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Salt Marshes Buffer El Niño Effects on Benthic Secondary Production

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Orientador: Dr Sérgio A. Netto

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Aos sete dias do mês de abril do ano de dois mil e vinte e um, às treze horas e trinta minutos, na sala online da plataforma digital Zoom: https://zoom.us/j/97184552552, realizou-se a sessão pública de apresentação e defesa de Dissertação de Mestrado de Mateus Floriano Stipp, como requisito para obtenção do título de Mestre em Ciências Ambientais, de acordo com o Regimento Interno do Programa de Pós-Graduação em Ciências Ambientais – PPGCA/UNISUL. Reuniu-se por videoconferência a comissão avaliadora composta pelos seguintes membros: Dr. Sérgio Antonio Netto, orientador e presidente da banca; Dr. Angelo Fraga Bernardino, avaliador externo da Universidade Federal do Espírito Santo (UFES); Dr. André Menegotto Domingos, avaliador externo da Universidade Federal de Goiás (UFG) para, sob a presidência do primeiro, arguirem o mestrando **Mateus Floriano Stipp**, sobre sua Dissertação intitulada: **"Salt marshes buffer El Niño effects on benthic secondary production"**, área de concentração "Tecnologia, Ambiente e Sociedade" e linha de pesquisa "Tecnologia & Ambiente". Após a apre-sentação, o mestrando foi arguido pelos membros da banca, tendo sido feitos os questionamentos e ouvidas às explicações a comissão avaliadora emitiu o conceito final:

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Observações:

Nada mais havendo a tratar, foram encerrados os trabalhos e, tendo sido lida e achada conforme, a presente ata foi assinada pelo presidente da sessão, em nome dos avaliadores presentes por videoconferência, pelo mestrando e pela secretária do PPGCA.

Dr. Sérgio Antonio Netto
Presidente da Sessão
Em nome da Comissão Avaliadora presente por videoconferência

Mateus Floriano Stipp

Mateus Floriano Stipp
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This dissertation is associated to the Sustainable Development Goals / SDGs 13 “Take urgent action to combat climate change and its impacts” and SDG 14 "Conserve and sustainably use the oceans, seas and marine resources for sustainable development”, of the 2030 Agenda of the United Nations (UN).

Our results contribute to Target 13.1 “Strengthen resilience and adaptive capacity to climate-related hazards and natural disasters in all countries” of the SDG 13, and Target 14.2 “By 2020, sustainably manage and protect marine and coastal ecosystems to avoid significant adverse impacts, including by strengthening their resilience, and take action for their restoration in order to achieve healthy and productive oceans” of the SDG 14.

RESUMO

O El Niño-Oscilação Sul (ENOS) influencia fortemente o clima e a hidrologia do planeta, consequentemente, a estrutura e funcionamento das comunidades biológicas estuarinas. No entanto, os efeitos do ENOS nas áreas costeiras são dependentes da escala espacial e das características intrínsecas do estuário, como seus diferentes habitats. Durante seis anos (2013 a 2018) investigamos a variabilidade interanual da produção secundária macrobêntica de marismas de *Spartina alterniflora* e áreas não-vegetadas adjacentes em uma lagoa costeira subtropical no sul do Brasil e testamos se os eventos ENOS (El Niño e La Niña) afetam de forma semelhante a produção secundária bêntica desses dois habitats. Nossos resultados mostram que a produção secundária da macrofauna variou ao longo do tempo, apresentando um aumento relacionado a ocorrência do evento El Niño 2015/2016 e consequente aumento na precipitação. No entanto, as marismas responderam de forma diferente das áreas não-vegetadas, com uma produção secundária mais estável. Há também uma distinção nos efeitos sobre diferentes táxons. Embora as espécies mais representativas, *Laeonereis acuta* e *Monokalliapseudes schubarti*, tenham apresentado aumento na produção secundária em áreas não-vegetadas, *L. acuta* apresentou aumento apenas na biomassa, enquanto para *M. schubarti* houve aumento na biomassa e densidade. Em contraste, ambas as espécies apresentaram densidade, biomassa e produção secundária sem diferenças significativas ao longo do tempo nas marismas. Esses achados reforçam que as variações climáticas podem influenciar a produção secundária, mas as marismas têm um efeito tampão sobre a influência do El Niño nas associações bênticas.

Palavras-chave: complexidade de habitat; comunidades estuarinas; marisma; produtividade; variabilidade climática; variabilidade de longo prazo.

ABSTRACT

The El Niño-Southern Oscillation (ENSO) strongly influences the planet climate and hydrology, consequently, the structure and functioning of estuarine biological communities. However, the effects of the ENSO on coastal areas are dependent of the spatial scale and the intrinsic characteristics of the estuary, such as different habitats. During six years (2013 to 2018) we investigate the interannual variability of macrobenthic secondary production of *Spartina alterniflora* marshes and adjacent unvegetated areas in a subtropical coastal lagoon in Southern Brazil and we tested whether the ENSO events (El Niño and La Niña) affect similarly the benthic secondary production of these two habitats. Our results show that the secondary production of benthic macrofauna varied over time, showing an increase related to the occurrence of the El Niño 2015/2016 event and consequent increase in precipitation. However, the salt marshes responded differently of the unvegetated areas, with a secondary production more stable. There is also a distinction in the effects on different taxa. Although the most representative macrobenthic species, *Laeonereis acuta* and *Monokalliapseudes schubarti*, increased secondary production in unvegetated areas, *L. acuta* showed an increase only in biomass, whereas for *M. schubarti* there was an increase in biomass and density. In contrast, both species showed density, biomass and secondary production with no significant differences over time in the salt marshes. These findings reinforce that climatic variations can influence secondary production, but the salt marshes have a buffering effect on the influence of El Niño on benthic associations.

Key words: climate variability; estuarine communities; habitat complexity; long-term variability; productivity; salt marshes.

SUMMARY

INTRODUCTION

Salt marshes have an important role in mitigating and promoting adaptation to climate change (Roberts and others 2017). They provide coastal protection (Serrano and others 2019), constitute blue carbon ecosystems (McLeod and others 2011), and support trophic webs, acting as a nursery and feeding grounds for many species, including those of economic interest (Kelleway and others 2017). Despite providing many ecosystem services (e.g., Lewis and others 2018) and supporting approaches that incorporate natural features and processes to reduce hazards and climate change risks, salt marshes have been systematically converted into harbors or urban areas. Besides that, pollution and human alteration of coastal zone result in decreased sediment supply, altered hydrological functioning, and increased subsidence, all of which contribute to marsh loss (e.g., Shepard and others 2011, Hoegh-Guldberg and others 2018).

Preservation and restauration of the salt marshes can, among other things, maintain the productivity and functionality of the estuarine environment (Rezek and others 2017). The vegetation increases the habitat complexity (Reis and others 2019), and, through primary production, salt marshes provide a more stable energy base for secondary production (Pettit and others 2016). Secondary production represents the amount of matter and energy incorporated in the biomass of heterotrophs by unit of time; it incorporates factors such as biomass, growth rate, survival, development time and other ecosystem processes, assessing community functionality (Benke and Huryn 2010, Dolbeth and others 2012). As benthic organisms form the basis of the estuarine trophic web, changes in benthic secondary production allows us to assume influences in the flows of matter and energy along the food web (Sánchez-Moyano and others 2017).

The variability of the estuarine benthic secondary production may provide key insights into ecosystem dynamics, as it envelops cumulative responses to both static and dynamic components (Dolbeth and others 2012) of a population's ecological performance. Thus, we can hypothesize that current global warming and/or global-scale events such as the El Niño Southern Oscillation (ENSO) may change climatic variables (i.e., temperature and precipitation) and affect benthic secondary production. Temperature, in particular, directly influences the feeding activities, reproduction and growth rates (Dolbeth and others 2012, McMeans and others 2015). Although productivity is related to organism size (Mahaut and others 1995), the exact effects of increased metabolism on biomass are uncertain (Gardner and others 2011, Sheridan and Bickford 2011) though it could influence the entire food web and represent an enormous risk to the services provided, with potential socioeconomic impacts (Sandifier and others 2015).

ENSO is the most important signal in the interannual variability of the global ocean–atmosphere system, fluctuating between anomalously warm (El Niño) and cold (La Niña) sea surface temperature (SST) conditions (Yeh and others 2018). ENSO phases strongly influence the planet climate and hydrology (Wang and Cai 2013), consequently, the structure and functioning of estuarine biological communities (e.g., Marques and others 2017, Francisco and Netto 2020). However, the effects of the ENSO on coastal areas are dependent of the spatial scale and the intrinsic characteristics of each estuary (Francisco and Netto 2020). Few studies related ENSO events to changes productivity in salt marshes, and most of them were focused on the vegetal structure (e.g., Canepuccia and others 2010, Marangoni and Costa 2012). To our knowledge, no study had been carried out on how benthic secondary production of the salt marshes responds to shift conditions experimented during ENSO events.

Here we investigate the interannual variability of macrobenthic secondary production of *Spartina alterniflora* marshes and adjacent unvegetated areas in a subtropical coastal lagoon in Southern Brazil. We tested whether the ENSO (El Niño and La Niña) events affect similarly the benthic secondary production of marshes and unvegetated flats. We expect that both vegetated and unvegetated area would respond to climatic variables, but in a different fashion, as vegetation would provide greater stability for the salt marshes.

METHODS

Study Site

Our study site is located in the southern and mixohaline portion of the Laguna Estuarine System (LES), the Santo Antônio lagoon, Southern Brazil (Figure 1). LES is a chocked lagoon of 184 km² (28º30'S/48°48'W), contained behind a sandy barrier (1-6 km wide) in a microtidal, wave-dominated coastal environment (Colonese and others 2017, Netto and others 2018). The mixohaline portion of LES is bordered by large *Spartina alterniflora* and *S. densiflora* marshes, with some isolated *Laguncularia racemosa* trees within the marshes (Netto and others 2018). The regional climate is subtropical and the mean air temperatures are below 16º C in winter and below 27º C in summer. About 1,340 mm of precipitation falls annually, without a defined rainy season; NE winds are dominant throughout the year, although, in the winter, the frequency of southern winds increases (Netto and others 2018).

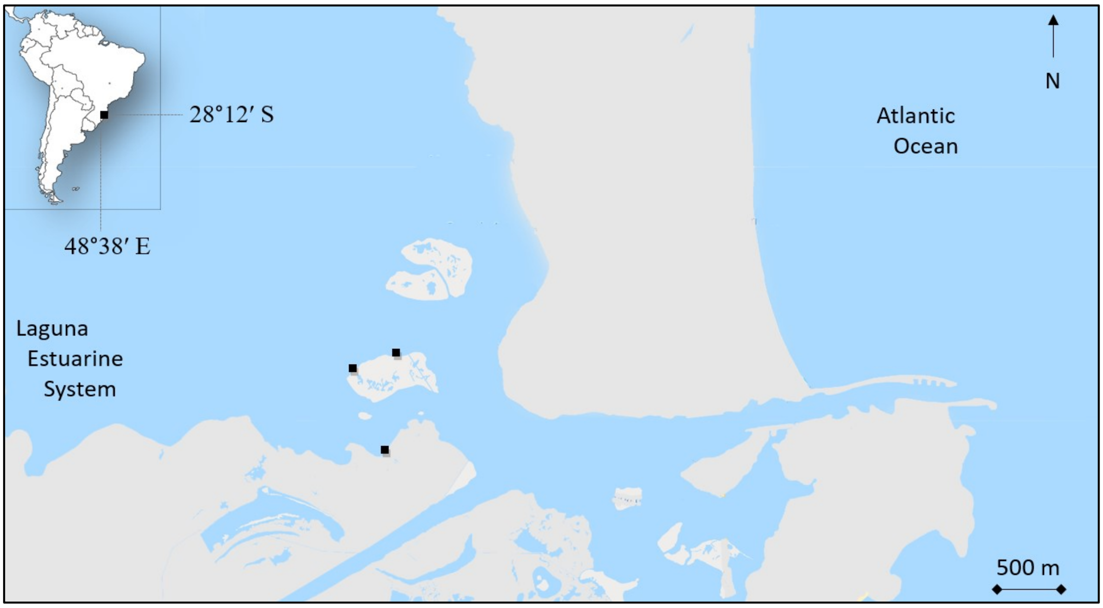

Figure 1. Map showing the sampling sites (black dots) within the mixohaline zone of the Laguna Estuarine System (Santo Antônio lagoon), South Brazil.

The study area is inside the Federal Right Whale Environmental Protection Area and represents one of the largest (more than 5 km^2) and well-preserved marshes in south Brazil. The region has been monitored seasonally over the past eight years, as part of the ReBentos project (Coastal Benthic Habitats Monitoring Network; www.rebentos.org) and is already suffering the effects of climate change with an increase in temperature (Bernardino and others 2015).

Benthic Fauna Sampling and Samples Processing

Benthic macrofauna were randomly collected twice during austral summer and twice during winter along six consecutive years (2013 to 2018). At each sampling date, three fixed sites, apart from each other for least 300 m, consisting of two habitats - *Spartina alterniflora* marshes and adjacent unvegetated area, were sampled (at most 25 meters from the edge). At each site, two macrofauna samples were taken in each habitat with a 0.03 m^2 PVC corer pushed to a depth of 20 cm. The samples were fixed in 10% formalin and sieved on a 0.5 mm mesh. The macrofauna, preserved with ethanol 70%, was identified to the lowest possible taxonomic level and counted. Once identified, individuals of each macrofauna species were dried (60°C for 48 hours) and weighed. The biomass in grams of dry weight was then converted into joule (J), using the conversion factors compiled in Brey (2001) and Brey and others (2010).

Estimation of the secondary production followed the methods proposed by Brey (2001, 2012). We used Brey's multi-parameter artificial neural network model to estimate macrobenthic invertebrate productivity from three continuous parameters (water depth and temperature – collected during the sampling – and biomass) and categorical parameters (taxon, mobility, feed type and habitat). The information on the categorical parameters of each taxon was collected from online database (MarLIN 2006), literature (e.g., Queirós and others 2013, Jumars and others 2015) and ad hoc information from specialists. From the result, in production / biomass ratio, the average secondary production for each taxon by area was calculated and converted in g C/m^2/ y^{-1} (Salonen and others1976).

ENSO and Environmental Data

ENSO events were analyzed using the Oceanic Niño Index (ONI), provided by the Climate Prediction Center of National Oceanic and Atmospheric Administration (NOAA). The ONI is a 3-month running mean anomalies of sea surface temperature data (Huang and others 2017) in the Niño 3.4 region (5ºN-5ºS, 120º-170ºW).

Average monthly data of air temperature, precipitation, north surface stress and north wind component trends were provided from the Giovanni online data system, developed by the NASA Goddard Earth Sciences Data and Information Services Center (NASA GES DISC, https://giovanni.gsfc.nasa.gov/giovanni/). The data were obtained from satellite MERRA-2 Model M2TMNXFLX v5.12.4 (GMAO 2015). The data collection from Laguna Estuarine System were limited by the coordinates of the Data Bounding Box -48.75W, -28.5S, -48.75W, -28.5S, and it was obtained from January/2013 to December /2018.

Data Analysis

In order to test the differences in macrofauna (total and the two most representative species) density, biomass and secondary production among years (fixed factor: 2013 to 2018), seasons (fixed factor: summer and winter) and habitats (fixed factor: salt marsh and unvegetated) were used a permutational analysis of variance (PERMANOVA) on Euclidian distances matrices with 9999 permutations (Anderson and others 2008).

The significance of the differences in the multivariate density, biomass and secondary production among years, seasons and habitats were tested with a permutational analysis of variance (PERMANOVA) on Bray-Curtis matrices with 9999 permutations (Anderson and others 2008). Faunal data ordination by nMDS (Multi-Dimensional Scaling) was used to visualize the similarities among years, season and habitats regarding density, biomass and secondary production.

To characterize the ENSO phases (El Niño, La Niña and Neutral) during the period of this study, data derived from ONI were used. The influence of the ENSO phases on the environmental variables (temperature, precipitation, north surface stress and north wind component) of the study area was tested with a permutational analysis of variance (PERMANOVA) among ENSO phases (fixed factor: El Niño, La Niña and Neutral), run on Euclidean distance matrices with 9999 permutations (Anderson and others 2008).

To test the relation between climatic factors and benthic secondary production in each habitat, the monthly data of ONI and environmental variables, recorded continuously, were transformed, through simple mean, into seasonal data (summer and winter for each of the 6 years), thus making correspondence to the fauna data that were seasonally sampled. In order to identify the contribution of predictor variables to the temporal variability of macrofauna secondary production, a distance-based linear model routine (DistLM, Legendre and Anderson 1999) was applied. The DistLM was based on similarity matrices of macrofauna secondary production data and the predictors: ONI, air temperature, precipitation, north surface stress and north wind component. A linear regression analysis (SAS Institute 1999) was used to determine if benthic secondary production variation had a functional relation with the SST anomalies recorded in the 2015/2016 El Niño event.

RESULTS

El Niño Southern Oscillation phases and Environmental data

From January 2013 to October 2014, the ENSO was characterized by a neutrality, followed by an intense increase in the temperature anomalies, with a peak of 2.6°C in December 2015 (Figure 2). These months of El Niño (SST anomalies higher than 0.5°C in the Pacific Ocean) last until mid-2016, when the water temperature dropped and periods of La Niña (late 2016, and late 2017/early 2018) and neutrality (mid 2017 and mid 2018) predominated (Figure 2).

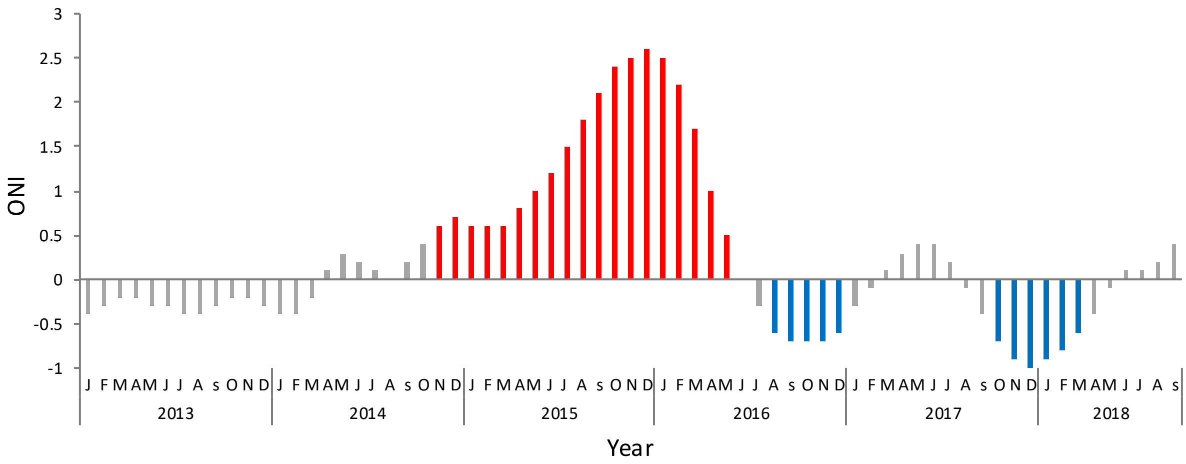

Figure 2. Three-month running mean of sea surface temperature anomalies in the Pacific Ocean (ONI) indicating different ENSO phases from January 2013 to September 2018. El Niño event in red, La Niñas in blue and neutrality in gray.

Most of environmental variables (temperature, north surface stress and north wind component) did not differ significantly between ENSO phases, except for precipitation (Table 1). Monthly precipitation totals during El Niño months were 70% higher than neutral and La Niña conditions (El Niño - 218 mm; La Niña - 159 mm and neutral 151 mm). Total monthly mean precipitation during La Niña and neutral conditions did not differ significantly during the studied period (Table 1). Higher volumes of precipitation rainfall were registered in October 2015 with a total of 424 mm.

Table 1. Mean value (±SD) of meteorological variables and summary results of the PERMANOVA tests for differences between the ENSO phases (El Niño, neutral and La Niña) for the Laguna Estuarine System area.

	EN	**LN**	**N**	**Pseudo-F**	**P(MC)**
Precipitation (mm)	218 (90)	158 (68)	151 (84)	4.3113	**0.0157**
Temperature (°C)	21.8 (2.77)	21.0 (2.61)	20.3 (3.16)	1.6404	0.2038
North surface stress (N/m²)	-0.01 (0.02)	-0.01 (0.01)	-0.02 (0.02)	2.6888	0.7623
North wind component (m/s)	-1.3 (1.41)	-1.4 (0.71)	-1.8 (1.51)	0.75891	0.4693

Precipitation pair-wise test

Groups	**t**	**perms**	**P(MC)**
Neutral, El Niño	3.433	9834	**0.0015**
Neutral, La Niña	0.1406	9840	0.8919
El Niño, La Niña	2.5654	9837	**0.0155**

Macrofauna Density, Biomass and Secondary Production

A total of 25,862 organisms (8,191 in salt marshes and 17,671 in unvegetated areas) belonging to 39 taxa (25 and 34 in marshes and unvegetated areas respectively) were collected throughout the study. The tanaid *Monokalliapseudes schubarti* (Mane-Garzon 1949), and polychaeta Nereididae *Laeonereis acuta* (Treadwell, 1923) were the most abundant species in both vegetated and unvegetated areas (representing 44.8% and 18.8% of the organisms collected), with higher biomass (26.1% and 32.1%) and productivity (25.9% and 39.0%).

In the salt marshes, both species showed little variation throughout the years (Figure 3, Table S1 and Table S2). Mean biomass of *M. schubarti* varied from 0.0002 to 0.03 g DW/0.03m^2; density from 0.2 to 82.7 individuals/0.03 m^2 and production from 1.05 to 60.7 g C/m^2/y-^{1}. However, in unvegetated areas, all descriptors of *M. schubarti* increased significantly during El Niño (2015/2016; Figure 3, Table S1). Compared to the other periods (neutral and La Niña), during El Niño the biomass of *M. schubarti* increased by an average of 4,059% (up to 0.08 g DW/0.03m^2), density increased 5,370% (up to 569.3 individuals/0.03 m^2) and production increased 2,688% (up to 201.09 g C/m^2/y-^{1}). *Laeonereis acuta* biomass and production also significantly increased in unvegetated areas during El Niño (mean biomass of 0.024 g DW/0.03m^2 during neutral/La Niña, 0.042 g DW/0.03m^2 during El Niño; mean production of 56.1 g C/m^2/y-^{1} during neutral/La Niña, and 117.01 g C/m^2/y-^{1} during El Niño). On the other side, densities of *L. acuta* in the unvegetated areas remained roughly similar over time, with a mean of 51.5 individuals/0.03 m^2 (Figure 3; PERMANOVA on Table S2).

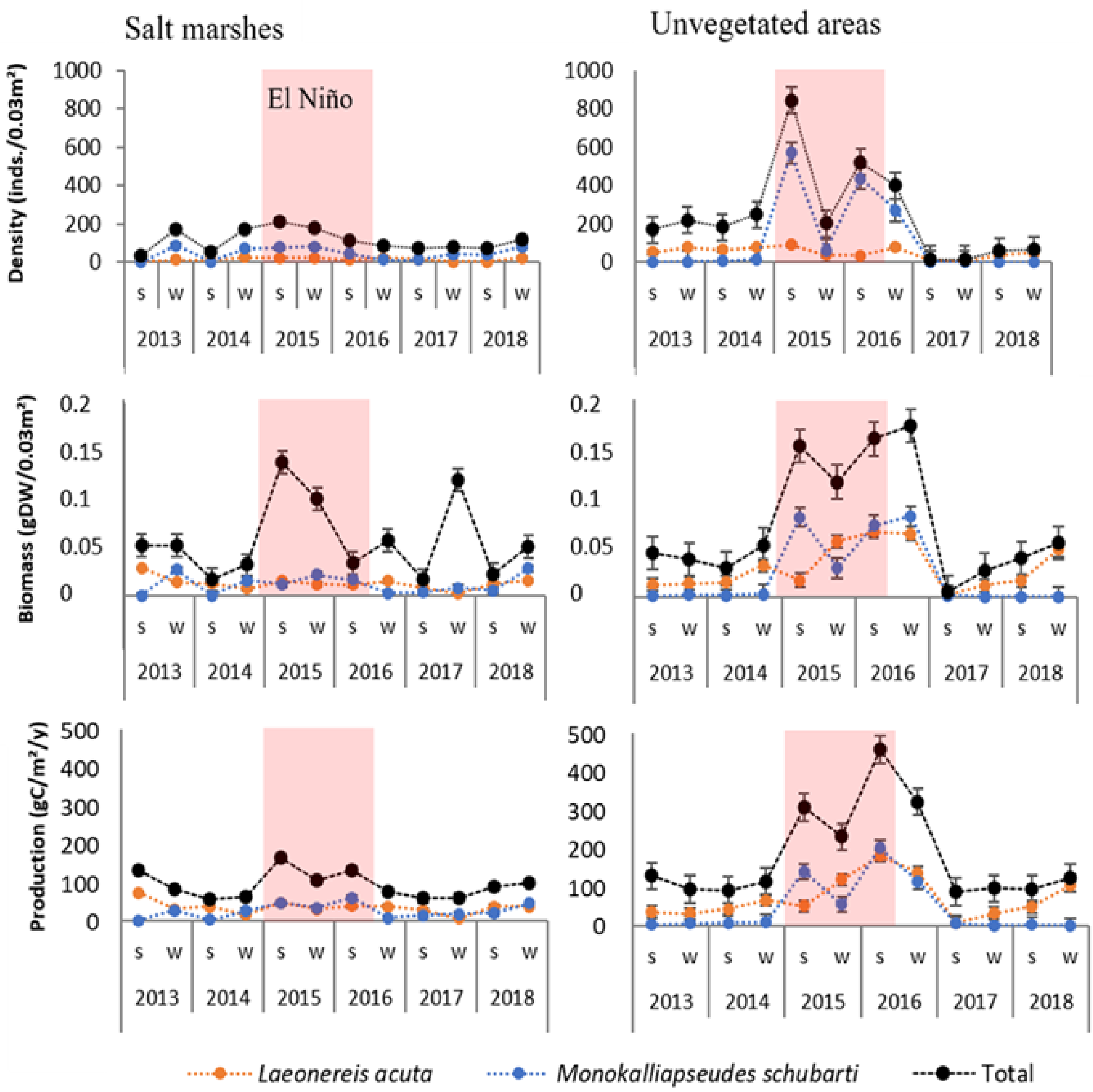

Figure 3. Mean values of density, biomass and secondary production of *Laeonereis acuta*, *Monokalliapseudes schubarti*, and total macrofauna in salt marshes and unvegetated areas from 2013 to 2018. Red boxes mark El Niño periods.

The total macrofauna density, biomass and secondary production, likewise, were less variable over the years in the marshes than in the unvegetated areas, though some significant effects during El Niño were detected (Figure 3; PERMANOVA on Table S3). In the salt marshes, total density did not vary significantly along the years (mean of 180 inds./0.03 m²), while biomass was higher in 2015/2016 (mean of 0.08 g DW/0.03m²) than 2014 (0.02 g DW/0.03m²). The increase on biomass in 2015 and winter 2017 was related to peaks on the biomass of the opportunistic gastropod *Heleobia australis*. The average secondary production in the salt marshes ranged from 55.8 g C/m²/y^{-1} (in the summer 2014) to 164.2 g C/m²/y-^{1} (in summer 2015) and their variation along the years were dependent of the season. Macrofauna production were higher in the summer periods between 2015/2016 (mean of 134.1 g C/m²/y-^{1}) and lower in 2014 and 2017 (57.1 g C/m²/y-^{1}) (Figure 3; PERMANOVA on Table S3).

In unvegetated areas, the variations of total macrofauna density, biomass and production mirrored the numerically dominant species, and were significantly higher during periods of El Niño. Compared to neutral and La Niña, total density and biomass increased more than 300% (density from 122 to 491 inds./0.03 m²; biomass from 0.04 to 0.2 g DW/0.03 m²), while production increased from 107.5 to 336.4 g C/m²/y (an increase of 216%) (Figure 3, PERMANOVA on Table S3).

Structure, Biomass and Production of Benthic Assemblages

The MDS ordination of densities, biomass and secondary production of the macrofaunal assemblages (Figure 4) showed a clear distinction between salt marshes and unvegetated areas. The variability of densities, biomass and secondary production along the years were higher in unvegetated areas than in salt marshes (PERMDISP all $p<0.04$). In general, the ordinations showed a seriation along the years (more evident along the horizontal plan) reflecting a gradation of densities, biomass and secondary production, where 2013/2014 (neutral years) were plotted on the right of the graphics, in opposition to 2015/2016 (El Niño years) on the left and 2017-2018 (La Niña and neutral years) in between then (Figure 4). This was particularly evident for the unvegetated areas, though salt marshes macrofauna biomass (Figure 4 B) and production (Figure 4 C) also showed samples form

2015 on the left side of the plots, indicating a breakdown of the temporal seriation with an increase of biomass and production.

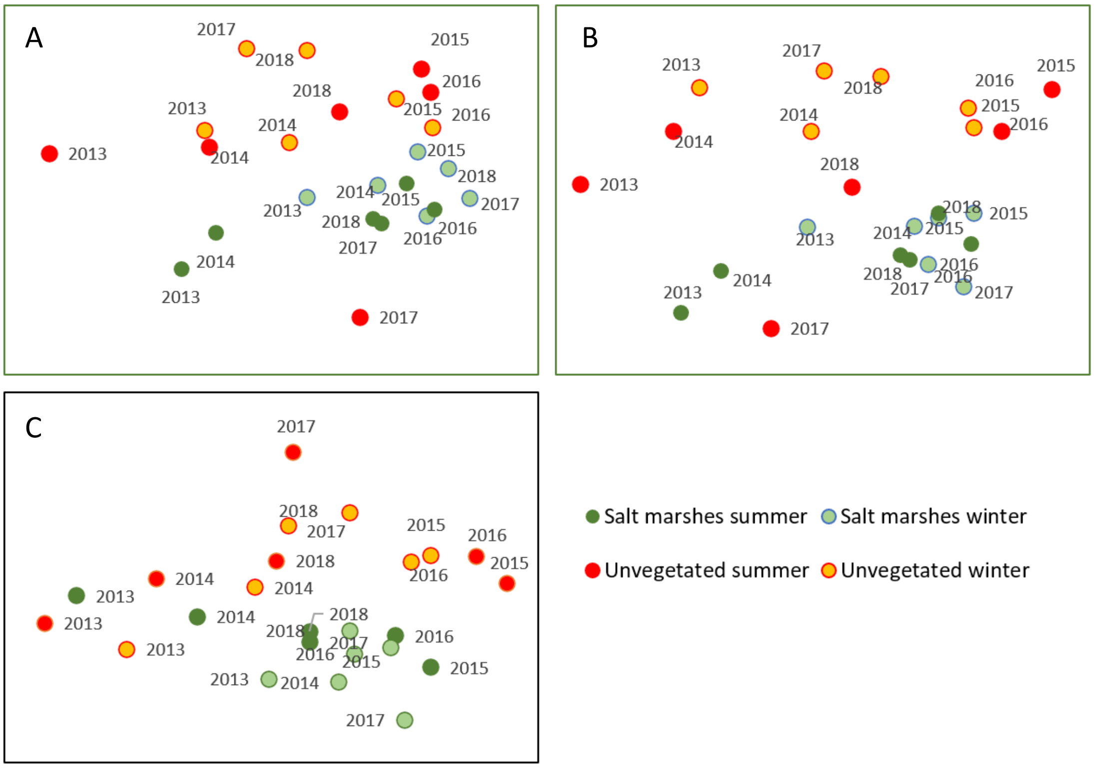

Figure 4. MDS ordination of (A) log-transformed benthic macrofauna density (stress 0.19), (B) fourth root transformed biomass (stress 0.17) and (C) log-transformed secondary production (stress 0.16) of the salt marshes and unvegetated areas from 2013 to 2018.

The results of PERMANOVA for the density of the macrobenthic assemblages indicated an interdependence between the habitats, years, and seasons (significant interaction habitat x year x period, Table S4). In general, the associations of unvegetated areas were more abundant, especially in the summers of El Niño years (for details see PERMANOVA on Table S4). The variation in the macrofauna biomass between habitats depended on years (in unvegetated areas 2015/2016 always higher; in salt marshes 2015/2016 higher than 2014 only). Benthic macrofauna secondary production were higher in unvegetated areas than in salt marshes, except in winter 2013 (significant interaction habitat x year), especially during in El Niño summers (significant interaction year x period; Table S4).

Interrelationships among Secondary Production, ENSO and environmental variables

While macrofauna secondary production of salt marshes did not correlate with sea surface temperature anomalies (ONI index), the unvegetated areas was positively correlated (p= 0.0002). The regression analysis showed that almost 70% of secondary production variability in unvegetated areas was explained by the variation in ONI index (R^2 = 0.6948). In the salt marshes this relationship explains only 20% of the production variability (Figure 5).

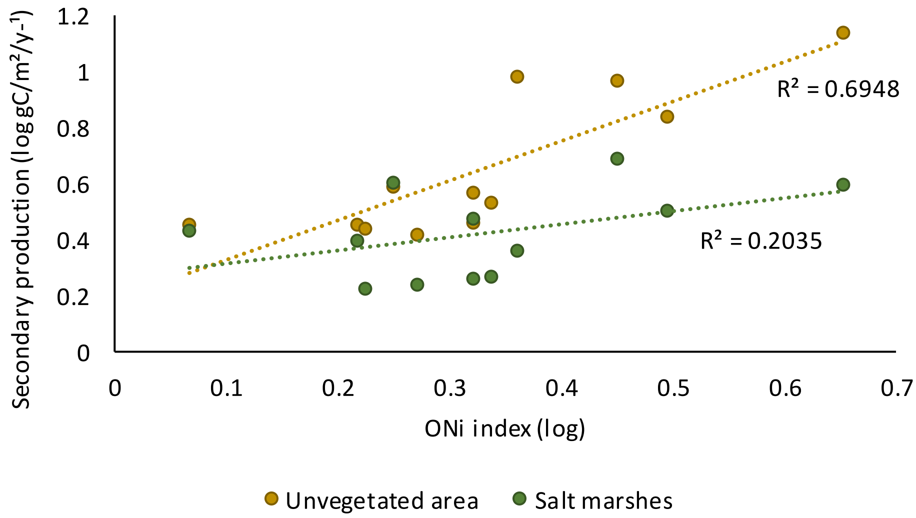

Figure 5. Regression of average secondary production by seasons of the six years shown functional relation to ONI.

The DistLM analysis detected significant correlation between macrofaunal secondary production and ONI index and precipitation, especially for the unvegetated areas in Laguna Estuarine System (Table 2). The marginal tests evaluating the contribution of individual variables to macrofaunal assemblages revealed that ONI has a 17.1% of contribution. Precipitation was the second variable in amount of contribution (11.1%).

Moreover, the sequential test that evaluated the effect of all predictors combined, showed significant correlation between production and ONI, precipitation and north surface stress. For the salt marshes, the DistLM analysis showed the higher correlation between production and ONI and precipitation, but the percentages of variance explained by these environmental variables were lesser than 6%.

Table 2. Results of the marginal test and sequential tests performed by DISTLM-forward analysis. "% var - percentage of variance explained in macrofauna secondary production; North surface stress – NSS; North wind component – NWC.

	Unvegetated				Salt Marsh		
Variable	Pseudo-F	p	% var	Variable	Pseudo-F	p	% var
ONI	14.475	0.0001	17.1	ONI	4.1208	0.0042	5.7
Precipitation	8.7817	0.0001	11.1	Precipitation	4.2708	0.0029	5.7
NWC	2.1097	0.0558	2.9	NWC	2.954	0.0185	4.1
NSS	1.9174	0.0751	2.7	Temperature	2.272	0.056	3.1
Temperature	1.8062	0.0925	2.5	NSS	1.9208	0.097	2.7
	Sequential tests				Sequential tests		
Precipitation	8.7817	0.0001	11.1	Precipitation	4.2708	0.0029	5.7
ONI	8.2999	0.0001	9.1	NSS	3.4742	0.0083	4.4
NSS	2.3827	0.0261	2.9	Temperature	2.1913	0.0623	2.9
Temperature	1.6101	0.1271	2.0	ONI	2.1621	0.067	2.7
NWC	1.2716	0.2433	1.6	NWC	0.68463	0.6315	0.9

DISCUSSION

Ocean-atmosphere interactions, such as those associated with ENSO, play a key role in shaping the climate and ecosystems (McPhaden and others 2006, Cai and others 2020). Wide variations in climatic conditions are accepted as an impact factor in biological communities, though the response of habitats is complex and uncertain (e.g., Dwire and others 2018). For example, the habitat complexity can affect the abundance, richness and composition of the assemblages, providing resources and mediating ecological interactions (Reis and others 2019), thus modulating the climatic influence on each habitat. In this study we tested whether the ENSO phases would affect benthic secondary production in different estuarine habitats, the salt marshes and unvegetated areas. Our results showed that estuarine unvegetated areas were strongly affected by the El Niño 2015/2016, when their benthic secondary production significantly increased. The higher secondary production was supported by greater abundance and/or biomass, which depended on the taxonomic group. The greater habitat complexity of the salt marshes, given by both below- and aboveground components, buffered the climatic variations and keeping benthic secondary production more stable.

The increase in secondary production in unvegetated areas was strongly related (~ 70%) to El Niño, as measured by the ONI index. Positive precipitation anomalies were associated with El Niño. Due to large amounts of rain during El Niño, the estuary receives large volumes of water from the drainage basin, which may reduce salinity and increase the flow of allochthonous organic and inorganic material (Panton and others 2020). This may be particularly important for the Laguna Estuarine System, a chocked microtidal lagoon with long residence time (Netto and others 2018). These two factors – salinity and organic material - individually or in combination, have strong impacts on growth and energy content and their effects can varied over time (Gomez and others 2019, Carrier-Belleau and others 2021).

Periods of abundant supply of nutrients can boost primary and secondary production (Kim and Montagna 2012). In addition, abnormally high temperatures can also favor populations dominated by juvenile organisms and young adults growing faster than normal, which leads to an increase in population production, as showed by Riascos and others 2017. In fact, in the studied unvegetated areas, the benthic secondary production more than quadrupled during the El Niño period. Our results contrast some observed in other marine ecosystems, especially those subjected to low nutrient inputs from continent and more dependent of processes such as upwelling. Under these conditions, it was observed a decrease in biomass and benthic production during El Niño conditions, possibly because the water temperature rises and the thermocline deepens, which limits the resurgence to the nutrient-poor surface layer and less energy can be assimilated by macrobenthic species (Thatje and others 2008, Yin and others 2021). Despite the increase in secondary production, abundance and biomass observed in the studied unvegetated areas during the El Niño event, there was an abrupt decrease in the following period, suggesting that long lasting or strong El Niños, such as the 2015/2016 event, may lead to environmental degradation, as also observed on a sandy beach in Uruguay (Jorge-Romero and others 2021).

In the *S. alterniflora* marshes of the Laguna Estuarine System, the benthic secondary production varied along the years but in a smaller scale than adjacent unvegetated areas and did not show significant relationships with the ENSO phases. Probably, vegetation enhances fauna survivorship, with vegetation providing greater stability to the benthic system (Tilman and Downing 1994) and increasing the habitat's resistance to climatic events (Isbell and others 2015, Liu and others 2021). In contrast, the unvegetated habitat ends up being more exposed to physical and biological stress during El Niño. The presence/absence of vegetation and sedimentary features associate to it, influences patterns in benthic communities, particularly for macroinvertebrates (Alsaffar and others 2020). Foundation species, such as *Spartina*, structure the habitat, resulting in a relatively high reduction in physical stress and provision of detritus and other food resources that affect biodiversity, population and community stability and ecosystem functioning (Bruno and Bertness 2001, Crotty and Bertness 2015). Plants stabilize the salt marshes by contributing to the deposition and retention of sediments and organic matter and providing resistance to compaction and erosion (Cahoon and others 2020). Increase in benthic secondary production of salt marshes during El Niño was also related precipitation, that could exert similar effect of increase of organic materials to low marshes, but in a less intense way due to the presence of vegetation. The relationship between the quality of organic matter and benthic secondary production has already been observed in other vegetated habitats such as mangroves (Wong and others 2011, Bissoli and Bernardino 2018).

As in the salt marshes, mangrove production also differs from areas without vegetation. In unvegetated areas with high production occur smaller organisms with faster reproduction, while in mangroves the organisms that incorporate more energy in biomass, such as annelids, dominate (Bissoli and Bernardino 2018). Ecosystems with larger and less productive animals, although more stable, are much more sensitive than more productive ecosystems and with a higher production/biomass ratio (P/B ratio). Greater P/B ratios, indicating whether populations accumulate energy in production or biomass, show greater resilience to stressors (Tumbiolo and Downing 1994, Bissoli and Bernardino 2018). In general, the salt marshes showed less biomass replacement (turnover; lower P/B) than unvegetated areas, therefore, despite having had greater stability in production over the years, once this habitat was affected it could have greater difficulty to recover.

Benthic secondary production of vegetated areas was also significant related to north wind surface stress. Shallowness and microtidal regime make wind and precipitation to exert key roles in the circulation and sediment movement of coastal lagoons (Kjerfve 1994). Locally, the dominant NE winds force lagoon water masses towards the southern margins (where there is the only lagoon inlet), decreasing salinity and increasing suspended materials from continental origin (Netto and others 2018). This process seems to be enhanced during periods of El Niño, further increasing the continental drainage towards the estuary. It is known that anomalous heat sources associated with El Niño perturb the Walker and Hadley circulations over South America and generate Rossby wave trains that affects subtropics and extratropics (Grimm 2003). During an El Niño events, the atmospheric pattern culminates in negative and positive pressure anomalies over the eastern mid- latitudes and eastern subtropical South America, respectively. These atmospheric-circulation anomalies favour north-westerly advection of moist warm air into south-east South America and an enhanced South American Low-Level Jet (Viale and others 2018) (i.e., locally winds from north quadrant).

The macrofauna of the salt marshes and unvegetated areas was numerically dominated by the polychaete *L. acuta* and by the tanaidaceous *M. schubarti*. The increase in secondary production in the benthic community observed in the El Niño period was strongly influenced by increases in the biomass of *L. acuta* and in the biomass and density of *M. schubarti*. Moreover, the variation observed on biomass in the salt marshes reflected the biomass of the *H. australis*, which had peaks in different ENSO phases; this mollusk generally presents an opportunistic behavior with oscillation in population descriptors and feeding habits (Magalhaes and others 2014) according to conditions and resources (Figueiredo-Barros and others 2006, Echeverría and others 2010). As for the two dominate species, *Monokalliapseudes schubarti* is an endemic estuarine species of South American that can reach high population densities (Drumm and Heard 2011, Freitas-Junior and others 2013). This species was practically absent in unvegetated areas during the periods of neutrality or La Niña, in the years 2013/2014 and 2017/2018, but in summer of 2015 reached values of almost 60,000 inds/m^2. During the El Niño years, *M. schubarti* was responsible for up to 80% of the density and 50% of the total fauna biomass in unvegetated areas. These marked interannual population fluctuations, clearly related to the El Niño periods, had already been observed in other estuaries in southern Brazil (e.g., Colling and others 2010, Netto and other 2018). The increase in density in years dominated by El Niño is possibly due to the more intense pattern of reproduction of the species and recruitment in periods of high temperature, decreasing in autumn and winter (Bemvenuti 1992, Freitas-Junior and others 2013). On the other hand, the populations of *M. schubarti* in the salt marshes were stable over time.

The Nereididae polychaete *L. acuta*, a widely spread and abundant species in South American Atlantic estuaries (Pamplin and others 2007, Netto and others 2018), also showed a significant increase in its biomass and secondary production in unvegetated areas during El Niño. However, the species did not show an increase in abundance throughout the study. The effects of El Niño on *L. acuta* in unvegetated areas seem to be related to an increase in body size and biomass. The increase of *L. acuta* biomass during El Niño could also be related to a drop in in the environmental quality of the estuary as suggested by Pagliosa and Barbosa (2006). Different responses according to species and habitats, as we shown in this study, reflect the complexity of the climate influence on biological communities. To understand the effects of climatic phenomena it is necessary to consider multiple stressors and their interactions and to consider multiple responses (Carrier-Belleau and others 2021). Thus future studies need to incorporate more both natural and anthropic factor, to assess their role on the responses of different species, so we can broaden our understanding climate change in coastal areas.

Our findings reinforce that large scale climatic oscillations can directly influence estuarine ecology. However, the results also showed that the effects are depend on the structural complexity of the estuarine habitat. While the salt marshes buffered the effects of El Niño, benthic associations of unvegetated were strongly affected, increasing their secondary production. Frequency of El Niño events is projected to increase with climate change (Peng and others 2019). Hence, regions with a robust El Niño signal in the current climate, such as South Brazil, are expected to experience an increase in ENSO-driven extreme events, as the impact superimposes on the mean state change (Power and Delage 2018). The capacity of salt marshes to buffer effects of El Niño emphasizes the need to protect this ecosystem and the services they provided, as salt marshes can be fundamental in mitigating impacts in the estuaries. The degradation of these habitats can decrease the resilience of the ecosystem (Hautier and others 2015), with consequences still uncertain for the food web.

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SUPPLEMENTARY MATERIAL

Table S1. Results of PERMANOVA tests for *Monokalliapseudes schubarti* density, biomass and secondary production.

	Source	df	SS	MS	Pseudo-F	P(MC)
Density	Ye	5	9.46E+05	1.89E+05	5.2283	**0.0002**
	Se	1	54990	54990	1.5195	0.2187
	Ha	1	1.66E+05	1.66E+05	4.5848	**0.0324**
	YexSe	5	4.10E+05	81946	2.2644	0.0501
	YexHa	5	8.40E+05	1.68E+05	4.6442	**0.0007**
	SexHa	1	1.86E+05	1.86E+05	5.1489	**0.0235**
	YexSexHa	5	2.52E+05	50313	1.3903	0.2328
	Res	120	4.34E+06	36189		
	Total	143	7.20E+06			

Pair-wise test of density for Year x Habitat and Season x Habitat interactions

	Groups	t	P(MC)
Unvegetated	2013, 2014	2.0607	0.0557
	2013, 2015	1.7873	0.0901
	2013, 2016	8.1756	**0.0001**
	2013, 2017	0.50355	0.6209
	2013, 2018	1.83	0.0846
	2014, 2015	1.7293	0.0979
	2014, 2016	7.8939	**0.0001**
	2014, 2017	1.9093	0.0719
	2014, 2018	2.4159	**0.0256**
	2015, 2016	0.2134	0.8335
	2015, 2017	1.7835	0.0896
	2015, 2018	1.7963	0.0896
	2016, 2017	8.1593	**0.0001**
	2016, 2018	8.2137	**0.0001**
	2017, 2018	2.1174	**0.0428**
Salt Marsh	2013, 2014	0.20516	0.8363
	2013, 2015	0.8316	0.4146
	2013, 2016	0.47353	0.6389
	2013, 2017	0.48521	0.6299
	2013, 2018	0.45884	0.6425
	2014, 2015	1.122	0.2724
	2014, 2016	0.35388	0.7391
	2014, 2017	0.36874	0.7111
	2014, 2018	0.75597	0.4573
	2015, 2016	1.3918	0.1825
	2015, 2017	1.3446	0.1874
	2015, 2018	0.43132	0.6664
	2016, 2017	8.46E-02	0.9374
	2016, 2018	1.0724	0.2991

	2017, 2018	1.0247	0.3195
Summer	Unvegetated, Salt Marsh	2.2964	**0.0234**
Winter	Unvegetated, Salt Marsh	0.22913	0.8167

	Source	df	SS	MS	Pseudo-F	P(MC)
Biomass	Ye	5	3.88E-02	7.75E-03	8.417	**0.0001**
	Se	1	1.64E-04	1.64E-04	0.17862	0.6739
	Ha	1	4.56E-03	4.56E-03	4.9467	**0.0279**
	YexSe	5	4.99E-03	9.97E-04	1.0828	0.3811
	YexHa	5	3.66E-02	7.32E-03	7.9482	**0.0001**
	SexHa	1	2.92E-03	2.92E-03	3.1755	0.0755
	YexSexHa	5	5.93E-03	1.19E-03	1.288	0.2794
	Res	120	0.1105	9.21E-04		
	Total	143	0.20441			

Pair-wise test of biomass for Year x Habitat interactions

	Years	t	P(MC)
Unvegetated	2013, 2014	0.87792	0.3941
	2013, 2015	2.1358	**0.0479**
	2013, 2016	11.375	**0.0001**
	2013, 2017	1.2253	0.2399
	2013, 2018	1.9802	0.0601
	2014, 2015	2.1059	**0.0489**
	2014, 2016	11.242	**0.0001**
	2014, 2017	2.0653	**0.0499**
	2014, 2018	2.695	**0.0133**
	2015, 2016	0.84359	0.4045
	2015, 2017	2.1643	**0.0438**
	2015, 2018	2.1786	**0.0424**
	2016, 2017	11.511	**0.0001**
	2016, 2018	11.571	**0.0001**
	2017, 2018	1.4612	0.1643
Salt Marsh	2013, 2014	0.56602	0.5724
	2013, 2015	0.26949	0.7883
	2013, 2016	0.4382	0.6718
	2013, 2017	0.78001	0.4579
	2013, 2018	0.29089	0.7771
	2014, 2015	1.0069	0.3228
	2014, 2016	0.22071	0.8216
	2014, 2017	0.39443	0.7032
	2014, 2018	1.3729	0.1878
	2015, 2016	0.85815	0.4041
	2015, 2017	1.2315	0.2309
	2015, 2018	2.48E-02	0.9835
	2016, 2017	5.91E-01	0.5587
	2016, 2018	1.1535	0.2631
	2017, 2018	1.6434	0.1193

	Source	df	SS	MS	Pseudo-F	P(MC)
Secondary production	Ye	5	153.3	30.661	14.087	**0.0001**
	Se	1	6.0707	6.0707	2.7891	0.0982
	Ha	1	12.093	12.093	5.5561	**0.0211**
	YexSe	5	36.344	7.2689	3.3396	**0.0076**
	YexHa	5	95.854	19.171	8.8078	**0.0001**
	SexHa	1	7.8042	7.8042	3.5856	0.0621
	YexSexHa	5	3.2432	0.64865	0.29802	0.9128
	Res	120	261.19	2.1766		
	Total	143	575.9			

Pair-wise test of secondary production for Year x Habitat and Year x Season interactions

	Groups	T	P(MC)
Unvegetated	2013, 2014	1.0988	0.2755
	2013, 2015	2.3183	**0.0298**
	2013, 2016	13.973	**0.0001**
	2013, 2017	0.41607	0.6849
	2013, 2018	1.6794	0.1084
	2014, 2015	2.2305	**0.0404**
	2014, 2016	13.42	**0.0001**
	2014, 2017	1.4627	0.1583
	2014, 2018	2.3401	**0.0281**
	2015, 2016	1.4238	0.1682
	2015, 2017	2.3403	**0.0292**
	2015, 2018	2.3934	**0.0248**
	2016, 2017	14.119	**0.0001**
	2016, 2018	14.38	**0.0001**
	2017, 2018	1.5057	0.1441
Salt Marsh	2013, 2014	5.88E-02	0.9557
	2013, 2015	1.4359	0.1697
	2013, 2016	1.4302	0.17
	2013, 2017	0.1612	0.8695
	2013, 2018	1.5799	0.131
	2014, 2015	1.5329	0.1399
	2014, 2016	1.6295	0.1191
	2014, 2017	0.14192	0.8914
	2014, 2018	1.8946	0.0676
	2015, 2016	0.31784	0.7493
	2015, 2017	1.3029	0.2081
	2015, 2018	0.35408	0.725
	2016, 2017	1.25E+00	0.223
	2016, 2018	2.31E-02	0.9826
	2017, 2018	1.3687	0.1859
2013	Summer, Winter	1.6698	0.1068
2014	Summer, Winter	2.3812	**0.0261**

2015	Summer, Winter	1.1336	0.2736
2016	Summer, Winter	4.5169	**0.0003**
2017	Summer, Winter	0.1657	0.8677
2018	Summer, Winter	1.2901	0.2043

Table S2. Results of PERMANOVA tests for *Laeonereis acuta* density, biomass and secondary production.

	Source	df	SS	MS	Pseudo-F	P(MC)
Density	Year (Ye)	5	23313	4662.7	3.2719	**0.0092**
	Season (Se)	1	1302	1302	0.91365	0.3326
	Habitat (Ha)	1	45121	45121	31.662	**0.0001**
	YexSe	5	11848	2369.6	1.6628	0.1476
	YexHa	5	13349	2669.8	1.8735	0.1001
	SexHa	1	50.174	50.174	3.52E-02	0.8616
	YexSexHa	5	6992.5	1398.5	0.98136	0.4267
	Residue	120	1.71E+05	1425.1		
	Total	143	2.73E+05			

Pair-wise test of density for year interactions

Years	t	P(MC)
2013, 2014	0.50683	0.6182
2013, 2015	0.53859	0.593
2013, 2016	2.95E-02	0.9757
2013, 2017	3.5717	**0.0008**
2013, 2018	1.05	0.3035
2014, 2015	0.11965	0.9051
2014, 2016	0.56772	0.5779
2014, 2017	2.82E+00	**0.0074**
2014, 2018	1.26E+00	0.2151
2015, 2016	0.66267	0.5158
2015, 2017	4.5157	**0.0002**
2015, 2018	1.7703	0.0852
2016, 2017	4.9741	**0.0002**
2016, 2018	1.3151	0.1902
2017, 2018	4.1427	**0.0002**

	Source	df	SS	MS	Pseudo-F	P(MC)
Biomass	Ye	5	1.51E-02	3.02E-03	4.2504	**0.0016**
	Se	1.00E+00	1.47E-03	1.47E-03	2.0688	0.1534
	Ha	1	1.04E-02	1.04E-02	14.673	**0.0005**
	YexSe	5	2.97E-03	5.94E-04	0.83575	0.5169
	YexHa	5	1.37E-02	2.74E-03	3.8602	**0.0036**
	SexHa	1	3.77E-03	3.77E-03	5.3002	**0.0229**
	YexSexHa	5.00E+00	2.00E-03	4.00E-04	0.56281	0.7276
	Res	1.20E+02	8.53E-02	7.11E-04		
	Total	143	0.13478			

Pair-wise test of biomass for Year x Habitat and Season x Habitat interactions

	Groups	t	P(MC)
Unvegetated	2013, 2014	1.3366	0.1917
	2013, 2015	1.6206	0.1189
	2013, 2016	3.0806	**0.0054**

	2013, 2017	1.59E+00	0.1265
	2013, 2018	2.3645	**0.0262**
	2014, 2015	0.84704	0.4096
	2014, 2016	2.3367	**0.0296**
	2014, 2017	2.3511	**0.024**
	2014, 2018	8.87E-01	0.3874
	2015, 2016	1.31E+00	0.208
	2015, 2017	2.1029	**0.0491**
	2015, 2018	0.27773	0.7809
	2016, 2017	3.5126	**0.0022**
	2016, 2018	1.8232	0.0856
	2017, 2018	3.3953	**0.0037**
Salt Marsh	2013, 2014	1.7625	0.0905
	2013, 2015	1.3013	0.2085
	2013, 2016	1.51E+00	0.1466
	2013, 2017	2.8594	**0.009**
	2013, 2018	0.97785	0.3388
	2014, 2015	0.68356	0.5028
	2014, 2016	0.65032	0.5161
	2014, 2017	9.72E-01	0.3399
	2014, 2018	6.06E-01	0.5581
	2015, 2016	0.13735	0.8894
	2015, 2017	2.0213	0.0573
	2015, 2018	8.96E-02	0.9265
	2016, 2017	2.3564	**0.0304**
	2016, 2018	0.18896	0.8477
	2013, 2014	1.7625	0.0905
Summer	Unvegetated, Salt Marsh	1.1365	0.2601
Winter	Unvegetated, Salt Marsh	4.1427	**0.0001**

	Source	**df**	**SS**	**MS**	**Pseudo-F**	**P(MC)**
Secondary production	Ye	5	79.44	15.888	5.3184	**0.0001**
	Se	1	0.13079	1.31E-01	4.38E-02	0.8406
	Ha	1.00E+00	42.623	4.26E+01	14.268	**0.0005**
	YexSe	5	13.162	2.63E+00	0.88117	0.4931
	YexHa	5	63.306	1.27E+01	4.2382	**0.0017**
	SexHa	1	11.492	1.15E+01	3.847	0.0507
	YexSexHa	5	12.043	2.41E+00	0.80628	0.5396
	Res	1.20E+02	358.49	2.99E+00		
	Total	1.43E+02	580.68			

Pair-wise test of secondary production for Year x Habitat interactions

	Years	**t**	**P(MC)**
Unvegetated	2013, 2014	1.2619	0.2231
	2013, 2015	1.796	0.0862
	2013, 2016	3.2824	**0.0038**
	2013, 2017	1.3651	0.1774

	2013, 2018	2.3809	**0.0252**
	2014, 2015	0.97484	0.3409
	2014, 2016	2.6074	**0.0201**
	2014, 2017	2.2541	**0.034**
	2014, 2018	1.0065	0.3263
	2015, 2016	1.6059	0.125
	2015, 2017	2.3315	**0.029**
	2015, 2018	0.26853	0.7893
	2016, 2017	3.6913	**0.0012**
	2016, 2018	2.0399	0.052
	2017, 2018	3.3783	**0.0035**
Salt Marsh	2013, 2014	1.6349	0.1207
	2013, 2015	0.91118	0.3758
	2013, 2016	1.0905	0.2907
	2013, 2017	2.6378	**0.0167**
	2013, 2018	0.8425	0.4064
	2014, 2015	0.89966	0.3821
	2014, 2016	0.9596	0.3508
	2014, 2017	0.84543	0.4091
	2014, 2018	0.59855	0.5601
	2015, 2016	8.5605E-2	0.9309
	2015, 2017	2.0309	0.0558
	2015, 2018	0.11391	0.9095
	2016, 2017	2.4494	**0.0236**
	2016, 2018	6.464E-2	0.954
	2017, 2018	1.3441	0.1944

Table S3. Results of PERMANOVA tests for total density, biomass and secondary production.

	Source	df	SS	MS	Pseudo-F	P(MC)
Density	Ye	5	1.71E+06	3.42E+05	6.1859	**0.0001**
	Se	1	41480	41480	0.75023	0.3911
	Ha	1	6.24E+05	6.24E+05	11.288	**0.0008**
	YexSe	5	7.89E+05	1.58E+05	2.853	**0.0151**
	YexHa	5	9.42E+05	1.88E+05	3.4078	**0.0069**
	SexHa	1	1.91E+05	1.91E+05	3.4619	0.0617
	YexSexHa	5	3.83E+05	76636	1.3861	0.2347
	Res	120	6.63E+06	55290		
	Total	143	1.13E+07			

Pair-wise test of density for Year x Habitat and Year x Season interactions

	Groups	t	P(MC)
Unvegetated	2013, 2014	0.28155	0.7762
	2013, 2015	1.6117	0.1179
	2013, 2016	4.1327	**0.0005**
	2013, 2017	3.8621	**0.0011**
	2013, 2018	2.7727	**0.0119**
	2014, 2015	1.471	0.1601
	2014, 2016	3.1436	**0.0044**
	2014, 2017	3.1647	**0.0049**
	2014, 2018	2.3928	**0.0236**
	2015, 2016	0.30981	0.7668
	2015, 2017	2.551	**0.0191**
	2015, 2018	2.3138	**0.031**
	2016, 2017	9.8657	**0.0001**
	2016, 2018	8.5595	**0.0001**
	2017, 2018	3.7129	**0.0013**
Salt Marsh	2013, 2014	2.48E-01	0.8011
	2013, 2015	1.4574	0.1624
	2013, 2016	1.77E-02	0.9849
	2013, 2017	0.65798	0.5136
	2013, 2018	0.1334	0.8887
	2014, 2015	1.2359	0.2277
	2014, 2016	0.25411	0.8022
	2014, 2017	0.81768	0.4162
	2014, 2018	0.3489	0.7328
	2015, 2016	1.4431	0.1633
	2015, 2017	1.8201	0.0869
	2015, 2018	1.4911	0.1562
	2016, 2017	6.08E-01	0.5446
	2016, 2018	1.11E-01	0.9118
	2017, 2018	1.3687	0.1859
Summer	2013, 2014	0.38295	0.7024
	2013, 2015	2.0625	0.0537

	2013, 2016	3.7521	**0.0011**
	2013, 2017	1.333	0.1979
	2013, 2018	0.79936	0.4332
	2014, 2015	1.9896	0.0635
	2014, 2016	3.7459	**0.0014**
	2014, 2017	2.1578	**0.0421**
	2014, 2018	1.4804	0.1608
	2015, 2016	1.0026	0.3283
	2015, 2017	2.3467	**0.0292**
	2015, 2018	2.2447	**0.0362**
	2016, 2017	5.6028	**0.0001**
	2016, 2018	5.10E+00	**0.0003**
	2017, 2018	0.81949	0.4216
Winter	2013, 2014	0.19425	0.849
	2013, 2015	0.11008	0.9162
	2013, 2016	1.0036	0.3219
	2013, 2017	3.4514	**0.0035**
	2013, 2018	2.2548	**0.0387**
	2014, 2015	0.27517	0.7858
	2014, 2016	0.45462	0.6468
	2014, 2017	2.3939	**0.0276**
	2014, 2018	1.6923	0.1091
	2015, 2016	1.1933	0.2515
	2015, 2017	3.5576	**0.0021**
	2015, 2018	2.263	**0.0352**
	2016, 2017	5.7896	**0.0001**
	2016, 2018	4.0033	**0.0008**
	2017, 2018	1.329	0.1988

	Source	df	SS	MS	Pseudo-F	P(MC)
Biomassa	Ye	5	0.19953	3.99E-02	6.4493	**0.0001**
	Se	1	6.99E-03	6.99E-03	1.1297	0.2815
	Ha	1	1.20E-02	1.20E-02	1.9409	0.1607
	YexSe	5	3.35E-02	6.69E-03	1.0812	0.3748
	YexHa	5	0.10283	2.06E-02	3.3236	**0.008**
	SexHa	1	2.64E-03	2.64E-03	0.42597	0.5193
	YexSexHa	5	7.85E-03	1.57E-03	0.25362	0.9397
	Res	120	0.74254	6.19E-03		
	Total	143	1.1078			

Pair-wise test of biomass for Year x Habitat interactions

	Years	t	P(MC)
Unvegetated	2013, 2014	4.25E-02	0.9674
	2013, 2015	2.215	**0.0396**
	2013, 2016	5.4173	**0.0002**
	2013, 2017	2.1302	0.0462
	2013, 2018	0.33456	0.7343
	2014, 2015	2.2459	**0.0363**

	2014, 2016	5.5954	**0.0001**
	2014, 2017	2.3418	**0.0307**
	2014, 2018	0.38745	0.707
	2015, 2016	0.69825	0.4886
	2015, 2017	2.8464	**0.0102**
	2015, 2018	2.0302	0.0544
	2016, 2017	6.7166	**0.0001**
	2016, 2018	4.7722	**0.0003**
	2017, 2018	2.0061	0.0578
Salt Marsh	2013, 2014	1.8045	0.0872
	2013, 2015	1.4281	0.175
	2013, 2016	0.34826	0.7321
	2013, 2017	0.45104	0.6603
	2013, 2018	0.89568	0.3658
	2014, 2015	2.0924	**0.0499**
	2014, 2016	2.1976	**0.0415**
	2014, 2017	1.3016	0.2067
	2014, 2018	1.0824	0.2873
	2015, 2016	1.5988	0.1209
	2015, 2017	0.91586	0.3708
	2015, 2018	1.8006	0.0877
	2016, 2017	0.64505	0.5316
	2016, 2018	0.75447	0.4751
	2017, 2018	0.91974	0.3668

	Source	df	SS	MS	Pseudo-F	P(MC)
Secondary production	Ye	5	542.57	108.51	10.613	**0.0001**
	Se	1	24.617	24.617	2.4075	0.1163
	Ha	1	236.12	236.12	23.093	**0.0002**
	YexSe	5	61.914	12.383	1.211	0.3212
	YexHa	5	316.38	63.275	6.1883	**0.0002**
	SexHa	1	0.40486	0.40486	3.96E-02	0.8434
	YexSexHa	5	10.192	2.0384	0.19935	0.962
	Res	120	1227	10.225		
	Total	143	2419.2			

Pair-wise test of secondary production for Year x Habitat interactions

	Years	t	P(MC)
Unvegetated	2013, 2014	2.87E-01	0.7789
	2013, 2015	2.1076	0.0503
	2013, 2016	5.2211	**0.0001**
	2013, 2017	0.67372	0.514
	2013, 2018	8.33E-02	0.9379
	2014, 2015	2.2971	**0.0322**
	2014, 2016	5.7428	**0.0001**
	2014, 2017	0.48244	0.6382
	2014, 2018	0.19685	0.8437
	2015, 2016	1.4326	0.169

	2015, 2017	2.4658	**0.0215**
	2015, 2018	2.1568	**0.0469**
	2016, 2017	6.0313	**0.0001**
	2016, 2018	5.3246	**0.0002**
	2017, 2018	0.59327	0.5602
Salt Marsh	2013, 2014	1.5868	0.127
	2013, 2015	0.73726	0.4709
	2013, 2016	0.12356	0.8995
	2013, 2017	1.4168	0.1753
	2013, 2018	0.35847	0.7249
	2014, 2015	3.0352	**0.0071**
	2014, 2016	2.5205	**0.0188**
	2014, 2017	3.77E-02	0.9705
	2014, 2018	1.4564	0.1604
	2015, 2016	1.1666	0.2523
	2015, 2017	2.6083	**0.017**
	2015, 2018	1.2686	0.219
	2016, 2017	1.9338	0.0677
	2016, 2018	0.34591	0.7317
	2017, 2018	1.2328	0.2274

Table S4. Results of the PERMANOVA tests for differences between the years, habitats and seasons on density, biomass and secondary production of benthic associations (Data log-transformed).

	Source	df	SS	MS	Pseudo-F	P(MC)
Density	Year (Ye)	5	68898	13780	11.763	**0.0001**
	Season (Se)	1	5835.2	5835.2	4.9812	**0.0002**
	Habitat (Ha)	1	18001	18001	15.367	**0.0001**
	Ye x Se	5	22762	4552.4	3.8862	**0.0001**
	Ye x Ha	5	21288	4257.5	3.6344	**0.0001**
	Se x Ha	1	1173.3	1173.3	1.0016	0.4254
	Ye x Se x Ha	5	10786	2157.2	1.8415	**0.0038**
	Residue	120	140570	1171.4		
	Total	143	289320			

Pair-wise test of density for Year x Habitat x Season interactions

		Years	t	P(MC)
Unvegetated	Summer	2013, 2014	1.3036	0.1775
		2013, 2015	4.9977	**0.0001**
		2013, 2016	5.6271	**0.0001**
		2013, 2017	3.212	**0.0002**
		2013, 2018	2.6075	**0.002**
		2014, 2015	3.5132	**0.0005**
		2014, 2016	4.0648	**0.0001**
		2014, 2017	3.0409	**0.0004**
		2014, 2018	2.3622	**0.0032**
		2015, 2016	2.5694	**0.0019**
		2015, 2017	3.2646	**0.0004**
		2015, 2018	2.3136	**0.0083**
		2016, 2017	3.1754	**0.0003**
		2016, 2018	2.3989	**0.0082**
		2017, 2018	1.3759	0.1397
Unvegetated	Winter	2013, 2014	1.7958	**0.0228**
		2013, 2015	3.8559	**0.0002**
		2013, 2016	4.3273	**0.0001**
		2013, 2017	2.9111	**0.0008**
		2013, 2018	3.666	**0.0001**
		2014, 2015	1.2295	0.2026
		2014, 2016	1.9527	**0.0069**
		2014, 2017	1.8904	**0.0078**
		2014, 2018	1.87	**0.0228**
		2015, 2016	2.4766	**0.0033**
		2015, 2017	2.6404	**0.001**
		2015, 2018	2.7035	**0.0015**
		2016, 2017	3.172	**0.0004**
		2016, 2018	3.7302	**0.0002**
		2017, 2018	1.7031	**0.042**

Salt Marsh	Summer	2013, 2014	0.87395	0.5316
		2013, 2015	2.6656	**0.0015**
		2013, 2016	2.7631	**0.0009**
		2013, 2017	2.2231	**0.0063**
		2013, 2018	2.3993	**0.003**
		2014, 2015	2.4875	**0.0022**
		2014, 2016	2.6352	**0.0012**
		2014, 2017	2.2292	**0.004**
		2014, 2018	2.4292	**0.0032**
		2015, 2016	0.64397	0.7965
		2015, 2017	1.5489	0.0712
		2015, 2018	1.6309	**0.0469**
		2016, 2017	1.4525	0.0966
		2016, 2018	1.4106	0.1083
		2017, 2018	0.91714	0.4654
Salt Marsh	Winter	2013, 2014	1.6363	0.0633
		2013, 2015	2.2579	**0.0069**
		2013, 2016	2.203	**0.007**
		2013, 2017	1.7419	**0.0227**
		2013, 2018	2.316	**0.0035**
		2014, 2015	1.7993	**0.0298**
		2014, 2016	1.9643	**0.0163**
		2014, 2017	1.3078	0.1606
		2014, 2018	1.5315	0.067
		2015, 2016	1.1339	0.2817
		2015, 2017	1.5107	0.0728
		2015, 2018	1.7322	**0.0497**
		2016, 2017	1.3168	0.1503
		2016, 2018	1.6218	0.0617
		2017, 2018	1.582	0.0613

	Source	df	SS	MS	Pseudo-F	P(MC)
Biomass	Year (Ye)	5	403.12	80.624	6.3034	**0.0001**
	Season (Se)	1	9.1628	9.1628	0.71638	0.5245
	Habitat (Ha)	1	151.87	151.87	11.874	**0.0001**
	Ye x Se	5	82.337	16.467	1.2875	0.2087
	Ye x Ha	5	345.47	69.094	5.402	**0.0001**
	Se x Ha	1	38.49	38.49	3.0093	**0.0392**
	Ye x Se x Ha	5	87.633	17.527	1.3703	0.1598
	Residue	120	1534.9	12.79		
	Total	143	2652.9			

Pair-wise test of biomass for Year x Habitat and Habitat x Season interactions

	Groups	t	P(MC)
Unvegetated	2013, 2014	1.6956	**0.0435**
	2013, 2015	2.5802	**0.0048**
	2013, 2016	5.7129	**0.0001**

	2013, 2017	1.8763	**0.0249**
	2013, 2018	2.4803	**0.0037**
	2014, 2015	2.018	**0.0246**
	2014, 2016	5.0296	**0.0002**
	2014, 2017	1.6182	0.0711
	2014, 2018	1.4255	0.1289
	2015, 2016	1.8857	**0.0258**
	2015, 2017	2.3458	**0.0099**
	2015, 2018	2.1153	**0.0192**
	2016, 2017	5.8049	**0.0001**
	2016, 2018	4.6601	**0.0001**
	2017, 2018	2.3077	**0.0058**
Salt Marsh	2013, 2014	1.2402	0.2059
	2013, 2015	1.9832	**0.0351**
	2013, 2016	2.0957	**0.0132**
	2013, 2017	1.9813	**0.0403**
	2013, 2018	1.3165	0.178
	2014, 2015	1.7473	0.0801
	2014, 2016	2.1462	**0.0142**
	2014, 2017	1.5678	0.1229
	2014, 2018	1.2348	0.2325
	2015, 2016	1.1088	0.2662
	2015, 2017	0.72723	0.5035
	2015, 2018	1.7769	0.073
	2016, 2017	1.2841	0.1982
	2016, 2018	2.0342	**0.0198**
	2017, 2018	1.863	0.0651
Summer	Unvegetated, Salt Marsh	1.7961	**0.0303**
Winter	Unvegetated, Salt Marsh	3.5183	**0.0001**

	Source	**df**	**SS**	**MS**	**Pseudo-F**	**P(MC)**
Secondary Production	Year (Ye)	5	33355	6671.1	8.8118	**0.0001**
	Season (Se)	1	1535.2	1535.2	2.0278	0.0623
	Habitat (Ha)	1	8171.6	8171.6	10.794	**0.0001**
	Ye x Se	5	9016.8	1803.4	2.3821	**0.0005**
	Ye x Ha	5	12613	2522.5	3.332	**0.0001**
	Se x Ha	1	2653.3	2653.3	3.5047	**0.0056**
	Ye x Se x Ha	5	4964.3	992.86	1.3115	0.1351
	Residue	120	90847	757.06		
	Total	143	163160			

Pair-wise test of secondary production for Year x Habitat and Year x Season interactions

	Groups	**t**	**P(MC)**
Unvegetated	2013, 2014	1.2215	0.1933
	2013, 2015	3.5352	**0.0001**
	2013, 2016	5.1589	**0.0001**
	2013, 2017	2.0388	**0.0014**

	2013, 2018	2.5527	**0.0005**
	2014, 2015	2.6747	**0.0001**
	2014, 2016	4.3854	**0.0001**
	2014, 2017	1.6573	**0.017**
	2014, 2018	1.8945	**0.0143**
	2015, 2016	2.4347	**0.0009**
	2015, 2017	2.6538	**0.0002**
	2015, 2018	3.0472	**0.0001**
	2016, 2017	4.237	**0.0001**
	2016, 2018	4.7035	**0.0001**
	2017, 2018	1.6978	**0.0265**
Salt Marsh	2013, 2014	1.5349	0.0631
	2013, 2015	2.1514	**0.0025**
	2013, 2016	2.2899	**0.0013**
	2013, 2017	1.8732	**0.015**
	2013, 2018	2.0679	**0.0072**
	2014, 2015	2.0434	**0.0036**
	2014, 2016	2.2055	**0.0013**
	2014, 2017	0.99101	0.4066
	2014, 2018	1.4665	0.0817
	2015, 2016	0.84788	0.5552
	2015, 2017	1.814	**0.0268**
	2015, 2018	1.6034	0.0583
	2016, 2017	2.0756	**0.0096**
	2016, 2018	1.4095	0.1172
	2017, 2018	1.6137	0.07
2013	Summer, Winter	1.6305	**0.0283**
2014	Summer, Winter	1.968	**0.0059**
2015	Summer, Winter	1.2299	0.1801
2016	Summer, Winter	1.7076	**0.0476**
2017	Summer, Winter	1.2314	0.1714
2018	Summer, Winter	1.451	0.1064
Summer	Unvegetated, Salt Marsh	2.0145	**0.003**
Winter	Unvegetated, Salt Marsh	3.3057	**0.0001**