UNIVERSIDADE FEDERAL DO ABC

BACHARELADO EM CIÊNCIAS BIOLÓGICAS

Marcos Vinícius Gonçalves da Silva

SEASONALITIES AND TRENDS IN A SUBTROPICAL ROCKY SHORE MIDLITTORAL BENTHIC COMMUNITY:

How fragile are these systems to change?

SAZONALIDADES E TENDÊNCIAS DE UMA COMUNIDADE BENTÔNICA DO MEDIOLITORAL EM UM COSTÃO ROCHOSO SUBTROPICAL:

O quão sensíveis às mudanças são estes ecossistemas?

Santo André - SP

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Trabalho de Conclusão de Curso apresentado ao curso de graduação em Ciências Biológicas da Universidade Federal do ABC como requisito parcial para obtenção do título de Bacharel em Ciências Biológicas.

Orientadora: Profª Drª Natalia Pirani Ghilardi-Lopes.

Santo André - SP

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ATA DE DEFESA DO TRABALHO DE CONCLUSÃO DE CURSO

No dia **01 de dezembro às 08 horas**, em uma sessão remota de defesa do Trabalho de Conclusão de Curso (TCC), a Banca Examinadora para avaliação do TCC em Ciências Biológicas da UFABC foi instalada pelo Professora **Dra. Natalia Pirani Ghilardi-Lopes**. Estiveram presentes professores, alunos e visitantes. A banca examinadora foi constituída pelos professores **Dr. Gustavo Muniz Dias** (membro Titular), **Dr. João Ricardo Sato** (membro Titular) e o **Dra. Natalia Pirani Ghilardi-Lopes** (Orientador) da monografia a quem coube a presidência dos trabalhos. Às **08:00** horas, a banca iniciou seus trabalhos, convidando o aluno **Marcos Vinicius Gonçalves da Silva** a fazer a apresentação da monografia intitulada *"Sazonalidades e tendências de uma comunidade bentônica do mediolitoral em um costão rochoso tropical: o quão sensíveis às mudanças são estes ecossistemas"*. Encerrada a apresentação, iniciou-se a fase de arguição pelos membros participantes. Em seguida, os membros reuniram-se para a apreciação do desempenho do estudante. Após a avaliação, os membros presentes da Banca Examinadora decidiram por sua **aprovação** (aprovação/reprovação), com conceito **A**.

Santo André, 01 de dezembro de 2020.

Natalia P Ghilardi Lopes

Profa. Dra. Natalia Pirani Ghilardi-Lopes (Presidente e orientador)

Gustavo Muniz Dias

Prof. Dr. Gustavo Muniz Dias (Titular)

Prof. Dr. João Ricardo Sato (Titular)

AGRADECIMENTOS

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Agradeço aos demais docentes da UFABC, especialmente aos das àreas da biologia, da matemática e da computação, pois em algum momento eu precisei de conceitos de todas essas áreas do conhecimento para concluir este trabalho. A interdisciplinaridade da UFABC é o que levarei de mais importante para o resto da minha vida, mesmo que às vezes eu tenha pensado em desistir pelas dificuldades que também se apresentaram durante minha formação.

Por fim, agradeço aos co-autores, Juliana Nascimento da Silva, Helena Rodrigues Fragoso e André Luís Faccini, que também foram imprescindíveis à conclusão deste trabalho. Eles foram responsáveis pelo monitoramento do costão rochoso do Guarujá quando eu sequer estava matriculado na UFABC, e eu não teria uma série temporal para analisar sem a ajuda deles. Eles também fizeram contribuições, na medida do possível, para o texto apresentado a seguir.

RESUMO

Os organismos da zona entre marés podem responder às condições climáticas com algum retardo temporal. A estrutura das populações de cracas e mexilhões de um costão rochoso subtropical do sudeste do Brasil, bem como sua relação com as variáveis ambientais, considerando dados contemporâneos e ainda dois possíveis retardos temporais, foram estudadas no período entre 2013 e 2019. Diferentes variáveis abióticas puderam prever (positivamente ou negativamente) as tendências e os padrões sazonais do agregamento de cracas e mexilhões na região, dentre eles principalmente os níveis das marés, a velocidade do vento e a temperatura da superfície do mar, cujas tendências locais foram consistentes com os cenários de mudanças climáticas globais. A evidência de como os regressores abióticos com um retardo temporal puderam prever mudanças bióticas, juntamente com o fato de as tendências de mudança das condições climáticas locais serem similares às tendências globais, chama a atenção para a preocupação constante em entender como as mudanças climáticas afetam os bentos marinhos.
Palavras-chave: Ecologia bentônica; Monitoramento; Clima; Análise de séries temporais; Resposta biótica; *Chthamalus* sp.; *Brachidontes* sp.; Costa Sul de São Paulo.

ABSTRACT

Intertidal organisms may respond to climatic conditions with a certain time delay. The structure of barnacles and mussels populations on a subtropical rocky shore community in southeast Brazil and its relation with abiotic variables, considering contemporaneous and two possible temporal delays, was studied between 2013 and 2019. Different abiotic variables could predict (positively or negatively) the trends and seasonal patterns of barnacles and mussels in the area, mainly the tidal levels, wind speed and SST, whose local trends were consistent with global climate change scenarios. The evidence of how lagged environmental regressors can predict biotic changes, along the fact that the trends of change in local environmental conditions were similar to the global trends, draws the attention to the recurring concern of understanding how climate change affects the marine benthos.

Keywords: Benthic ecology; Monitoring; Climate; Time series analysis; Biotic response; *Chthamalus* sp.; *Brachidontes* sp.; São Paulo Southern coast.

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LIST OF ABBREVIATIONS AND ACRONYMS

BSTS	Bayesian Structure Time Series
BVS	Bayesian Variable Selection
CAP	Combined Active Passive
CPCe	Coral Point Count with Excel extension
JAGS	Just Another Gibbs Sampler
MCMC	Markov Chain Monte Carlo
MODIS	Moderate-Resolution Imaging Spectroradiometer
NASA	National Aeronautics and Space Administration
NOAA	National Ocean and Atmospheric Administration
PAR	Photosynthetically Available Radiation
S.I.	Système International d'unités (International System of Unit)
SASA	South Atlantic Subtropical Anticyclone
SD	Standard Deviation
SMAP	Soil Moisture Active Passive
SSS	Sea Surface Salinity
SST	Sea Surface Temperature

SUMMARY

INTRODUCTION [1]

The intertidal zone of rocky shores is occupied by macrofaunal invertebrates and macroalgae, whose community structure is organized by well-delimited dominance zones, which follow a universal zonation pattern described in the mid 1900's (Stephenson and Stephenson, 1949). The combination of biotic interactions, such as interspecific competition, and physiological responses to environmental conditions, such as temperature and tidal level, determine the temporal dynamics and the spatial distribution of the intertidal organisms (Stephenson and Stephenson, 1949; Crisp, 1961).

In the São Paulo State coast, Brazil, the upper intertidal zone is dominated by barnacles of the genus *Chthamalus* Ranzani, 1817, the intermediate intertidal is dominated by mussels of the genus *Brachidontes* Swainson, 1840, and the lower intertidal is dominated by macroalgae (Leite *et al*., 2011). Barnacles are capable of surviving higher on the rocky shore because the shell anatomy and color are different from those of mussels, which make them less susceptible to death when exposed to high radiation and temperature (Eston *et al*., 1986). Furthermore, barnacles settle preferentially on bare rock (Crisp, 1961), while mussels benefit from the presence of recruitment mediators such as barnacle clumps and filamentous macroalgae to settle (Navarrete and Castilla, 1990).

Several studies focused on understanding how environmental conditions can affect the spatial and temporal distribution of barnacles and mussels. Examples of such environmental conditions comprise air and wave exposure, air and sea temperature, wind strength and direction, solar radiation and tidal level (Hawkins and Hartnoll, 1982; Southward *et al*., 1995; Tanaka and Duarte, 1998; Pannacciulli and Relini, 2000). The mechanisms behind these community structure changes include physiological signaling resulting in differential larval emission, growth rate and survival of settled juvenile and adult individuals (Bueno *et al*., 2010; Skinner *et al*., 2010; Freuchet *et al*., 2015).

Furthermore, there is evidence that since barnacles and mussels are sessile organisms, an elapsing time occurs between climatic exogenous signaling and

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1 O presente trabalho está apresentado aqui em inglês, da forma como foi submetido como artigo: Silva, M.V.G.; Silva, J.N.; Faccini, A.L.; Fragoso, H.R.; Ghilardi-Lopes, N.P. Seasonalities and trends in a subtropical rocky shore midlittoral benthic comunity: how fragile are these systems to change? *Marine Environmental Research.*

physiological responses leading to changes in community structure. That delayed biotic response encompasses time periods ranging from 1-4 days (e.g. Kasten and Flores, 2013; Shanks, 1986), 6 months (e.g., Poloczanska *et al*., 2008), and up to 1 year (e.g. Mieszkowska *et al*., 2014). Besides observing a 6-months delayed response of barnacle settlement to sea surface temperature, Poloczanska *et al*. (2008) simulations suggested the disappearance of one barnacle genus and an increase in the vertical range of another genus in response to future scenarios of ocean warming. That study highlights the concern to understand how climate changes may affect the rocky shore community structure, while emphasizing the necessity of considering temporal lags in predictive models.

The objective of the present study was to evaluate how temporal abiotic oscillations can affect the aggregation pattern and vertical position of barnacles and mussels and find possible temporal delays in the biotic response. This study also represents an effort to understand the potential effects of climate change in local intertidal communities of subtropical rocky shores.

MATERIALS AND METHODS

2.1. Time series data acquisition

2.1.1. Historical environmental data

Historical climatic data for locations near Mar Casado Beach (Guarujá, São Paulo State, Brazil, Figure 1) were gathered between July 2012 and December 2019 from online public repositories. Given that each climatic variable selected was presented with a specific spatial resolution, specific locations were chosen for each one (Table 1).

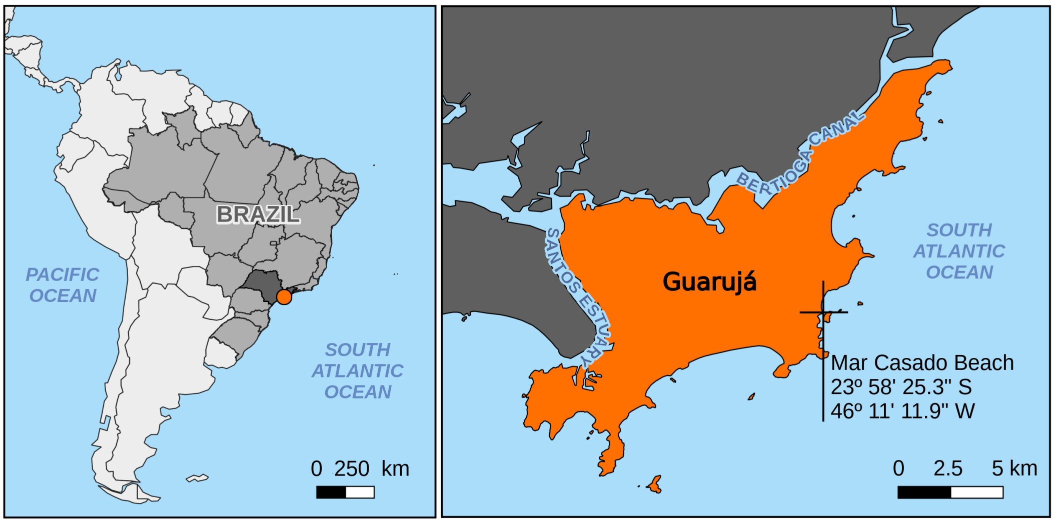
Sea Surface Temperature (SST, °C), Photosynthetically Available Radiation (PAR, E/m²s = 1 mol of photons/m²s in S.I.), Sea Surface Salinity (SSS, PSU), and wind speed (m/s) monthly averages were collected from remote sensing initiatives' databases. Since NASA Aquarius mission was discontinued in June 2015, data for SSS was also collected from Remote Sensing Systems (RSS) SMAP mission database between April 2015 (mission launching month) and December 2019 for a pair of coordinates within the range of Aquarius spatial resolution. Atmospheric pressure (hPa) and relative humidity (%) were collected from WeatherUnderground, an initiative by The Weather Company that uses a network of weather stations. Maximum and minimum tidal level (m) and total rainfall (mm) were collected from Brazilian Navy and Air Space Control Institute, respectively, which are government institutions that monitor these climatic factors locally. Any missing data points in these databases were filled with the monthly average of the last five years of analysis (Table 1). In the NASA monthly SST dataset there were 4 missing data points, which corresponds to 4.44% of the data, while for the monthly PAR dataset there was only 1 missing data point, regarding 1.11% of the data. In the WeatherUnderground daily relative air humidity, there were 102 missing data points, corresponding to 3.72% of the data, while in the daily atmospheric pressure dataset, there were 55 missing data points corresponding to 2.01% of the data. In the RSS monthly wind speed dataset only 1 missing data point was observed, which corresponds to 1.11% of the data. In the RSS monthly SSS dataset there was also only 1 missing data point, which corresponds to 1.75% of the data collected from this database, and 1.11% of all the data collected for the SSS variable.

2.1.2. ReBentos' rocky shore monitoring protocol

A rocky shore community in Mar Casado Beach (Figure 1) has been monitored from March 2013 until December 2019. The rocky shore monitoring protocol of the Coastal Benthic Habitats Monitoring Network (ReBentos) in Brazil proposes a long-term monitoring of the vertical amplitude of the zones and the percentual cover of organisms inhabiting the subdivisions of the intertidal zone (Coutinho *et al*., 2015), intending to study the potential effects of climate change on the community structure.

Five upright transects were fixed at the studied rocky shore: the upper intertidal is dominated by barnacles of the genus *Chthamalus* (from now on "barnacle dominance zone"), the intermediate intertidal is dominated by mussels of the genus *Brachidontes* (from now on "mussel dominance zone"), and the lower intertidal is dominated by macroalgae. In each dominance zone, one photographic 20 x 20 cm fixed sampling unit was taken in each transect. Also, the superior and inferior limits of each dominance zone were measured *in situ* in relation to a fixed point at the top of each transect. The samplings occurred each year in March, June, September, and December, months that mark the end of climatic seasons (Summer, Autumn, Winter and Spring, respectively, in the Southern Hemisphere).

Figure 1 - On the left, the South America map constrasting Brazil. The São Paulo State, where the studied rocky shore is located, is evidenced in darker grey, and the orange dot represents the approximate location of Guarujá city. On the right, the location and coordinates of the rocky shore studied between the years of 2013 and 2019, in Guarujá city. Coordinates in WGS84 datum.



In the present study only the barnacle and mussel dominance zones were analyzed. In each dominance zone, the following variables were obtained from the photographic sampling units: percent cover (%) of (i) barnacle, (ii) dead barnacle (barnacle lacking the operculum), (iii) mussel and (iv) available space; (v) basal plate and (vi) opercular diameter (mm) of barnacles, the latter only in barnacle dominance zone. Besides, in order to allow the understanding of the relative position shift of each dominance zone, the lowest value obtained for the measure of the inferior limit of each dominance zone was taken as its zero mark; allowing for the determination of a time series for their (vii) superior limit, (viii) inferior limit, and (ix) vertical amplitude (m).

Table 1 - Abiotic/climatic variables, units of measure, temporal and spatial resolution, geographical position (latitude and longitude), locality, the version of the algorithms and the sources of their online repositories. *Coordinates in WGS84 datum. **Coordinates according to the initiative's own geolocation system, which considers an equatorial radius of 6,378,137 m and a polar radius of 6,356,752 m.

Variable	Unit of measure	Algorithm version	Temporal resolution	Spatial resolution	Latitude	Longitude	Locality	Website reference
Sea Surface Temperature	ºC	MODIS-Terra Level-3 Mapped SST Data Version 2018	Monthly	0.042°	-23.97917*	-46.18750*	–	NASA Ocean Color https://oceandata.sci.gsfc.nasa.gov/opendap/MODIST/L3SMI/
Atmospheric pressure	hPa	–	Daily	–	–	–	Santos Air Base	WeatherUnderground https://www.wunderground.com/history/daily/br/guaruja/SBST
Relative humidity	%	–	Daily	–	–	–	Santos Air Base	WeatherUnderground https://www.wunderground.com/history/daily/br/guaruja/SBST
Photosynthetically Available Radiation	E/m²s	MODIS-Terra Level-3 Mapped PAR Data Version 2018	Monthly	0.042°	-23.97917*	-46.18750*	–	NASA Ocean Color https://oceandata.sci.gsfc.nasa.gov/opendap/MODIST/L3SMI/
Wind speed	m/s	Version-7 Release-01 Wind Speed CDR	Monthly	1°	-24.5**	-46.5**	–	Remote Sensing Systems ftp://ftp.remss.com/wind/monthly_1deg/
Tidal level (max and min)	m	–	Daily	–	–	–	Santos Port	Brazilian Navy https://www.surfguru.com.br/previsao/mare/50225
Sea Surface Salinity	PSU	Version 5.0 Aquarius Combined Active Passive (CAP) algorithm Level 3	Monthly	1°	-24.5*	-46.5*	–	NASA Aquarius https://podaac-opendap.jpl.nasa.gov/opendap/SalinityDensity/aquarius/
Sea Surface Salinity	PSU	SMAP Salinity V4 Validated Release	Monthly	0.25°	-24.875*	-46.125*	–	Remote Sensing Systems https://doi.org/10.5067/SMP40-3SOCS
Total rainfall	mm	–	Monthly	–	–	–	Santos Air Base	Air Space Control Institute http://clima.icea.gov.br/clima

Percent cover of organisms and available space were measured using Point Count with Excel Extensions (CPCe) 4.1. software (Kohler and Gill, 2006) with 50 random points in each image (Murray *et al*., 2006). Average operculum and basal plate diameters were measured over the carina - rostrum axis using ImageJ software considering those individuals under one of the 50 random points in each image. Time series for all biotic variables were defined by averaging the values obtained for the five transects in each sampling event.

2.2. Bayesian Structural Time Series (BSTS) Models

In order to standardize the sampling frequency of abiotic and biotic time series, data was averaged over the quarters of the year. Averages were obtained using the values from January to March (summer in the southern hemisphere), April to June (autumn), July to September (winter), and October to December (spring).

With the aim of understanding general temporal patterns and eventual seasonal patterns in environmental factors mean values, a “basic structural model” (Scott and Varian, 2014) was applied to abiotic time series ranging from winter 2012 to spring 2019. This model included a local linear trend component, and a seasonal component with four seasons per year. Concerning the biotic data, besides the basic structural model, a regression component was added based on results of the variable selection method (described ahead in section 2.3). Abiotic predictors that showed a weak evidence of having an effect were not considered (classification criterion also presented in section 2.3). For these variables, time series ranged from summer 2013 to spring 2019. Model fit was carried using the *bsts* (0.9.2 version) R package (Scott, 2019) using Markov chain Monte Carlo (MCMC) algorithm using 100,000 iterations and considering a 5,000 iterations burn-in period. All analyses were carried out using R 4.0.1 version (R Core Team, 2020).

Comparisons between the BSTS model considering only trend and seasonal effects, and the one with the addition of abiotic factors as a linear regression component were made by plotting both models in the same graph.

2.3. Bayesian Variable Selection (BVS)

Considering the small sample size (N = 28) and the large amount of plausible predictors (p = 27), Bayesian Variable Selection was used to identify important abiotic factors with high probability of having an effect on observed changes in community structure. We implemented the Kuo and Mallick (1998) Gibbs sampler to a linear regression model (O'hara and Sillanpää, 2009). Since barnacles and mussels are sessile organisms, there is evidence that an elapsing time occurs between climatic physiological signaling and significant changes in community structure (e.g., Lively *et al.*, 1993; Kasten and Flores, 2013). Thus, lagged climatic variables were considered in the predictors data frame. Lag 0 refers to contemporary climatic conditions, lag 1 to the previous season, and lag 2 to the season before the previous season (from now on "previous semester"). A Bernoulli prior was assumed for the indicator variable, $\gamma_p \sim Be(0.5)$[2], so a priori all models were equally likely. A weakly informative prior was assumed for linear regression coefficients β_p[3], using $\sigma_p^2 \sim$ Inverse-Gamma(10^{-4},10^{-4})[4] (Lemoine, 2019), shrinking coefficients estimation towards zero unless there is a strong posterior evidence of an effect (McElreath, 2015). During variable selection, a two-chains Gibbs sampler was carried over 100,000 iterations with a 5,000 iterations burn-in period. It was implemented in R using the JAGS program within the *rjags* package version 4-10 (Plummer, 2019). Convergence of MCMC simulations was assessed by the Gelman and Rubin's convergence diagnostic (estimated potential scale reduction factor < 1.1) and the analysis of density plots, both available in *coda* package version 0.19-3 (Plummer *et al.*, 2006).

Considering that the chosen environmental variables imply multiple different units of measure, a centering and scaling transformation was performed to minimize the intrinsic variance of different scales. Regarding the interpretation of γp posterior probabilities, the Jeffreys (1961) categorization was adopted. Hence, posterior probabilities values between 0.5 and 0.75 were considered as weak evidence, values between 0.75 and 0.95 a positive evidence, values between 0.95 and 0.99 a strong

2 $\gamma p \sim$ *Be*(0.5) is the indicator variable introduced by Kuo and Mallick (1998) to the Gibbs Sampler method, which follows a Bernoulli distribution including, *a priori*, half of the predictors in each MCMC iteration.
3 β_p is the linear regression coefficient for each *p* variable, which follows a normal distribution *a priori* ($\beta_p \sim \gamma_p N(0,\sigma_p^2)$).
4 $\sigma p^2 \sim$ Inverse-Gamma(10^{-4},10^{-4}) is the standard deviation of the normal distribution of β_p, which follows a weakly informative Inverse-Gamma distribution *a priori.*

evidence, and values above 0.99 a decisive evidence for an effect of the climatic predictors on the response biotic variable.

RESULTS AND DISCUSSION

3.1. Environmental trends and seasonal effects

The BSTS models uncovered a clear seasonality in several abiotic variables, with periods of time with high radiation levels and temperatures, heavier rainfall, slower winds and low atmospheric pressure (typical of Summer periods - December to February in the Southern Hemisphere); and other periods with low radiation levels, low temperatures and air humidity, less rainy, and with a peak in atmospheric pressure and maximum tidal levels (typical of Winter periods - June to August) (Figure 2). Also, low SSS events occurred biannually during winter. Interestingly, the high air humidity seasonal peaks occurred during autumn, despite these peaks being expected for Summer periods in subtropical zones (Peel *et al*., 2007).

Considering the more evident temporal trends, during the seven years of monitoring, it was possible to notice: (i) a mean increase of around 1.375 cm in the maximum tidal level, which was not followed by an increase in minimum tidal level; (ii) an increase of around 0.275 $m\ s^{-1}$ in the wind speed; (iii) an increase of around 0.875 ºC in the SST time series, which was followed by a 0.75 $E\ m^{-2}\ s^{-1}$ mean increase in PAR and (iv) a decrease of more than 40 mm of rainfall.

3.2. Community structure trends and seasonal effects

Regarding the barnacle dominance zone, the BSTS decomposition uncovered a trend of increase in mussel cover from 2013 until at least the early 2017, when there was a decrease of mussel cover concomitant to an accentuated trend of increase in available space. Contrastingly, there was a continuous trend of decrease in barnacle cover within this same period. In the beginning of 2019, mussel cover abruptly dropped. Both the superior limit and the vertical amplitude of barnacle dominance zone registered a mean increase of around 1 meter along the study period. Nevertheless, the inferior limit went up only 30 cm until early 2016 and stabilized until early 2018, when it went down 45 cm by the end of the monitoring (Figure 3).

In the mussel dominance zone, the time series decomposition showed a trend of near stability for mussel cover and available space until early 2015. At this moment, available space and barnacle cover increased, while mussel cover decreased.

Around mid 2017 and early 2018 all these trend patterns changed, with available space and barnacle cover decreasing, while mussel cover increased. The superior limit followed a similar trend pattern to that described for the inferior limit of barnacle dominance zone. From these results it is possible to infer that, due to the appearance of patches of free space within the mussel bed there was an opportunity for barnacles to also settle lower on the rocky shore. Additionally, it is evident that the superior limit of mussel dominance zone and the inferior limit of barnacle dominance zone follow the same trend pattern over time, probably as a result of the intense interspecific competition for space (Figure 4).

3.3. Delayed biotic responses to environmental changes

Concerning the barnacles dominance zone, there was no strong or decisive evidence of an effect of climatic predictors on response biotic variables (Table 2), while no decisive evidence of an effect was found regarding the mussel dominance zone (Table 3). Herein we focus the discussion on abiotic predictors with at least a positive evidence of an effect.

The temporal oscillations of the superior limit of barnacle dominance zone could be predicted by contemporary maximum tidal level, contemporary wind speed and previous semester air humidity, with positive correlations. Moreover, the amplitude of this dominance zone could be predicted by contemporary maximum tidal level and previous semester air humidity, also with positive correlations (Tables 2 and 4). These results indicate that the seasons with high maximum tidal levels and the ones with faster winds could be held responsible by barnacle cyprid larvae recruiting higher on the rocky shore, resulting in a vertically wider dominance zone. Furthermore, seasons with high air humidity possibly allowed these new individuals to survive higher on the rocky shore until one semester later, maintaining the shift in the position of the superior limit along this period.

While shifts in the position of the superior limit of barnacle dominance could be predicted by environmental conditions, the evidence for an effect of the predictors on the inferior limit was weak. These results are consistent with conclusions from a study performed in Scotland (Connel, 1961), which showed that the upper limit of the barnacle *Chthamalus stellatus* (Poli, 1791) dominance zone was limited by physical factors, such as heat and desiccation stress, while the inferior limit was more strongly influenced by interspecific competition for space. The same phenomenon could be observed for the vertical distribution of the barnacles *C. stellatus* and *Chthamalus montagui* Southward,1976 in the Mediterranean (Pannacciulli and Relini, 2000).

Figure 2 - Time series decomposition of abiotic variables. (A) Maximum tidal level (m); (B) wind speed (m/s); (C) minimum tidal level (m); (D) Sea Surface Temperature (°C); (E) Sea Surface Salinity (PSU); (F) Photosynthetically Available Radiation (E m^2 s^1); (G) mean relative air humidity (%); (H) mean atmospheric pressure (hPa); (I) total rainfall (mm).

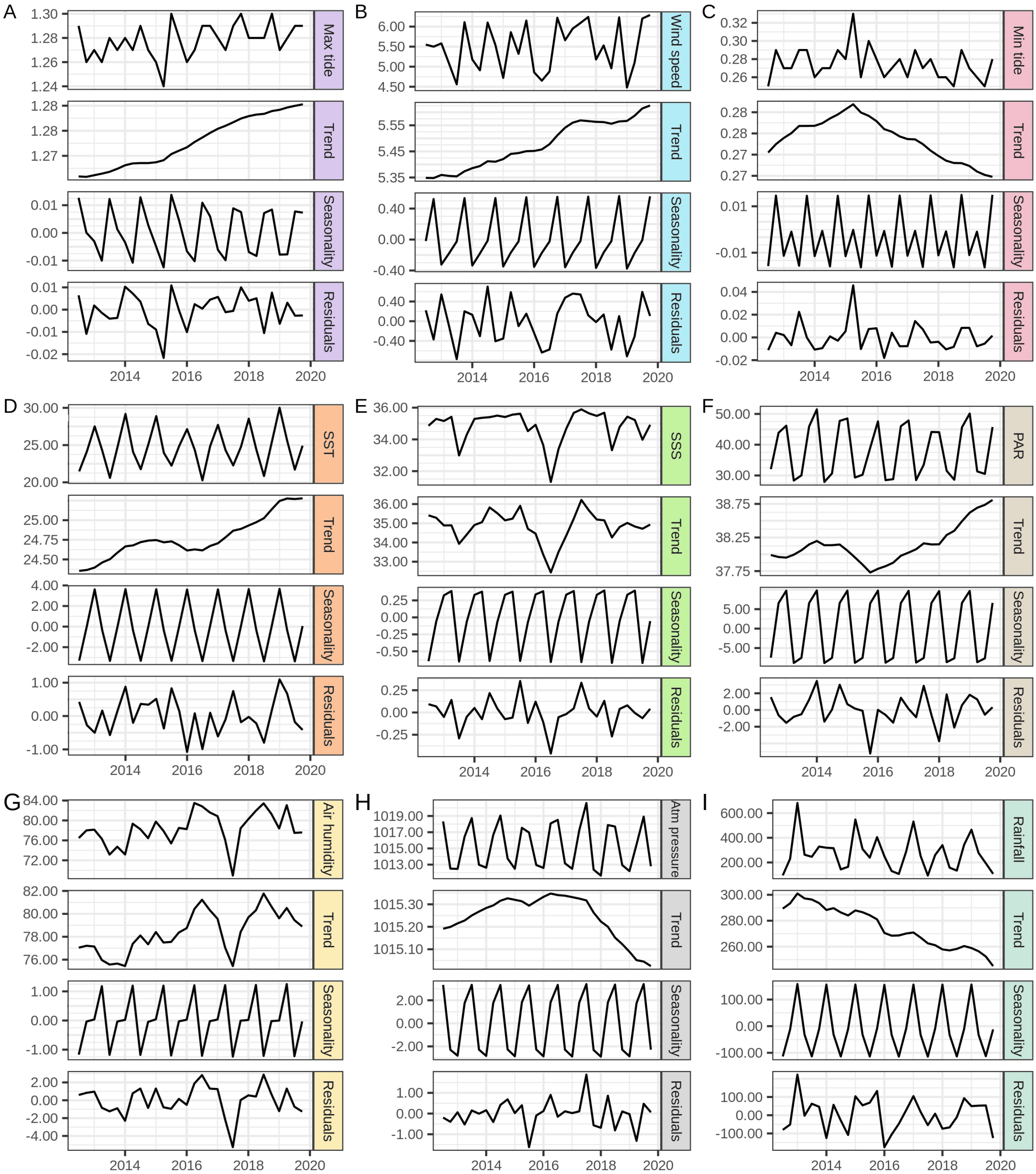


Figure 3 - Time series decomposition of the barnacle dominance zone variables. (A) Dominance zone amplitude (m); (B) dominance zone superior limit (m); (C) barnacle cover (%); (D) mussel cover (%); (E) barnacle lacking operculum cover (%); (F) dominance zone inferior limit (m); (G) mean opercular diameter (mm); (H) mean basal diameter (mm); (I) available space (%).

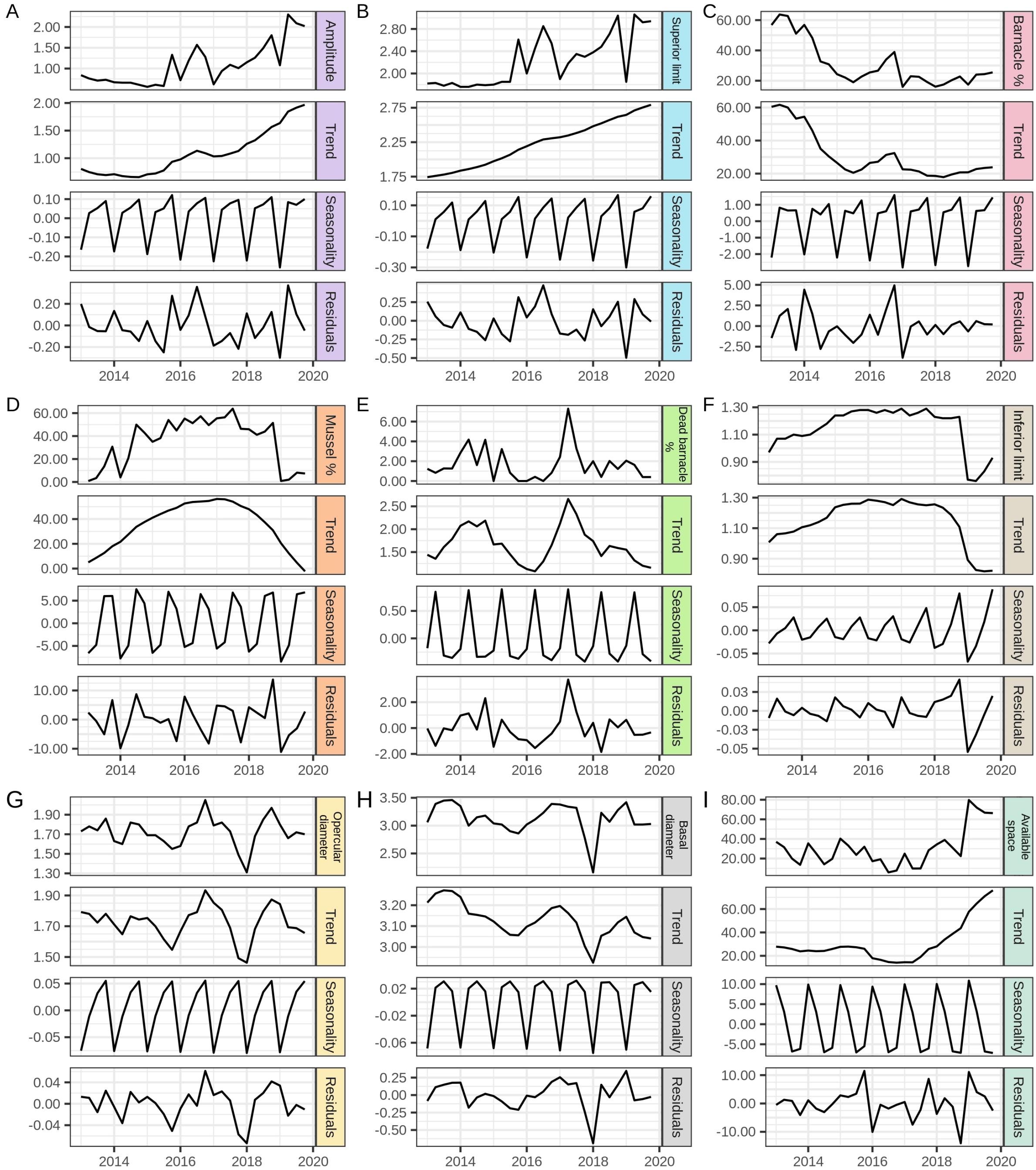


Figure 4 - Time series decomposition of the mussel dominance zone variables. (A) Available space (%); (B) mussel cover (%); (C) barnacle cover (%); (D) dominance zone superior limit (m); (E) dominance zone inferior limit (m); (F) dominance zone amplitude (m).

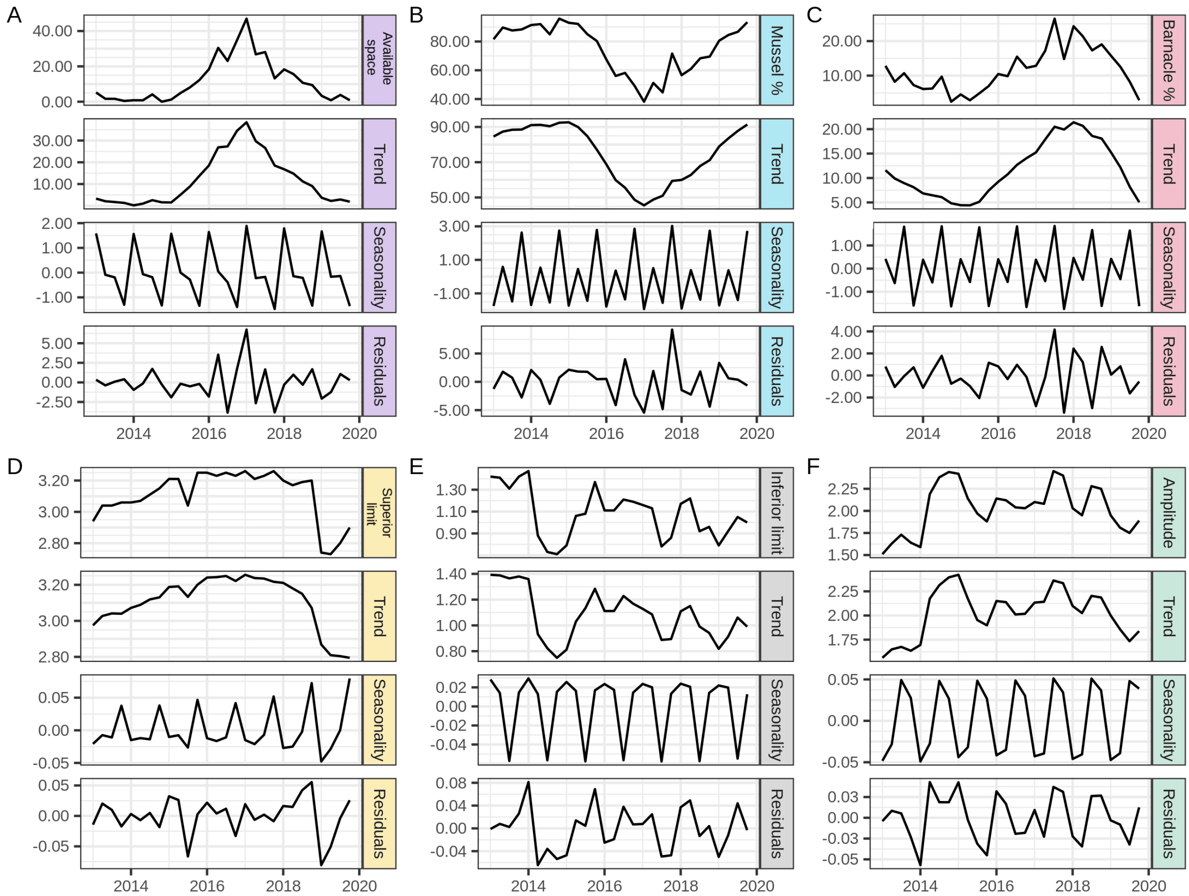


Table 2 - Posterior Inclusion Probabilities of the abiotic variables as predictors for the temporal variance of the barnacle dominance zone aggregation pattern. Values obtained by the BVS method (see section 2.3). lag 0 = contemporaneous time series, lag 1 = 3-months delayed time series and lag 2 = 6-months delayed time series. Values in bold (0.75< value< 0.95) refer to a positive evidence, those with a single asterisk (0.95<value<0.99) refer to a strong evidence, and those with double asterisk (> 0.99) refer to a decisive evidence for an effect of the climatic predictors on the response biotic variable.

(to be continued)

		Barnacle cover	Dead barnacle cover	Mussel cover	Available space	Superior limit	Inferior limit	Amplitude	Opercular diameter	Basal diameter
lag 0	SST	0.4522	0.4477	0.6316	**0.8211**	0.6387	0.7495	0.7457	0.4072	0.4162
	Relative air humidity	**0.8287**	0.4519	0.4851	0.2599	0.3320	0.3765	0.2740	0.2922	**0.8052**
	Atmospheric pressure	0.4577	0.3645	0.6301	0.6564	0.4298	0.6328	0.4687	0.6619	0.6410
	Wind speed	0.6650	0.2520	0.3771	0.2352	**0.8581**	0.2519	0.6362	0.2900	0.3810
	Max. tide level	0.3739	0.3940	0.2801	0.3440	**0.9089**	0.3025	**0.7972**	0.5261	0.2889
	Min. tide level	0.5448	0.5342	0.4191	0.3047	0.3735	0.3937	0.4768	0.2648	0.2449
	PAR	0.4288	0.4570	0.4565	0.5008	0.4070	0.4971	0.4195	0.4139	0.6315
	SSS	0.4208	0.7097	0.3193	0.2986	**0.9128**	0.2844	**0.7935**	0.3799	0.2794
	Rainfall	0.4564	0.2956	0.5685	0.3149	0.6886	0.3648	0.3761	0.3050	0.3242
lag 1	SST	0.4947	0.3666	0.4737	0.6723	0.6585	0.5099	0.6558	**0.7982**	0.5017
	Relative air humidity	0.6797	0.2861	0.6168	0.3267	0.4184	0.3302	0.2933	0.5193	0.3251
	Atmospheric pressure	0.4887	0.4147	0.4879	0.4154	0.4558	0.3847	0.4151	0.3959	0.3634
	Wind speed	0.5644	0.2781	0.4950	0.3664	0.2625	0.6536	0.3363	**0.9277**	**0.8318**
	Max. tide level	**0.8714**	0.3377	0.3741	0.3812	0.4186	0.3164	0.3848	0.3704	0.2719
	Min. tide level	**0.9131**	0.3488	**0.9059**	0.5953	0.4499	0.6986	0.7486	0.3599	0.3486
	PAR	0.3981	0.4683	0.4934	0.4461	0.4818	0.4152	0.4300	0.4347	0.4514
	SSS	0.5987	0.2847	0.4125	0.7219	0.3226	0.4834	0.2997	0.4956	0.4957
	Rainfall	0.4916	0.2835	0.3944	0.2749	0.2802	0.4195	0.3091	0.3245	0.3807
lag 2	SST	0.5500	0.3913	0.4344	**0.7537**	0.4336	0.5604	0.5974	0.4794	**0.8293**
	Relative air humidity	0.5697	0.2949	0.3596	**0.7749**	**0.9182**	0.3467	**0.8852**	**0.8950**	**0.7599**
	Atmospheric pressure	0.4610	0.3742	0.5598	0.4678	0.5005	0.5991	0.4201	0.6072	**0.9000**
	Wind speed	0.4368	0.3057	**0.8209**	0.7104	0.3575	0.6308	0.2693	0.3421	0.3709
	Max. tide level	0.5129	0.2721	0.3735	0.2651	0.4075	0.3674	0.2666	0.3205	0.2695
	Min. tide level	0.4899	0.3022	0.4701	0.2354	0.4294	0.6551	0.2449	**0.7592**	0.3728
	PAR	0.4752	0.4232	0.3948	0.4230	0.4268	0.4129	0.4274	0.5252	0.5289

Table 2 - Posterior Inclusion Probabilities of the abiotic variables as predictors for the temporal variance of the barnacle dominance zone aggregation pattern. Values obtained by the BVS method (see section 2.3). lag 0 = contemporaneous time series, lag 1 = 3-months delayed time series and lag 2 = 6-months delayed time series. Values in bold (0.75< value< 0.95) refer to a positive evidence, those with a single asterisk (0.95<value<0.99) refer to a strong evidence, and those with double asterisk (> 0.99) refer to a decisive evidence for an effect of the climatic predictors on the response biotic variable.

(conclusion)

		Barnacle cover	Dead barnacle cover	Mussel cover	Available space	Superior limit	Inferior limit	Amplitude	Opercular diameter	Basal diameter
lag 2	SSS	0.2707	**0.9157**	0.4965	0.5213	**0.9301**	0.2698	**0.8494**	0.6700	0.7145
	Rainfall	0.3655	0.2846	0.5070	0.3329	0.3120	0.5673	0.3103	0.4484	0.3423

Table 3 - Posterior Inclusion Probabilities of the abiotic variables as predictors for the temporal variance of the mussel dominance zone aggregation pattern. Values obtained by the BVS method (see section 2.3). lag 0 = contemporaneous time series, lag 1 = 3-months delayed time series and lag 2 = 6-months delayed time series. Values in bold (0.75<value< 0.95) refer to a positive evidence, those with a single asterisk (0.95<value<0.99) refer to a strong evidence, and those with double asterisk (> 0.99) refer to a decisive evidence for an effect of the climatic predictors on the response biotic variable.

(to be continued)

		Barnacle cover	Mussel cover	Available space	Superior limit	Inferior limit	Amplitude
lag 0	SST	0.4113	0.5738	0.5685	0.7421	0.5064	0.4323
	Relative air humidity	0.4257	0.3640	0.7164	0.3484	0.5843	0.7098
	Atmospheric pressure	0.6994	0.7342	**0.7667**	0.7340	0.5291	**0.7823**
	Wind speed	0.2485	0.7361	**0.9109**	0.2476	0.6134	0.3834
	Max. tide level	**0.8451**	0.5140	0.2573	0.3553	0.3390	0.3991
	Min. tide level	0.4018	0.4056	0.2357	0.3813	0.3768	0.5806
	PAR	0.4604	0.4864	0.4669	0.4854	0.4683	0.4166
	SSS	0.3417	0.7288	**0.8587**	0.2670	**0.9079**	**0.8232**
	Rainfall	0.2584	0.4804	0.4772	0.3955	0.3081	0.3941
lag 1	SST	0.3852	0.4099	0.3912	0.5035	0.5813	0.3928
	Relative air humidity	0.5438	**0.7989**	0.6445	0.2896	0.3667	0.3044
	Atmospheric pressure	0.3832	0.3774	0.3730	0.3844	**0.8220**	0.6889
	Wind speed	0.2547	0.7264	**0.8984**	0.5638	0.2588	0.5633
	Max. tide level	0.6681	0.6634	0.4234	0.2707	0.4816	0.2902
	Min. tide level	0.4413	**0.9140**	**0.96593***	0.4072	0.2508	0.2638
	PAR	0.4757	0.4749	0.4338	0.4026	0.4268	0.3721
	SSS	0.2463	0.5765	0.6450	0.4161	0.3610	0.2815
	Rainfall	0.2905	0.3067	0.3092	0.3771	0.6631	0.7009
lag 2	SST	0.6319	0.6058	0.5479	0.6286	0.5969	0.3827
	Relative air humidity	0.2325	0.2683	0.2555	0.3713	0.3441	0.2195
	Atmospheric pressure	0.4185	0.4790	0.5399	0.6747	0.3980	0.4988
	Wind speed	**0.9171**	**0.9627***	**0.96401***	0.6133	0.2566	0.3921
	Max. tide level	0.3950	0.4263	0.2995	0.3870	0.3468	0.3458
	Min. tide level	0.6258	0.2702	0.3289	0.5594	0.5205	0.2415
	PAR	0.4117	0.4301	0.4486	0.4438	0.4554	0.3970

Table 3 - Posterior Inclusion Probabilities of the abiotic variables as predictors for the temporal variance of the mussel dominance zone aggregation pattern. Values obtained by the BVS method (see section 2.3). lag 0 = contemporaneous time series, lag 1 = 3-months delayed time series and lag 2 = 6-months delayed time series. Values in bold (0.75<value< 0.95) refer to a positive evidence, those with a single asterisk (0.95<value<0.99) refer to a strong evidence, and those with double asterisk (> 0.99) refer to a decisive evidence for an effect of the climatic predictors on the response biotic variable.

(conclusion)

		Barnacle cover	Mussel cover	Available space	Superior limit	Inferior limit	Amplitude
lag 2	SSS	0.2657	**0.7904**	**0.9390**	0.2807	0.3420	0.3202
	Rainfall	0.4992	0.4704	0.3650	0.5562	0.3414	0.3583

Table 4 - *A posteriori* estimated linear regression coefficients of the abiotic variables as predictors for the temporal variance of the barnacle dominance zone aggregation pattern. Values obtained by the BVS method (see section 2.3). lag 0 = contemporaneous time series, lag 1 = 3-months delayed time series and lag 2 = 6-months delayed time series. Post. Mean = Posterior mean value for the regression coefficient. Post SD = Posterior Standard Deviation of the mean value for the regression coefficient. Bold values refer to an at least positive evidence for an effect of the climatic predictors on the response biotic variable (see Table 2).

(to be continued)

		Barnacle cover		**Dead barnacle cover**		**Mussel cover**		**Available space**		**Superior limit**		**Inferior limit**		**Amplitude**		**Opercular diameter**		**Basal diameter**	
		Post. Mean	**Post. SD**	**Post. Mean**	**Post. SD**	**Post. Mean**	**Post. SD**	**Post. Mean**	**Post. SD**	**Post. Mean**	**Post. SD**	**Post. Mean**	**Post. SD**	**Post. Mean**	**Post. SD**	**Post. Mean**	**Post. SD**	**Post. Mean**	**Post. SD**
lag 0	SST	-1.47	4.32	-0.21	0.55	-7.82	9.59	**13.44**	**9.88**	0.12	0.15	-0.10	0.09	0.23	0.21	-0.002	0.03	-0.01	0.06
	Relative air humidity	**-6.34**	**4.29**	-0.24	0.38	3.54	5.43	0.21	2.21	0.02	0.06	0.01	0.03	0.01	0.06	-0.002	0.01	**-0.08**	**0.06**
	Atmospheric pressure	-1.60	4.06	0.03	0.40	7.87	9.29	-7.00	7.69	-0.04	0.10	0.06	0.07	-0.07	0.13	0.04	0.04	0.08	0.09
	Wind speed	-3.33	3.25	0.01	0.19	1.74	3.45	0.12	1.93	**0.16**	**0.09**	0.002	0.02	0.11	0.11	-0.004	0.01	-0.02	0.03
	Max. tide level	-1.13	2.54	-0.16	0.32	-0.12	2.84	1.24	2.96	**0.19**	**0.09**	-0.01	0.02	**0.17**	**0.12**	-0.02	0.02	-0.01	0.03
	Min. tide level	-2.37	2.94	0.27	0.34	2.24	3.75	-0.94	2.35	-0.03	0.06	0.02	0.03	-0.06	0.09	-0.001	0.01	0.0007	0.02
	PAR	-0.38	3.90	-0.25	0.54	-2.05	7.57	3.64	7.36	-0.003	0.09	-0.03	0.07	0.03	0.12	0.001	0.03	0.07	0.09
	SSS	-1.46	2.95	0.51	0.44	0.89	3.31	-0.85	2.78	**-0.22**	**0.11**	0.00	0.02	**-0.19**	**0.14**	0.01	0.02	0.001	0.03
	Rainfall	1.72	2.88	-0.08	0.23	-4.45	5.41	0.82	2.83	-0.09	0.09	-0.01	0.03	-0.04	0.07	0.0003	0.01	0.01	0.04
lag 1	SST	-2.44	4.57	-0.04	0.42	-3.29	6.96	7.41	7.93	0.13	0.14	-0.03	0.06	0.15	0.17	**-0.06**	**0.05**	-0.04	0.07
	Relative air humidity	-4.17	4.02	0.08	0.26	5.63	6.25	-0.77	3.09	0.04	0.07	0.01	0.03	0.02	0.06	0.02	0.02	0.01	0.03
	Atmospheric pressure	-2.05	4.45	0.21	0.47	3.84	7.16	-1.68	5.16	-0.04	0.10	0.01	0.04	-0.04	0.11	0.01	0.03	0.01	0.05
	Wind speed	-2.74	3.36	0.06	0.22	3.57	5.03	-1.43	3.27	-0.005	0.04	0.05	0.05	-0.03	0.07	**-0.06**	**0.03**	**-0.09**	**0.06**
	Max. tide level	**-6.54**	**3.70**	0.11	0.25	1.76	3.76	1.60	3.21	0.03	0.06	-0.01	0.03	0.04	0.07	-0.01	0.02	-0.01	0.03
	Min. tide level	**-7.74**	**3.60**	-0.12	0.24	**10.89**	**5.36**	-3.61	3.91	-0.04	0.06	0.05	0.04	-0.13	0.10	-0.01	0.02	-0.01	0.03
	PAR	-0.10	3.50	0.30	0.58	-3.80	7.27	1.84	6.13	0.05	0.11	-0.01	0.05	0.03	0.13	0.01	0.03	-0.03	0.06
	SSS	-3.02	3.48	0.05	0.24	-2.37	4.54	6.37	5.52	0.01	0.05	-0.03	0.04	0.01	0.07	-0.02	0.03	-0.04	0.06
	Rainfall	2.18	3.21	-0.04	0.24	-2.02	4.24	0.29	2.52	-0.001	0.04	-0.02	0.04	0.02	0.06	0.004	0.02	0.02	0.04
lag 2	SST	-3.41	5.13	0.06	0.46	-2.18	6.66	**10.22**	**8.97**	0.03	0.10	-0.05	0.07	0.13	0.17	-0.01	0.03	**-0.14**	**0.10**
	Relative air humidity	-2.41	2.83	-0.08	0.22	-1.58	3.58	**6.06**	**4.48**	**0.17**	**0.08**	-0.01	0.03	**0.18**	**0.09**	**0.05**	**0.02**	**0.06**	**0.05**
	Atmospheric pressure	-1.16	4.32	0.06	0.42	5.57	8.54	-2.55	6.73	0.05	0.12	0.06	0.08	-0.002	0.13	-0.03	0.04	**-0.18**	**0.10**
	Wind speed	-1.57	2.78	0.09	0.25	**10.18**	**6.79**	-6.24	5.41	0.02	0.06	0.04	0.05	-0.01	0.05	-0.01	0.02	-0.02	0.04
	Max. tide level	-2.52	3.52	0.05	0.21	1.93	4.63	-0.39	2.36	0.04	0.07	0.01	0.03	0.01	0.05	-0.003	0.02	0.002	0.02

Table 4 - *A posteriori* estimated linear regression coefficients of the abiotic variables as predictors for the temporal variance of the barnacle dominance zone aggregation pattern. Values obtained by the BVS method (see section 2.3). lag 0 = contemporaneous time series, lag 1 = 3-months delayed time series and lag 2 = 6-months delayed time series. Post. Mean = Posterior mean value for the regression coefficient. Post SD = Posterior Standard Deviation of the mean value for the regression coefficient. Bold values refer to an at least positive evidence for an effect of the climatic predictors on the response biotic variable (see Table 2).

(conclusion)

		Barnacle cover		**Dead barnacle cover**		**Mussel cover**		**Available space**		**Superior limit**		**Inferior limit**		**Amplitude**		**Opercular diameter**		**Basal diameter**	
		Post. Mean	**Post. SD**	**Post. Mean**	**Post. SD**	**Post. Mean**	**Post. SD**	**Post. Mean**	**Post. SD**	**Post. Mean**	**Post. SD**	**Post. Mean**	**Post. SD**	**Post. Mean**	**Post. SD**	**Post. Mean**	**Post. SD**	**Post. Mean**	**Post. SD**
lag 2	Min. tide level	-2.29	3.36	-0.09	0.22	3.11	4.70	-0.32	1.91	0.04	0.07	0.05	0.04	0.01	0.04	**-0.03**	**0.02**	-0.02	0.03
	PAR	-1.47	4.32	0.18	0.49	-0.67	5.86	0.89	5.93	0.01	0.10	-0.01	0.05	0.02	0.13	-0.02	0.04	-0.05	0.08
	SSS	-0.05	1.58	**-0.86**	**0.41**	-3.32	4.70	3.46	4.73	**0.20**	**0.09**	-0.004	0.02	**0.19**	**0.11**	-0.03	0.03	-0.07	0.06
	Rainfall	-0.01	2.77	-0.01	0.25	-3.80	5.65	1.05	3.25	-0.004	0.05	-0.04	0.05	0.02	0.07	-0.01	0.02	-0.01	0.04

Table 5 - *A posteriori* estimated linear regression coefficients of the abiotic variables as predictors for the temporal variance of the mussel dominance zone aggregation pattern. Values obtained by the BVS method (see section 2.3). lag 0 = contemporaneous time series, lag 1 = 3-months delayed time series and lag 2 = 6-months delayed time series. Post. Mean = Posterior mean value for the regression coefficient. Post SD = Posterior Standard Deviation of the mean value for the regression coefficient. Bold values refer to an at least positive evidence for an effect of the climatic predictors on the response biotic variable (see Table 3).

(to be continued)

		Barnacle cover		Mussel cover		Available space		Superior limit		Inferior limit		Amplitude	
		Post. Mean	Post. SD	Post. Mean	Post. SD	Post. Mean	Post. SD	Post. Mean	Post. SD	Post. Mean	Post. SD	Post. Mean	Post. SD
lag 0	SST	-0,30	1,78	3,88	6,00	-2,68	4,14	-0,09	0,08	-0,04	0,09	-0,004	0,09
	Relative air humidity	-0,79	1,42	-0,91	2,60	3,21	2,80	0,01	0,03	-0,05	0,06	0,09	0,08
	Atmospheric pressure	2,61	2,52	-6,95	6,43	**5,56**	**4,71**	0,08	0,08	-0,05	0,08	**0,17**	**0,13**
	Wind speed	-0,05	0,68	-4,98	4,06	**5,86**	**2,81**	0,002	0,02	0,05	0,05	-0,03	0,05
	Max. tide level	**2,81**	**1,71**	-2,19	3,09	0,08	1,09	-0,01	0,03	0,01	0,03	-0,03	0,05
	Min. tide level	-0,64	1,20	1,23	2,28	-0,11	0,91	0,01	0,03	-0,02	0,03	0,05	0,06
	PAR	-0,75	2,22	2,39	5,52	-1,30	3,47	-0,03	0,07	-0,03	0,08	0,01	0,09
	SSS	-0,42	1,00	5,51	4,67	**-5,36**	**3,22**	0,0009	0,02	**-0,13**	**0,07**	**0,12**	**0,08**
	Rainfall	-0,07	0,71	1,95	3,13	-1,34	2,20	-0,02	0,03	0,01	0,03	-0,03	0,05
lag 1	SST	-0,10	1,58	0,83	3,84	-0,25	2,46	-0,03	0,06	-0,06	0,09	0,01	0,08
	Relative air humidity	1,18	1,51	**-5,37**	**3,82**	2,50	2,59	0,005	0,03	-0,02	0,04	0,01	0,04
	Atmospheric pressure	-0,35	1,47	0,37	3,26	-0,53	2,15	0,01	0,04	**-0,14**	**0,10**	0,12	0,12
	Wind speed	0,13	0,68	-4,81	4,14	**5,60**	**2,95**	0,04	0,04	-0,001	0,03	0,05	0,07
	Max. tide level	1,62	1,54	-3,72	3,65	1,04	1,81	-0,004	0,02	-0,03	0,04	0,01	0,04
	Min. tide level	0,74	1,21	**-8,12**	**3,90**	**6,46**	**2,27**	0,02	0,03	0,003	0,02	0,01	0,03
	PAR	-1,07	2,07	2,07	4,62	-1,00	2,74	-0,01	0,05	-0,02	0,06	0,01	0,07
	SSS	-0,01	0,66	3,29	4,14	-2,75	2,94	-0,02	0,04	-0,02	0,04	0,003	0,04
	Rainfall	0,12	0,86	0,45	2,08	-0,23	1,48	-0,02	0,03	0,07	0,07	-0,10	0,09
lag 2	SST	-2,20	2,57	4,46	5,89	-2,24	3,56	-0,06	0,07	-0,07	0,09	0,001	0,07
	Relative air humidity	-0,09	0,58	0,20	1,59	-0,11	1,03	-0,01	0,03	-0,01	0,03	-0,0003	0,02
	Atmospheric pressure	0,57	1,77	-2,20	4,71	2,21	3,49	0,07	0,08	-0,003	0,06	0,05	0,10
	Wind speed	**3,44**	**1,70**	**-11,62**	**4,27**	**7,40**	**2,64**	0,04	0,04	-0,003	0,03	0,03	0,05
	Max. tide level	0,58	1,25	-1,69	3,02	0,44	1,58	0,02	0,04	-0,01	0,04	0,02	0,04
	Min. tide level	-1,36	1,42	-0,15	1,72	0,61	1,53	0,04	0,04	0,03	0,04	-0,003	0,03

Table 5 - *A posteriori* estimated linear regression coefficients of the abiotic variables as predictors for the temporal variance of the mussel dominance zone aggregation pattern. Values obtained by the BVS method (see section 2.3). lag 0 = contemporaneous time series, lag 1 = 3-months delayed time series and lag 2 = 6-months delayed time series. Post. Mean = Posterior mean value for the regression coefficient. Post SD = Posterior Standard Deviation of the mean value for the regression coefficient. Bold values refer to an at least positive evidence for an effect of the climatic predictors on the response biotic variable (see Table 3).

(conclusion)

		Barnacle cover		**Mussel cover**		**Available space**		**Superior limit**		**Inferior limit**		**Amplitude**	
		Post. Mean	**Post. SD**	**Post. Mean**	**Post. SD**	**Post. Mean**	**Post. SD**	**Post. Mean**	**Post. SD**	**Post. Mean**	**Post. SD**	**Post. Mean**	**Post. SD**
lag 2	PAR	0,31	1,84	1,08	4,18	-1,16	2,96	-0,02	0,06	-0,03	0,07	0,01	0,07
	SSS	-0,03	0,75	**5,52**	**4,08**	**-5,55**	**2,55**	-0,01	0,02	0,01	0,03	-0,02	0,04
	Rainfall	-1,11	1,64	2,05	3,39	-0,59	1,90	-0,04	0,05	0,0008	0,04	-0,02	0,05

We could observe trends of increase for maximum tidal level (Figure 2.A) and wind speed (Figure 2.B), which are consistent with the trends of increase in the vertical amplitude and the superior limit of barnacle dominance zone (Figures 3.A and 3.B, respectively). Furthermore, a recent study showed that global mean sea level has risen around 3 mm yr^{-1} between 1993 and 2018 (Nerem *et al*., 2018), while in the present study we observed an increase of around 2 mm yr^{-1} (Figure 2.A). Another study gathered evidence that between 2010 and 2017 wind got 0.02 m s^{-1} yr^{-1} faster globally, in which global warming played an important role (Zeng *et al*., 2019). In the present study the same tendency was observed, but the mean increase of wind speed was around 0.04 m s^{-1} yr^{-1} (Figure 2.B). Nevertheless, these trends address the concern that global climate change may affect a marine community structure at local level, once the local climatic conditions followed the global trends.

While changes in the percentual barnacle cover in barnacle dominance zone could be predicted by previous season maximum and minimum tidal levels with a negative correlation, changes in the mussel cover in the same zone was predicted by previous season minimum tidal level with a positive correlation (Tables 2 and 4). Regarding the mussel dominance zone, changes in the percentual mussel cover could be predicted by previous season minimum tidal level with a negative correlation, while a positive correlation was observed between available space and the same predictor. A positive correlation was also observed between changes in the percentual barnacle cover and contemporary maximum tidal level (Tables 3 and 5). These results suggest that the tidal level oscillations may have accounted for the changes in abundance of mussels and barnacles in both dominance zones. A study conducted at the California coast gathered evidence that daily barnacle *Chthamalus* sp. settlement was cross correlated to maximum daily tidal levels, while also hypothesizing that tidal level oscillations account for the onshore transport of cyprids - along other site-specific coastal features such as tidal range, type of bottom topography, and water column density structure (Shanks, 1986). Another study at an Indian mangrove showed that the preferential settlement height of barnacles *Balanus amphitrite amphitrite* Darwin, 1854 and oysters *Crassostrea madrasensis* (Preston, 1916) and *Saccostrea cuccullata* (Born, 1778) is due the tolerance to extended submergence and emergence caused by tidal oscillations. In that intertidal environment, oysters are not able to withstand extended periods of emergence, and thus settle lower than barnacles (Karuppaiyan and Raja, 2007).

The oscillations in percentual mussel cover in barnacle dominance zone could be predicted by previous semester wind speed with a positive correlation (Tables 2 and 4). Concerning the mussel dominance zone, oscillations in barnacle cover and available space could be predicted by contemporary, previous season, and previous semester wind speed, all with positive correlations, while mussel cover was predicted by previous semester wind speed with a negative correlation (Tables 3 and 5). The presented results emphasize the synergistic influence of tidal levels and wind speed variations on a local intertidal community. In a similar way, an experimental study on the embryos of the gastropods *Dolabrifera brazieri* G. B. Sowerby II, 1870 and *Bembicium nanum* (Lamarck, 1822) brought evidence that radiation, sea temperature and salinity interplay a synergistic effect on their mortality and development rate (Przeslawski *et al*., 2005). Although studies regarding barnacles and mussels are still necessary, the study with gastropds indicates the possibility of synergistic effects of environmental conditions on intertidal organisms' reproduction. As sessile organisms, the only way changes in barnacle and mussel abundances can be observed is through recruitment and growth of new individuals, and by extension, the organisms' reproduction. In addition, as discussed previously, the vertical position of both dominance zone limits could be predicted by sea level rise and faster winds. Considering the environmental changes that will possibly happen as a consequence of global climate change, the knowledge about synergistic effects of abiotic conditions is key for the understanding of changes in community structure and diversity and, ultimately, of the emergence of novel ecosystems (Doney *et al*., 2011).

Acknowledging the constant trend of increase in maximum tidal level (Figure 2.A), the constant trend of increase in wind speed (Figure 2.B), and also the trend of increase in minimum tidal level until mid-2015 (Figure 2.C) allowed the inference that environmental changes enabled mussels to survive higher on the rocky shore. The trend of increase in mussel cover (Figure 3.D) along the trend of decrease in barnacle cover (Figure 3.C) in barnacle dominance zone might mistakenly lead to the conclusion that mussels have elapsed barnacles in upper midlittoral zone. Considering this accentuated upwards shift in position of the superior limit, and since the monitoring protocol is based on quadrats positioned at fixed heights, it is evident that barnacles were not necessarily substituted by mussels, but rather barnacles and mussels were both able to settle and survive higher on the rocky shore. Yet, barnacles were also able to settle in patches of free space within mussel dominance zone.

In central Chile, for example, recruitment of the mussel *Perumytilus purpuratus* (Lamarck, 1819) in the intertidal zone depends upon the presence of recruitment mediators, such as mussel or barnacle clumps (Navarrete and Castilla, 1990). Also, in the Gulf of California, field experiments showed that the presence of barnacle *Chthamalus anisopoma* Pilsbry,1916 clumps enhanced the settlement of the mussel *Brachidontes semilaevis* (Menke, 1848) (Lively and Raimondi, 1987). Thus, generally barnacles are primary space colonizers while mussels benefit on this colonization to occupy the rocky shore. These evidences, along with those presented previously, may explain why mussels never completely dominated the rocky shore. Then, the observed increase of mussel abundance in barnacle dominance zone might have been a combination of favorable conditions for barnacles and mussels' survival higher on the rocky shore, and also changes in barnacle recruitment pattern benefiting mussel settlement. Moreover, barnacles were also able to settle in patches of free space within the mussel dominance zone, which possibly was an important condition for mussels to recolonize those spaces when environmental conditions were not suitable for their survival in the upper midlittoral zone.

The variance in available space in barnacle dominance zone could be predicted by contemporary and previous semester SST with a positive correlation, and there was also a positive correlation for air humidity during the previous semester predicting the availability of space. Additionally, barnacle cover was negatively influenced by contemporary air humidity (Tables 2 and 4). In the mussel dominance zone, the oscillations of mussel cover could be predicted by previous season relative air humidity, with a negative correlation (Tables 3 and 5). These results indicate that the dynamics of available space in both dominance zone might have been attributed to the SST and the air humidity temporal oscillations. While the process behind the available space temporal dynamics might seem vague, looking at weak evidence (Tables 2 and 4) it is possible to notice that changes in mussel cover in barnacle dominance zone could be predicted by contemporary SST (negative correlation) and also by previous season air humidity (positive correlation), which can be related to those results. Regarding the mussel dominance zone, yet still looking at weak evidence of an effect, oscillations of mussel cover could be predicted by contemporary and previous semester SST (positive correlation), while availability of space could be predicted by contemporary and previous semester SST (negative correlation). This full scenario elucidates that summer high temperatures usually predicts a reduction in mussel cover within the barnacle dominance zone, concomitantly to the appearance bare rock patches in the upper midlittoral zone. Also, the same predictor was related to an increase in the abundance of mussels in the mussel dominance zone. Contrastingly, autumn high air humidity predicted the persistence of mussels within the barnacle dominance zone, which elapsed the barnacle cover within the fixed quadrats. High relative air humidity was also predicted a decrease in the mussel abundance within the mussel dominance zone, indicating that even when climatic conditions favored their survival in the upper midlittoral, mussels were not able to dominate the lower midlittoral zone.

The relation between mussel cover and temperature could be expected, as it was previously reported in São Sebastião city (northern São Paulo State Coast) for mussels *Mytilaster solisianus* (d'Orbigny, 1842) (as *Brachidontes solisianus*) which, due to differences in shell anatomy and color, were more susceptible to death during late summer than barnacles *Chthamalus bisinuatus* (Pilsbry, 1916) (Eston *et al*., 1986). Furthermore, summer 2019 was the hottest (Figure 2.D) over the seven years of monitoring. Also, the October 2019 Climate Report from NOAA showed that the first ten months of that year was globally one of the hottest in 140-years of monitoring. Additionally, the January-October mean ocean temperature anomalies have been increasingly warmer since 1980 all around the world (NOAA, 2019). Thus, the warmer ocean might have accounted for the sudden disappearance of mussels from barnacle dominance zone observed after summer 2019 (Figure 3.D). Presumably, this scenario emphasizes that global warming may have influenced community structure changes at the local level.

The opercular and basal diameters of barnacles in barnacle dominance zone could be predicted by the wind speed during the previous season, both with a negative correlation. While the opercular diameter could be predicted by previous season SST, the basal diameter could be predicted by previous semester SST, both with a negative correlation (Tables 2 and 4). *C. bisinuatus* increases its larvae release rate one day after being exposed to extremely hot temperatures, which can be understood as a last reproduction effort when mortality risk is high (Kasten and Flores, 2013). Thus, the prediction of the appearance of smaller barnacles after summer high temperatures could be expected and was measured as a decrease in mean opercular and basal diameters. Apparently, seasons with high wind speed may have also accounted for the appearance of smaller barnacles, which could possibly be explained by the faster winds carrying the cyprids onshore. In fact, Hawkins and Hartnoll (1982) observed a peak in settlement of barnacle *Semibalanus balanoides* (Linnaeus, 1767) in Isle of Man in response to faster onshore winds. Although it was not possible to analyze wind direction in the present study, for missing data regarding the years of 2018 and 2019 at the studied locality in NOAA's Blended Sea Winds database, an earlier study in Mar Casado Beach showed that winds blow essentially onshore all over the year at this locality (Silva et al., 2019).

The oscillations of the mean opercular diameter of barnacles could be predicted by previous semester air humidity with a positive correlation, and also by previous semester minimum tidal level however with a negative correlation. Mean basal diameter was negatively affected by contemporary air humidity, while being positively affected by previous semester air humidity (Tables 2 and 4). These results indicate that seasons with high air humidity are marked by the arrival of new barnacles, which can be predicted by the air humidity conditions during the previous semester. Not only, the seasons with low minimum tidal levels also predict the appearance of smaller individuals of barnacles.

Knowing that the seasonal peak of high air humidity occurs during autumn and the lowest minimum tidal levels during winter, these results corroborate the hypothesis of an arrival of new individuals to the barnacle dominance zone predicted by summer environmental conditions, as discussed previously. Furthermore, the air humidity conditions during spring also predicts the decrease of barnacle opercular and basal diameters. While dryer springs augment the arrival of new individuals, moister springs suppress this biotic response resulting in an increase in the mean size of individuals.

Both the shifts in position of the superior limit and the changes in amplitude of barnacle dominance zone could be predicted by contemporary SSS with a negative correlation, and a positive correlation regarding previous semester SSS (Tables 2 and 4). In the mussel dominance zone, the shift in the position of the inferior limit could be predicted by contemporary SSS with a negative correlation, while there was a positive correlation between the vertical amplitude and the same predictor (Tables 3 and 5). These results reveal that while the barnacle dominance zone amplitude variation is more strongly influenced by the temporal trends of its superior limit, in the mussel dominance zone the influence of the temporal trend in the inferior limit is stronger.

The position of mussel dominance zone inferior limit could be predicted by previous season atmospheric pressure with a negative correlation, whereas the amplitude of that zone could be predicted by contemporary atmospheric pressure with a positive correlation (Tables 3 and 5). These results alone might suggest that there was a delay between the change in dominance zone amplitude and the inferior limit position shift, given the different lags of the environmental predictor. Yet, a peek at the weak evidence reveals that the position of the mussel dominance zone superior limit could be predicted by contemporary atmospheric pressure with a positive correlation, while the position of the inferior limit could be predicted by the same predictor, yet with a negative correlation. So, in fact, oscillations in the dominance zone amplitude are caused by concomitant variations of the superior and inferior limits, possibly in response to environmental conditions.

The seasonality observed for SSS reaches its lowest levels during winter (Figure 2.E), when atmospheric pressure reaches its highest peak (Figure 2.G). There is evidence that the seasonal oscillation of SSS in the South Atlantic coast is related to river discharges into the ocean, along the intensity and direction of wind stress, with less salty waters occurring during winter (Dessier and Donguy, 1994; Piola, 2005). This kind of influence could be observed extending along a coastal strip of 1.300 Km from the Plata River estuary (Piola *et al*., 2005). Presumably, the same seasonality and causal relation could be expected for the studied location. In fact, the Guarujá city is an island surrounded by the Santos Estuary and the Bertioga Canal (Figure 1) which could be influencing seasonal oscillations in SSS, yet further studies are necessary. Regarding the atmospheric pressure, seasonal oscillations are directly related to the influence of the South Atlantic Subtropical Anticyclone (SASA). SASA extends over southeastern Brazil during winter, causing an increase in mean sea level atmospheric pressure. This seasonal displacement of SASA hinders precipitation and decreases the wind intensity in the southern Brazil coast (Reboita *et al*., 2019). Although the reviewed literature brought no evidence that atmospheric pressure is capable of inducing physiological responses in barnacles or mussels, our results bring evidence that those climatic conditions affected by seasonal variations of SASA and also seasonal oscillations of SSS are good predictors for changes in the abundances of mussels and barnacles in the rocky shore and the size of barnacles.

From the perspective of the winter peak of both environmental conditions mentioned above, it is possible to evaluate that during this season a widening in the barnacle dominance zone amplitude can be expected, concomitant to the superior limit rise. Also, the SSS during the previous semester predicted that superior limit rise. We could not find any published studies that focused on understanding the relation between the seasonal oscillations in sea salinity and changes in the vertical aggregation pattern of intertidal organisms, indicating a gap of knowledge that can be further investigated. Regarding the mussel dominance zone, it was evident that SSS and atmospheric pressure performed antagonistic effects on dominance zone inferior and superior limits. The prediction of a wider or narrower dominance zone depended on the strength of the environmental signaling.

The availability of space in the mussel dominance zone could be predicted by contemporary and previous semester SSS with a negative correlation, and also by contemporary atmospheric pressure but with a positive correlation. Also, oscillations of the mussel abundance in that zone could be predicted by previous semester SSS as well, with a positive correlation (Tables 3 and 5). Thus, during the winter peak of both SSS and atmospheric pressure an increase in available space can be expected, as a result of the decrease in mussel cover. This relation may be corroborated when taking into account the weak evidence, which showed a negative correlation between mussel cover and contemporary atmospheric pressure and a positive correlation between mussel cover and contemporary SSS, which predict a decrease in mussel cover after those winter conditions.

Regarding the barnacle dominance zone, dead barnacle cover could be predicted by previous semester SSS with a negative correlation and mean basal diameter could be predicted by previous semester atmospheric pressure also with a negative correlation (Tables 2 and 4). Winter environmental conditions are correlated with an increase in the recruitment of new barnacles individuals, viewed as a decrease in mean basal diameter of barnacles one semester after winter high atmospheric pressure. This result is consistent with the observation that barnacles *C. bisinuatus* can settle throughout the whole year in the northern São Paulo coast

(Eston *et al.*, 1986). Additionally, the seasonal low SSS during winters predicted an increase in dead barnacles cover in the barnacle dominance zone.

3.4. Environmental predictors influence on BSTS modeling of biotic variables

It was possible to infer that only a trend and a seasonal component were not enough to describe precisely at least some of the community structure changes observed during the monitoring time span (see the evident distance of the red lines, which represent trend and seasonal effects only, in relation to the black lines with dots, which represent original data, in Figures 5 and 6). Thus, there may be other temporal components that influenced these changes.

Our initial hypothesis was that environmental factors could predict changes in the community structure, given the extensive literature that brings evidence of how environmental variables affect the growth, survival and reproduction of barnacles and mussels. In fact, by analyzing the goodness of fit of the BSTS modeling (Table 6) it is evident that only in some cases the addition of abiotic predictors could be considered as an improvement in the models, when compared to those with only a trend and a seasonal oscillation. Such cases were the models for the superior limit, the opercular and the basal diameter of barnacles within the barnacle dominance zone. These results indicate that taking environmental conditions into consideration enhanced the prediction of those changes related to the shifts in the position of the barnacle dominance zone superior limit, the recruitment of barnacle propagules, and also their growth (increase in the mean diameter of the individuals). Regarding the mussel dominance zone, the models that considered only a trend and a seasonal effect performed better in describing the observed data. These results indicate that taking the environmental conditions into consideration does not enhance the prediction of the changes in the community structure lower on the rocky shore. The differential results of the goodness of fit measure regarding the two dominance zones seem to indicate that environmental conditions might be more important for the individuals that settle higher on the rocky shore, and thus are most strongly affected by the cyclical oscillations of the tidal levels.

Nevertheless, for most environmental predictors it was possible to elicit a reasonable physiological background responsible for the biotic responses to the observed environmental changes. Yet, there may be also unexplored factors that could predict the observed changes in the community structure. Examples of these unexplored factors are microenvironmental factors, such as surface topography, which affects settlement (Mullineaux and Butman, 1991), anthropogenic impacts, such as trampling, which affects percent cover (Smith and Murray, 2005), and biotic interactions, such as interspecific competition for space (Connell, 1961). The latter could be indirectly observed, however was not addressed as a predictor during the modeling process. Another aspect of the adopted modeling approach was that it was possible to identify the cumulative effect of previous seasons and previous semesters environmental conditions in predicting the contemporary state of the biotic variables.

Figure 5 - Comparative graph of BSTS models describing the barnacle dominance zone variables temporal oscillation. The models consider trend and seasonal components only (red line), trend, seasonal and the linear regressor component of abiotic predictors (blue line), and original data (black line with dots).

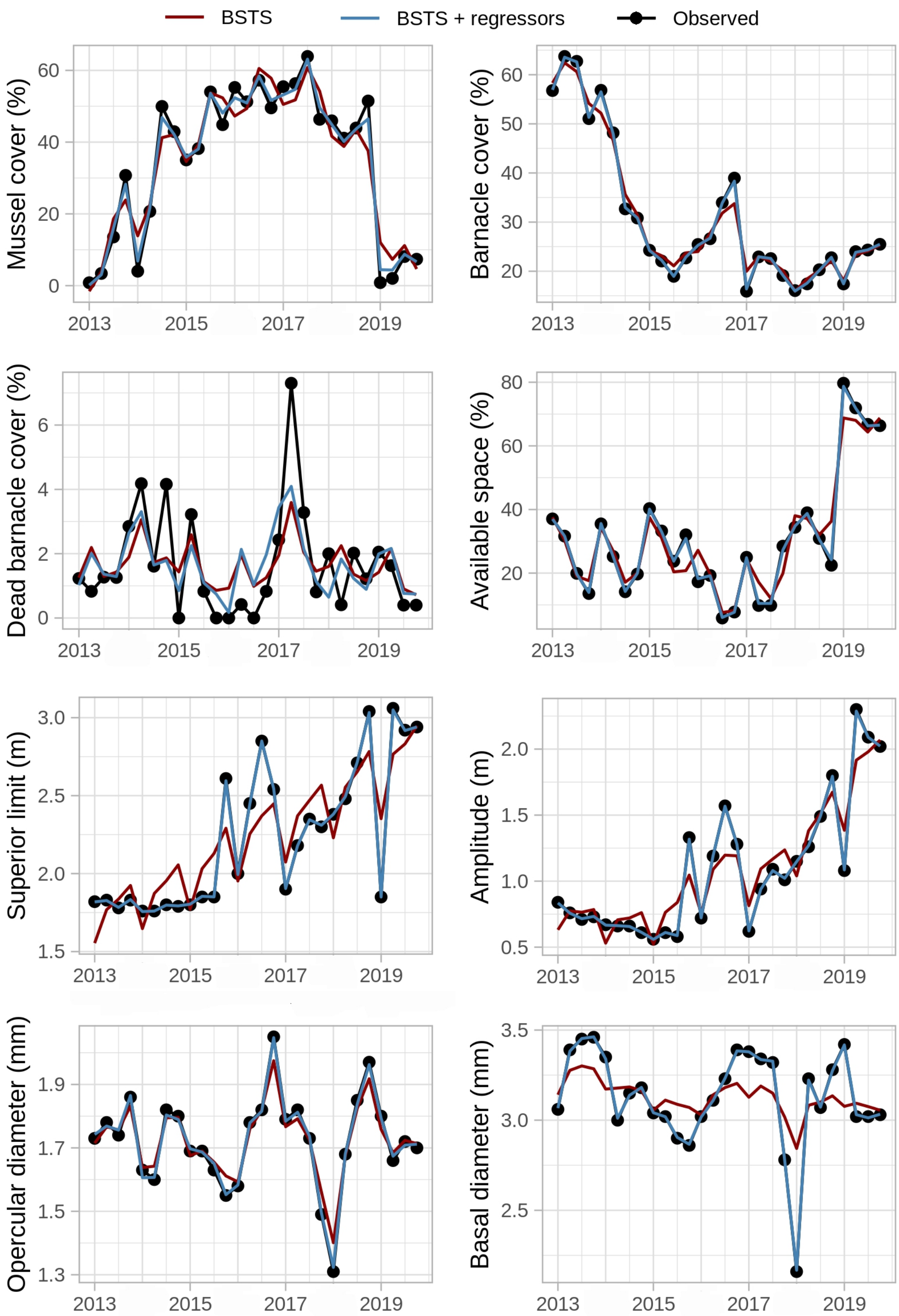


Figure 6 - Comparative graph of BSTS models describing the mussel dominance zone variables temporal oscillation. The models consider trend and seasonal components only (red line), trend, seasonal and the linear regressor component of abiotic predictors (blue line), and original data (black line with dots).

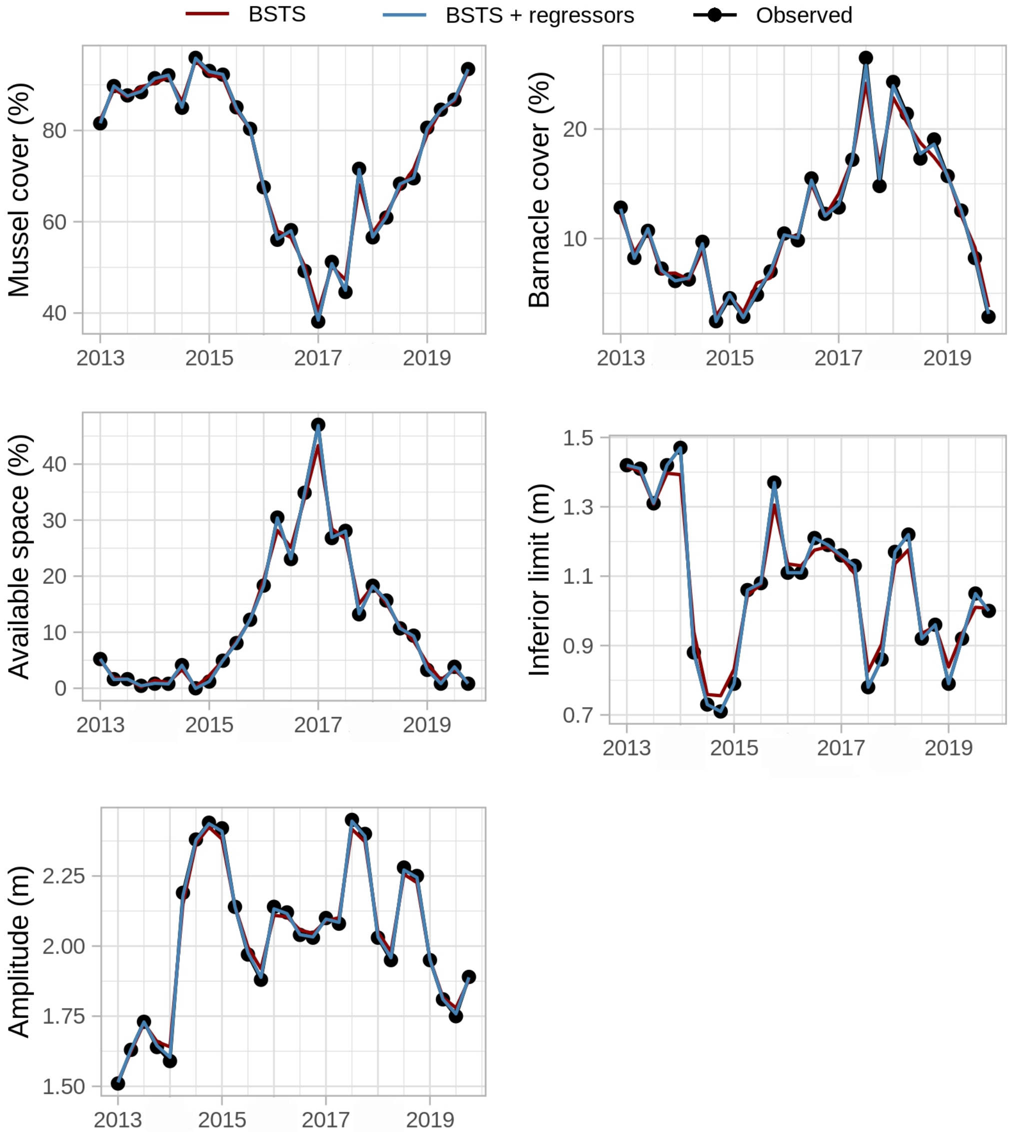


Table 6 - Comparison of the Bayesian Information Criterior (BIC) values for the BSTS modelling of the barnacle and mussel dominance zones variables. The BSTS model that considers only a trend and a seasonality is compared to the model that considers a trend, a seasonality and the linear regressor component of abiotic predictors identified through BVS method.

	Barnacle dominance zone		**Mussel dominance zone**	
Biotic variable	**BSTS**	**BSTS + regressors**	**BSTS**	**BSTS + regressors**
Superior limit	40.43545	36.72108	-21.85671	-2.739402
Amplitude	43.5665	49.2916	15.45945	22.24406
Inferior limit	-23.32421	1.193772	11.15517	13.99565
Barnacle cover	221.2543	231.3854	184.2178	189.8658
Mussel cover	247.5622	255.3525	227.8782	236.2533
Available space	246.9374	256.7998	215.243	232.958
Opercular diameter	-4.672612	-13.53013	-	-
Basal diameter	36.38653	29.70821	-	-
Dead barnacle cover	136.3615	139.2364	-	-

CONCLUSIONS

The aggregation pattern of barnacles and mussels was monitored between the years of 2013 and 2019, and during this period there was an upwards shift in the superior limit of barnacle dominance zone, causing an widening in that zone over time. Some environmental conditions were good predictors for these changes, such as the temporal trend of increase in tidal levels and wind speed, which followed the global climate change trends. Physiological responses that could explain the observed correlations include the desiccation stressors possibly allowing barnacles to survive higher on the rocky shore. In addition, mussels were able to settle within the barnacle dominance zone, viewed as an increase in their percentual cover, that could be predicted by the interannual variations of the same environmental conditions. Additionally, reduction of mussel cover and increase in available space in the barnacle dominance zone were related to high SST events. Also, the barnacle settlement was predicted by wind speed and tidal level seasonal oscillations, along the summer SST and air humidity conditions, as well as the winter SSS conditions.

Although mussels were able to survive increasingly higher on the rocky shore, they did not dominate the midlittoral region. Conversely, there was an increase in available space concomitant to this upwards occupation that could be predicted by wind speed, tidal levels, air humidity, and SSS. Besides colonizing primary space higher on the rocky shore, barnacles could also colonize the patches of free space within the mussel dominance zone, possibly because mussels do this less efficiently. The settlement of barnacles in the mussel dominance zone could be predicted by the temporal oscillations of tidal levels and wind speed. As mussels benefit from the presence of barnacle clumps to settle, this colonization was possibly important for mussels to recolonize their own zone when environmental conditions were not favorable to their survival higher on the rocky shore.

It was possible to identify the scarcity of studies concerned at analyzing the physiological responses of barnacles *Chthamalus* and mussels *Brachidontes* to environmental stressors, which are commonly found organisms inhabiting the intertidal zone of rocky shores worldwide. In addition, no study has focused on understanding how the seasonal fluctuations of salinity can influence changes in the vertical aggregation pattern of intertidal organisms, although correlational evidence could be found in the present study.

The fact that the trends of change in local environmental conditions were similar to the global trends draws the attention to the recurring concern of understanding how climate change affects the marine benthos. The present study represents a multispecies approach to track, and possibly forecast, the responses of a marine ecosystem to the synergistic influence of environmental variations. Beyond that, the inclusion of lagged abiotic predictors improved the descriptive precision of at least some of the adopted models. This effect was possibly due to a delay between physiological responses of the intertidal organisms to the climatic conditions and significant changes in aggregation pattern. Thus, predictive models aiming at understanding how future scenarios of climate change could affect intertidal communities should consider those lagged predictors.

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