tolerance limits, so small changes in certain environmental parameters (e.g. pH, temperature, light) could generate significant physiological and ecological responses (Russell et al. 2013). For example, a decrease in microphytobenthic biomass (as a proxy for productivity) was experimentally observed with increasing temperatures (Hicks et al. 2011). Likewise, an increase in the susceptibility to photoinhibition at high temperatures was observed in diatom-dominated microphytobenthic communities (Laviale et al. 2015) as well as a reduction in microphytobenthic primary productivity (measured as chlorophyll *a* concentration) due to SLR (O'Meara et al. 2017) and hypoxic conditions combined with darkness (Villnäs et al. 2013). However, other studies have shown positive effects (e.g. Alsterberg et al. 2012) or even null ones (as in this study) under different stressors (e.g. acidification, Hicks et al. 2011; sediment nutrient enrichment, Mangan et al. 2020).

The fact that there were no differences between treatments could be due to particular environmental conditions (e.g. turbidity and desiccation in the IIT and NIT treatments, respectively) that could have

equalized microphytobenthic primary production. In this sense, suspended sediment concentration in the water column increases turbidity, which negatively impacts microphytobenthic primary production (Pratt et al. 2014). In the IIT treatment, turbidity was observed (C. Diaz de Astarloa pers. obs.), probably due to the activity (i.e. burrow construction) of *N. granulata*, and it would have been expected that this would impact microphytobenthic primary production. In another direction, exposure to desiccation decreases microphytobenthos diversity and richness, and thus, negatively affects its primary production (McKew et al. 2011). Following this line of reasoning, the EUs were set up in the marsh–mudflat edge so that desiccation stress in the NIT treatment would have been greater than in a lower tidal height. In addition, during air exposure, sediment–water content is mostly maintained by water held in *N. granulata* burrows. In March 2018 when we estimated microphytobenthic primary production, the NIT treatment presented almost half the number of burrows compared with the IIT treatment (see Section 3.1), reinforcing the desiccation stress hypothesis. Therefore, in the experimental situation developed in this study, the negative effects (i.e. a reduction in microphytobenthic metabolism) associated with turbidity (IIT treatment) and increased desiccation (NIT treatment) could have had similar net impacts on benthic metabolism, thus explaining the results obtained here. Another explanation for the achievement of the same productivity values among treatments could have been an effect of functional redundancy (Walker 1992, Naeem 1998): when individual species are lost because of their susceptibility to a specific disturbance, functional redundancy can provide continuity of ecosystem function because biological traits are shared by different species (e.g. Tsikopoulou et al. 2020). In this experiment, functional redundancy in microphytobenthic primary production (species being lost but without a corresponding loss of function) is of great importance since it could indicate ecosystem resilience under one potential negative impact of SLR, maintaining ecosystem function and services in this system.

5. CONCLUSION

As discussed before, intertidal environments are subjected to intense and highly variable dynamics in terms of their disturbance regimes (Griffiths et al. 2017), so it is challenging to understand what the effects of the forces associated with GCC on ecosys-

tem functioning will be. Our work shows that at our study site, increased inundation time—which is likely to occur as the sea level rises—does not affect microphytobenthic primary production or the intensity of bioturbation of the dominant intertidal species, *Neohelice granulata*, in summer. Nevertheless, inundation time increased this crab's digging activity in winter and spring and greatly decreased the variability of *Spartina densiflora* decomposition rate and OM content compared to the NIT treatment.

Overall, in our system, inundation reduced NIT treatment variability of some of these ecosystem functions. This finding could be relevant because organisms vary in their sensitivity and response to disturbance. Some organisms are more susceptible to certain disturbances (or degrees of disturbance) while others are more tolerant. Therefore, in a high-diversity ecosystem, we expect that the ecosystem functions would not be lost because duplication of species traits can provide a degree of functional redundancy (Walker 1992, Naeem 1998), whereas in a low-diversity ecosystem, the response capability might be more limited. Therefore, in the context of GCC, flooding frequency is predicted to rise, which could lead to a decrease in the ecosystem functioning variability in low-diversity communities. A decrease in ecosystem function variability might be indicative of a less resilient system (Peterson et al. 1998). In this sense, it has been shown that low-diversity ecosystems are more vulnerable to environmental change and have lower resilience than high-diversity ecosystems (Tilman et al. 2014, Isbell et al. 2015). As resilience declines, the ecosystem becomes more vulnerable to changes that could previously be tolerated. As a consequence, vital ecosystem functions may be altered or lost along with the ecosystem services provided to society.

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