

Temporal variation in intertidal community recruitment and its relationships to physical forcings, chlorophyll-*a* concentration and sea surface temperature

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Abstract We investigated the recruitment of intertidal barnacles and mussels at three temporal scales (months, weeks and days), and its relationships to physical forcings, chlorophyll-*a* concentration (Chla) and sea surface temperature (SST), at both a local (km) and a regional (10–100 km) resolution. The study was conducted in the South Brazilian Bight, a subtropical region influenced by upwelling and meteorological fronts, where recruitment rates were measured monthly, biweekly and daily, from 2012 to 2013 using artificial substrates fixed in the intertidal zone. The strength of the relationship between recruitment and physical forcings, Chla and SST depended on the temporal scale, with different trends observed for barnacles and mussels. Barnacle recruitment was positively correlated with wind speed and SST and negatively related to the wind direction, cold front events and Chla. Wind direction

was positively correlated with mussel recruitment and negatively covaried with SST. We calculated net recruitment (NR) to estimate the differences in recruitment rates observed at longer time scales (months and weeks), with recruitment rates observed at shorter time scales (weeks and days), and found that NR varied in time and among taxa. These results suggest that wind-driven oceanographic processes might affect onshore abundance of barnacle larvae, causing the observed variation in recruitment. This study highlights the importance of oceanic–climatic variables as predictors of intertidal invertebrate recruitment and shows that climatic fluctuations might have different effects on rocky shore communities.

Introduction

Models and algorithms developed to describe ecological relationships serve as a basis for predicting future consequences of climatic conditions for marine communities. However, even simple empirical relationships between ecological processes and environmental variables are still fairly scarce in the literature (Walther et al. 2002; Harley et al. 2006). As it is practically impossible to reproduce realistic climatic conditions in laboratory conditions, temporal replications of natural phenomena over time series are a valuable tool for investigating and detecting covariation with ecological processes (Parmesan et al. 2000; Stenseth et al. 2002).

Recruitment rates provide crucial information for understanding temporal patterns of adult abundances, distributions and intraspecific and interspecific interactions (Roughgarden et al. 1988; Caley et al. 1996; Kinlan and Gaines 2003). Settlement and recruitment are also used to address benthic–pelagic coupling of intertidal populations and communities (Navarrete et al. 2008; Jenkins et al.

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2008; Jacinto and Cruz 2008; Lathlean et al. 2010; Gyory and Pineda 2011). Thus, the description of ecological dynamics of intertidal organisms depends on knowledge of recruitment rates and how they vary in time and space.

Recruitment, defined as the number of settled larvae that survive the initial post-settlement period (Keough and Downes 1982; Connell 1985; Jenkins et al. 2008), is partially dependent on the number of competent larvae near settlement sites. Consequently, one would expect recruitment and the supply of competent larvae to be correlated. However, settlers and recruits are exposed to very different environmental conditions than they experience as meroplankton, and conditions change within a short period of time from the water column to the benthos (Crisp 1976; Okubo 1994). Recruitment is influenced by many factors that impact the growth and survival of settlers and recruits (e.g., Nasrolahi et al. 2013). Recent settlers suffer high mortality rates (e.g., Nasrolahi et al. 2013), consequently affecting recruitment rates. Variations in recruitment rates are related to biotic (e.g., larval competency, Satuito et al. 1997; biofilms, Wieczorek and Todd 1998; gregarious behavior, Knight-Jones and Stevenson 1950) and abiotic factors (e.g., substrate heterogeneity, Bers and Wahl 2004; hydrodynamic characteristics, Eckman et al. 1990; mesoscale features, Woodson et al. 2012). Furthermore, in natural habitats, these factors may interact with each other, and their effects vary with the scale of observation. Therefore, explaining variation in recruitment requires measurements at multiple spatial and temporal scales (Pineda et al. 2009).

Correlations between recruitment rates and oceanographic–meteorological variables at different temporal scales have been used as evidence that pelagic processes regulate recruitment. For rocky shore intertidal invertebrates, most information is from areas with persistent coastal upwelling regimes where wind, sea surface temperature (SST) and chlorophyll-*a* concentration (Chla) correlate with recruitment (Range and Paula 2001; Menge et al. 2009, 2011; Iles et al. 2012). Variation in sea surface is caused by several oceanographic phenomena, and these processes may affect the transport of larvae and the mortality of settlers and recruits (Jenkins and Hawkins 2003; McQuaid and Lindsay 2000; Hunt and Scheibling 1997). For example, variation in sea surface height may be correlated with fluctuations in recruitment rates, although processes that influence sea level (i.e., storms, coastally trapped waves and large-scale currents) are rarely considered in recruitment studies (but see Pineda and López 2002). Correlations between recruitment rates and oceanographic variables depend on the temporal frequency of recruitment measurements (Tapia and Navarrete 2010), but most studies have not investigated more than one temporal scale simultaneously. Due to the level of intrinsic

stochasticity in meteorological and oceanographic processes, it is crucial to consider temporal resolution to improve the predictive capability of models of recruitment dynamics. Additionally, time is required for recruitment to respond to a change in the pelagic environment, and time series investigations should include time lags in correlation analyses of physical variables and recruitment rates (e.g., McCulloch and Shanks 2003; Narváez et al. 2006).

Barnacles and mussels are important components of intertidal communities and are frequently used as model organisms in recruitment studies. However, they respond differently to variations in the pelagic environment, such as changes in SST (Dudas et al. 2009; Iles et al. 2012). Differences in larval behavior (Shanks and Brink 2005) and in tolerance of recruits to environmental stress (Wetthey et al. 2011) can also explain recruitment variation between barnacles and mussels. For example, barnacle and mussel larvae may not concentrate at the same depth prior to settlement (Miron et al. 1995; Graham and Sebens 1996), have different swimming capabilities (Young 1995) and hence are exposed to different currents and transport mechanisms (McCulloch and Shanks 2003). In addition, the seasonality and frequency of reproduction in both groups are often distinct (Starr et al. 1991), resulting in contrasting larval abundances between the two taxa, potentially affecting recruitment rates.

We measured recruitment, wind, waves, sea surface height (SSH), Chla and SST in a subtropical area that is influenced by a meteorological regime that alternates between two relatively opposite phases. First, when a warm high-pressure center dominates the regional meteorological fields, N–E–NE winds prevail, and surface waters are transported offshore. Second, during meteorological cold fronts, low-pressure centers cross the region, coinciding with periods of onshore surface water transport (Carbonel 2003; Lorenzetti et al. 2009). These two meteorological regimes can be distinguished by their specific wind and wave fields, as well as by their SST and Chla signatures. During cold fronts, winds and waves are from SW–S–SE and surface waters are approximately 20–23 °C, in the opposite condition, winds are from N–E–NE, waves are from E and surface waters may be above 26 °C, when warmed by solar radiation, or drop below 18 °C if upwelling occurs (Valentin et al. 1987; Stech and Lorenzetti 1992; Gonzalez-Rodriguez et al. 1992; Stevenson et al. 1998; Campos et al. 2000; Carbonel 2003; Pianca et al. 2010). Chla and SST variability is locally driven, but strong N–E–NE winds may cause upwelling of nutrient-rich waters and phytoplankton blooms (Castelao and Barth 2006).

The alternation between these two dominant oceanographic regimes is highly stochastic, resulting in varying SSH wave, wind, SST and Chla fields, from days to seasons. Depending on their duration and strength, both phases

might influence the dynamics of the pelagic system. Cold fronts last from 2 to 7 days (Stech and Lorenzetti 1992; Gallucci and Netto 2004). N–E–NE wind conditions may last from 2 to 10 days (Gonzalez-Rodriguez et al. 1992). Moreover, both regimes have cumulative monthly and seasonal effects, for example in sea surface temperatures and wave height (Franchito et al. 2008; Pianca et al. 2010). To evaluate the importance of these physical processes on recruitment, it is necessary to measure recruitment at scales of months, weeks and days.

We tested the hypothesis that during meteorological cold fronts, larvae are transported to the nearshore near settlement sites, resulting in increased recruitment rates as long as the Chla and SST are favorable for larval metamorphosis and juvenile growth during the post-settlement period. This hypothesis was tested by evaluating changes in recruitment rates of rocky shore invertebrates at monthly, weekly and daily temporal scales in response to fluctuations in physical forcings, such as SSH and winds. It was expected that higher recruitment rates would be observed when cold fronts dominate, winds and waves are strong and from SW–S–SE, and sea level near the coast (SSH) rises. Since larval development and recruitment are affected by Chla and SST (Hoegh-Guldberg and Pearse 1995; Phillips 2002; Thiagarajan et al. 2005), the relationships between recruitment rates and Chla and SST were also investigated. We assumed that a linear relationship between recruitment rates and a given variable would be a strong indicator of either potential mechanisms of larval transport, or oceanographically favorable conditions for the onset of recruitment.

Materials and methods

Study area and region

This study was carried out along rocky shores located on the E–SE side of the Island of São Sebastião at Castelhanos Bay and at Fortaleza Bay, located in the South Brazilian Bight, in the Southwest Atlantic Ocean (Fig. 1). This region is characterized by abundant granitic rocky shores exposed to wave action alternating with shallow bays and sandy beaches along a complex coast line, and it integrates two marine protected areas. This study area was chosen because the influence of cold fronts and upwelling events is expected to be pronounced, due to the greater distance from the coast (for Island São Sebastião), and given the variability in currents, wave action, sea water temperature and food availability in the water column associated with these oceanographic regimes (Valentin et al. 1987; Stech and Lorenzetti 1992; Gonzalez-Rodriguez et al. 1992; Stevenson et al. 1998; Campos et al. 2000; Carbonel 2003; Pianca

et al. 2010). The intertidal communities found along these rocky shores are rich, varying in their abundance, distribution and composition (Coutinho and Zalmon 2009), mainly due to differences in wave exposure, geomorphology, pelagic productivity and anthropogenic impacts (Christofolletti et al. 2011).

To investigate variation at the scale of months or weeks, three sites located 5 km apart in Castelhanos Bay (Fig. 1) were sampled. The three sites had similar wave exposure, orientation, geomorphological features, depths (20-m isobaths), anthropomorphic pressure and accessibility. Additional daily samples were taken in Bravinha Beach in Fortaleza Bay, 30 km from the Castelhanos Bay sites, along the coast of the island (Fig. 1). The Fortaleza Bay site was chosen for daily sampling because during cold fronts and other large wave conditions, the three sites in Castelhanos Bay are inaccessible. Bravinha Beach is shallower than Castelhanos Bay and differs in orientation to the open ocean (Castelhanos Bay, >20 m, open to the E; Fortaleza Bay, <12 m, open to the SE). The duration of the monitoring included the meteorological–oceanographic conditions of interest.

Physical forcings, Chla and SST

Data collected at local (km) and regional (10–100 km) scales included physical forcings (wind field, wave height and sea surface height), Chla and SST. The local scale measurements were taken in situ or estimated from data available in the study area. Regional estimates were made for the entire study region, including areas along the continental shelf. In situ measurements of physical forcings were obtained from the oceanic–meteorological stations of the Oceanographic Institute/USP located near Fortaleza Bay (monthly and weekly scales) and of the Agronomic Institute of Campinas located in São Sebastião Channel, close to Castelhanos Bay (daily scales). Data from the station with the longest continuous time series were chosen for the analyses. In situ Chla and SST were measured at the same nearshore location where recruitment was measured. Other estimates (zonal u and meridional winds v , significant wave height SWH, sea surface height SSH, Chla and SST) were obtained from a specific global database generated from remote sensing data and numerical modeling, which are detailed below.

Wind field was described by in situ wind speed (ws) and direction (wd), the intensity of the decomposed zonal (u) and meridional winds (v), and the number of cold fronts. Sampling period in situ wind data was 15 min. Meteorological cold fronts were observed when winds were from the S–SE–SW, and upwelling was observed when winds from N–NE–E. Estimates of u and v were made from the NCEP/NCAR database (Kalnay et al. 1996) at resolutions of 4 h,

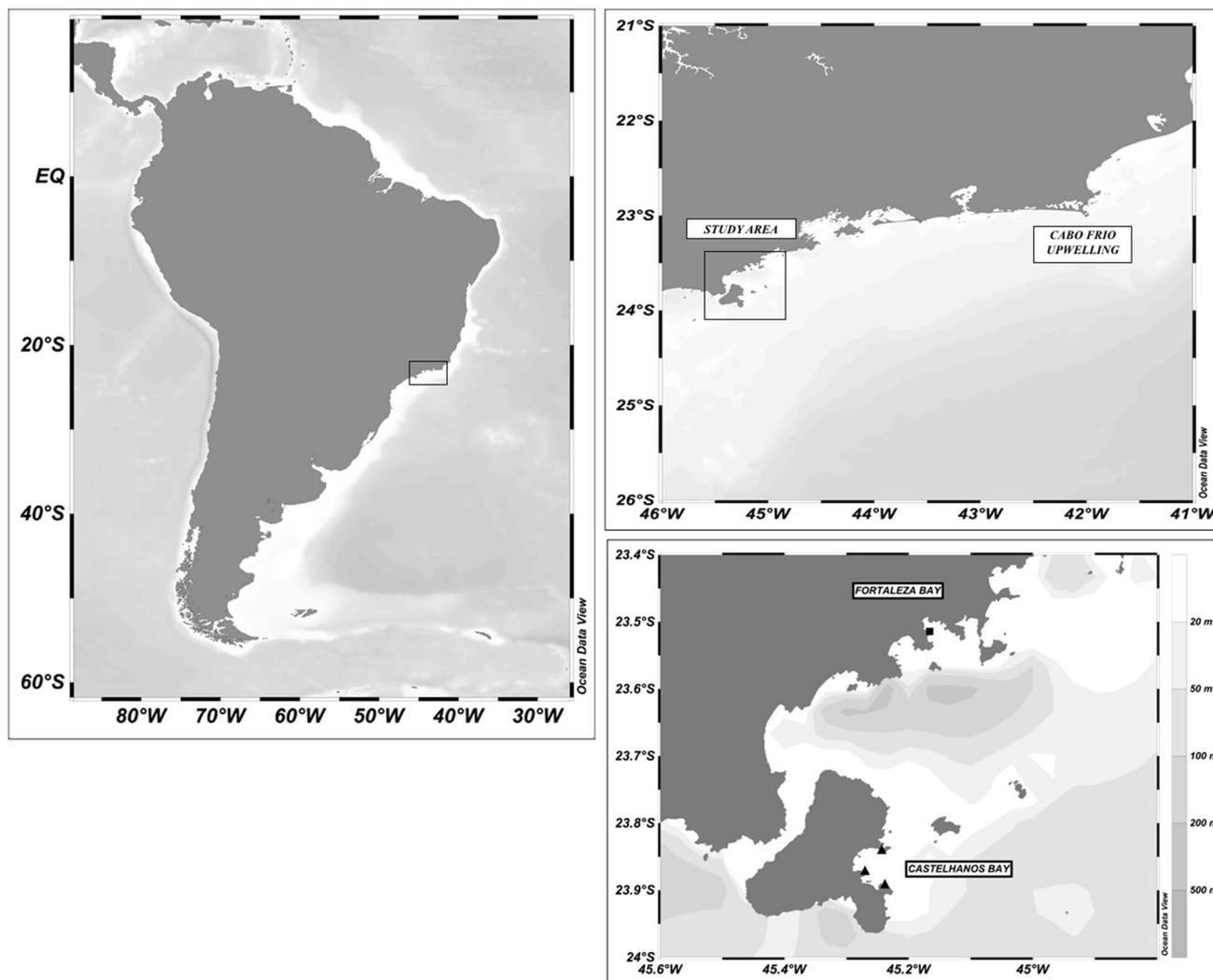


Fig. 1 Continental and regional views of study areas. The Brazilian coast in the South Atlantic Bight (*upper left*); Cabo Frio upwelling center, encompassing the study region (*upper right*); study sites

for the investigations performed at the scales of months and weeks (Castelhanos Bay), and at the scale of days (Fortaleza Bay), *lower right*

and 2.5° latitude \times 2.5° longitude. Local estimates were averaged for 25°S , and regional estimates were averaged from 21 to 26°S and 41° to 46°W . The number of meteorological cold fronts that passed over the Brazilian coast and reached the study region was determined from the monthly report of CPTec for 2012/2013 (reference area: Ubatuba-SP, Center for Weather Forecasting and Climate Research). Cold front conditions last longer than 1 day, but no index of cold front intensity at the daily scale is available. Therefore, the events are described as present or absent, and quantitative information for cold front intensity was not included in the daily resolution analysis.

Wave height was obtained from the Aviso database (MSS_CNES_CLS10, <http://www.aviso.oceanobs.com/>), which uses altimeter radar measurements from the satellites

Jason-1, Jason-2 and Envisat to generate the daily average significant wave height (SWH) at a spatial resolution of 1° latitude \times 1° longitude. Local estimates were averaged for a specific area of the shelf (23° to $25^\circ\text{S}/46^\circ$ to 44°W). Regional estimates were averaged for the area from 21 to 26°S and 41° to 46°W . Sea surface height (SSH) was measured in situ with a tide gauge at a temporal resolution of 3 min between acquisitions.

Chla derived from satellite, an indicator of phytoplankton biomass in the upper water column, was determined monthly and weekly by remote sensing from the GIOVANNI database (Acker and Leptoukh 2007), which generates these estimates using radiometers on the MODIS-Aqua satellite at temporal and spatial resolutions of 8 days and 4 km. Local estimates were averaged for a specific

area of the shelf (23° to 25°S/46° to 44°W). Regional estimates were averaged for the area from 21 to 26°S and 41° to 46°W. Additionally, regional satellite maps that included the presence and extension of the Cabo Frio plume, and estimates of Chla inside the plume, were used to describe the regional Chla field. Daily local and regional estimates of Chla are not available from remote sensing, and they were estimated from in situ fluorescence measurements made during the study, measured twice a day. In situ measurements of natural fluorescence of sea water were converted into Chla values according to the procedure to fluorescence of extracted chlorophyll-*a* from particulate matter (Welschmeyer 1994). Natural fluorescence was measured in three samples of 20 ml each of surface sea water collected adjacent to the shore twice a day (morning and afternoon). After acclimation in the dark for 30 min, fluorescence was measured in a 5-ml aliquot using a portable fluorometer (AquaFluor[®], Turner Designs, Sunnyvale, CA, USA). Chlorophyll extraction was carried out six times during the sampling campaign. For this purpose, three samples of 500 ml of surface sea water were filtered through GF/F glass fiber filters (0.7 µm, Whatman[®]) after 30 min of acclimation in the dark. Filters and the retained material were displaced in a 90 % acetone solution for 48 h, and after extraction, fluorescence was measured using the same fluorometer.

SST data were obtained from the NOAA OI SST V2 database (Reynolds et al. 2007), which incorporates corrected estimates of temperature obtained from a high-resolution radiometer (AVHRR) at a temporal and spatial resolution of 1 day and 0.5° latitude × 0.5° longitude. Local and regional SST estimates were taken at the same coordinates as the measurements of Chla. Additional regional SST ocean surface images were derived from the GIOVANNI database (MODIS-Aqua; 1 month, 4-km resolution, Kalnay et al. 1996). Patterns detected in the maps included the presence or absence of the upwelling plume, the area of the plume and the SST associated with the plume. During the daily campaigns, in situ SST was also measured through averaging in situ observations conducted twice per day using a portable handheld temperature system (YSI Model 30).

Recruitment

Recruitment rates (RRs) were measured on artificial substrates, plates for barnacles (all Cirripedia) and Tuffys for mussels (all Bivalvia), placed in the intertidal zone along the rocky shore. Plates were flat PVC squares (8 cm × 8 cm × 0.2 cm) covered with Safety Walk[®] 3 M anti-slip tape, which provides adequate rugosity to stimulate barnacle settlement. Tuffys are traps made of a multi-filament plastic mesh (typically used for dishwashing;

S.O.S. Tuffy[®]) and provide a complex substrate for settling mussel larvae. All substrates were placed at the mid-intertidal zone about 5 m apart. The dominant species in this zone is the barnacle *Tetraclita stalactifera* although other species of barnacles and mussels were present. For mussels, the most abundant is *Perna perna* (Coutinho and Zalmon 2009). Plates and Tuffys were secured to the rocks with stainless steel screws and washers. At the end of each sampling period, the experimental substrates were replaced with fresh ones, and plates and tuffys containing settlers were transported to the laboratory and frozen at -20 °C until being processed (minimum freezing time: 1 day). In the laboratory, barnacle recruits on the plates were counted using a stereomicroscope (Zeiss Discovery v.08). Tuffys were washed in fresh water, and recruits longer than 100 µm were separated using a calibrated metal mesh (100 µm) and then preserved in an ethyl alcohol solution (70 %) until being counted under a stereomicroscope.

Recruitment can be defined as the number of settled larvae that survive the initial post-settlement period (Keough and Downes 1982; Connell 1985; Jenkins et al. 2008), and different studies define the post-settlement period in different ways, that is, the post-settlement period is arbitrarily defined. Here, we define ‘settlers’ as individuals encountered after 1 to 3 days of trap deployment (scale: days); ‘early recruits’ are the individuals encountered after approximately 15 days of trap deployment (scale: weeks); finally, ‘late recruits’ are the individuals encountered after approximately 1 month of trap deployment (scale: months).

‘Net recruitment’ (NR) was calculated to estimate differences in recruitment rates measured at longer time scales (months or weeks), with recruitment rates measured at shorter time scales: months versus weeks and weeks versus days. Considerations of this analysis include: first, that recruitment is greater when more free space is available for settlement, and the settlement substrate saturates (Minchinton and Scheibling 1993; but see Pineda and Caswell 1997); second, that the longer the recruitment sampling period, the greater the mortality of the settlers; third, a potential positive effect of early recruits on posterior settlement (Michener and Kenny 1991; Pineda 2000); and fourth, a potential reduction in mortality of settlers due to buffering of stressful conditions by early recruits (e.g., Bertness 1989). Therefore, we expect that longer sampling intervals will result in lower recruitment rates than consecutive shorter sampling periods if free space and increases in post-settlement mortality factors dominate. Alternately, if recruitment rates measured at longer time scales are higher than those observed using consecutive shorter time-scale measurements, early recruits might have a positive effect on new settlers because of, for example, gregarious settlement (discussed in Pineda 2000), or settler mortality may be reduced due to thermal buffering effects (Bertness

1989). The NR (see ‘Data analysis’) allows comparisons between recruitment measurements at different temporal scales. NR was calculated using data from Castelhanos Bay (months vs. weeks) and from the Bravinha site (weeks vs. days).

Temporal scales and sampling design

Recruitment rates (RRs) of barnacle and mussels were measured at three temporal scales: months, weeks and days. Monthly estimates were made from April 18, 2012, to June 12, 2013, resulting in 13 sampling events of approximately 30-day intervals. Barnacles and mussel recruitment were measured simultaneously during these periods. However, in the monthly samplings performed in July and August 2012, the plates were not replaced, consequently barnacle recruitment was measured continuously during both months, and all calculations accounted for this issue.

Recruitment rates were also measured biweekly (approximately 15 days, scaled as ‘weeks’), in 3 periods simultaneously to the monthly measurements. There were a total of 10 biweekly sampling events: six consecutive sampling events in winter, from April 18 to August 21, 2012; two consecutive sampling events in summer, from November 27 to January 8; and two consecutive sampling events at the end of summer, from January 29 to March 1, 2013. Biweekly sampling was discontinued because accessing the shores was not possible due to adverse wave conditions. For the biweekly and monthly temporal scales, recruitment was estimated along the three Castelhanos Bay shores using 5 to 10 replicates of each sampling device, and replicates were averaged for each period.

Daily samples at Fortaleza Bay were taken continuously from March 6, 2013, to March 24, 2013, according to the following design: Eight replicates of each substrate were replaced daily (total of 15 sampling events), four replicates of each substrate were replaced every 3 days (total of 5 sampling events) and four replicates of each substrate remained in place from 6 to 24 March (one sampling event). Tuffys and plates were interspersed and placed at two areas 50 m apart along the shore, but this spatial structure was not accounted for in this analysis, and the two areas were treated as one. In two cases, the daily samplings comprised 2 to 3 days (March 14 to 16 and March 17 to 20) because it was impossible to safely access the intertidal zone during large wave conditions.

Data analysis

RR [(settlers.d⁻¹) and (early or late recruits.d⁻¹)] was obtained by calculating the average recruitment rate standard deviation in each of the two study sites. Physical forcings were described with using the following

variables: wind speed w_s [m s⁻¹] and wind direction w_d [degrees], zonal and meridional u and v [m s⁻¹], number of cold fronts [units], significant wave height SWH [m] and sea surface height SSH [m]. The average concentration of chlorophyll-*a* Chla [mg m⁻³] and the average temperature in surface waters SST [°C] were calculated for each recruitment sampling period (months, weeks and days). Two scales of representation, regional and local, were included for the physical forcings, SST and Chla data.

Temporal variation of the oceanographic–meteorological conditions was assessed as follows: (1) regional trends over time were described from graphs made for representative periods of time at scales of months, weeks and days; (2) w_s and w_d were categorized according to the origin, speed and percentage of time the wind assumed a determined orientation (%); and (3) maps of Chla and SST were analyzed to infer the presence and characteristics of the Cabo Frio upwelling plume.

To test the hypothesis that recruitment is related to cold fronts, we assessed the (1) temporal synchrony and (2) the linear correlation between continuous time series of RR and each variable for the physical forcings, Chla and SST through correlation analysis (Sokal and Rohlf 2003). The series were considered synchronous when $r \geq 0.51$. Time-lagged analyses (obtained by cross-correlation analysis) were conducted only for the daily comparisons (+ or -1 and 2 days), which had sufficient time measurements. We assumed $\alpha = 0.05$ and determined the significant p values using the false discovery rate method (Garcia 2004; Verhoeven et al. 2005, Pike 2011). Temporal autocorrelation was assessed by comparing each variable versus time with a simple correlation analysis. Variables were considered autocorrelated when testing whether the null hypothesis that the correlation coefficient was not equal to 0 with $p \leq 0.05$. The following variables were temporally autocorrelated (see Electronic Supplementary Material Table S1): scale of months, number of cold fronts (total), SWH (regional), SST (local); scale of weeks, w_d , v (local and regional), Chla (regional), SST (local and regional); scale of days, SWH (regional), Chla (in situ), SST (local and in situ). We removed the autocorrelation by taking the differences between the averages of consecutive periods (e.g., Pineda and López 2002) (see Electronic Supplementary Material Table S2) and used the differences to conduct the final analyses for those variables. In the scale of weeks, summer data (December and February) were not analyzed because of insufficient data. We used R-project (R Development Core Team 2005), ODV (Schlitzer 2013) and Panoply 3.1.8 (Schmunk 2013) software to conduct the statistical analyses and as graphical tools.

Net recruitment (NR) was calculated by the following formulas

$NR = [R_m - (R_1 + R_2)]/T_m$ for net recruitment differences between months [late recruits. d^{-1}] and weeks [early recruits/d]. Here, R_m is the average recruitment measured during the month [late recruits], R is the average recruitment measured during the biweekly intervals (R_1 and R_2 , 15 days each) within the respective month, and T_m is the total sampling time in that month, with units days [d];

$NR_{3D} = [R_w - (RR_{3d} \cdot T_w)]/T_w$ for net recruitment differences between weeks (15 days) [early recruits. d^{-1}], and the corresponding 3-day periods [settlers/d]. R_w is the average recruitment measured during these weeks [early recruits], RR_{3d} is the average recruitment rate for the 3-day periods [settlers. d^{-1}], and T_w is the total sampling time in this period, with units days [d];

$NR_{1D} = [R_w - (RR_{1d} \cdot T_w)]/T_w$ for net recruitment differences between weeks (15 days) and the corresponding 1-day periods [recruits. d^{-1}]. Here, R_w is the average recruitment measured during these weeks [recruits], RR_{1d} is the average recruitment rate of the 1-day period [recruits, d^{-1}], and T_w is the total sampling time in this period, with units days [d].

Note that the scale of weeks refers to samplings conducted biweekly (approximately 15 days) and that this sampling was simultaneous to the monthly sampling. The comparisons of NR were made only for the periods when both the monthly and the biweekly sampling were available. We calculated a total of 4 NR for barnacles and 5 NR for mussels.

Results

Oceanic–meteorological conditions

The wind field was mostly influenced by winds from the N–E quadrant, which is the prevailing condition from winter to summer (higher values on the map) (Fig. 2a to d). In winter, the intensity of the wind velocity field was higher than in summer (4 to 7 m/s) (Fig. 2a) and gradually increased from western to eastern areas near the Cabo Frio upwelling center (Fig. 2c). In spring, wind speed was highest (6 to 9 m/s), with prevailing winds from the NE and E, and a smooth spatial gradient from W to E (Fig. 2b). Spatial variation was greater in summer (Fig. 2c) than in winter (Fig. 2a), but the summer average wind speeds were the lowest among all seasons (1 to 3 m/s). In fall, the influence of the SE winds was the most significant, and the average wind speeds were similar to those observed in spring (6 to 9 m/s) (Fig. 2d). Cold fronts reached the study region most frequently in late fall (May and June), but they were also

present in October (Fig. 2, see Electronic Supplementary Material Table S3). The number of cold fronts that reached the study area was always lower than the total number of fronts that reached the Brazilian coast (see Electronic Supplementary Material Table S3).

In situ winds from the NE and NW were dominant in the study area (observed in 20 to 30 % of the sampling period) (see Electronic Supplementary Material Table S3). Highest wind speeds usually originated from the NE (4 to 7.7 m/s), but SW winds also ultimately reached maximal speeds. Minimum values ($ws < 6$ m/s) were observed from May to August and in October and December of 2012 and April to June of 2013. Two periods with fewer cold fronts, relevant to this study, must be highlighted, November 2012 and March 2013, when winds from the S were more frequent than in the other months (frequency: SW, 10 %; SE, >5 %) (see Electronic Supplementary Material Table S3). In December and March, winds from the E reached their maximum frequency and cold fronts were absent in the study region (see Electronic Supplementary Material Table S3). The remote sensed zonal (u) winds were dominated by W winds (negative averages), with a greater influence of E winds observed in May and June of 2012 and in January, April and June of 2013 (Fig. 4c). The meridional component v was most affected by S winds during May, October and November of 2012 and by N winds in May and June (Fig. 4d).

Average significant wave height SWH in the region varied from 1 to 3.5 m, with maxima in winter and minima in summer, with a gradient of wave height from W to E (Fig. 2e to Fig. 2h). In spring and fall, SWH was similar, but the spatial gradient was from N to S (Fig. 2f and Fig. 2h). Within the study area, wave height varied from 1.5 to 2.5 m, with maxima in October and minima in February (Fig. 2e to h, Fig. 4e). Maximum sea surface height SSH was in June, and minimum levels were observed in spring (September) and the beginning of summer (January) (Fig. 4g).

For the entire region, higher levels of Chla were observed in spring (Fig. 3f), when SST was lower compared to the other seasons (Fig. 3e, g, h). The upwelling plume influenced Chla in the surface waters over the shelf throughout the year whereas it only influenced waters close to the study sites from August to November (late winter–spring) (see Electronic Supplementary Material Table S4, Fig. 3f), when Chla was the highest inside the plume. Within the study area, the Chla levels in the surface waters over the continental shelf were highest between June and August 2012 (Fig. 4h), when temperatures were the lowest (Fig. 4i), being influenced by cold currents from the southern shelf (Fig. 3a).

The daily recruitment samples were obtained during at least two cold fronts that corresponded with a wind direction change from N to S and increased wind speeds before and after the events (Fig. 7b). The cold fronts were

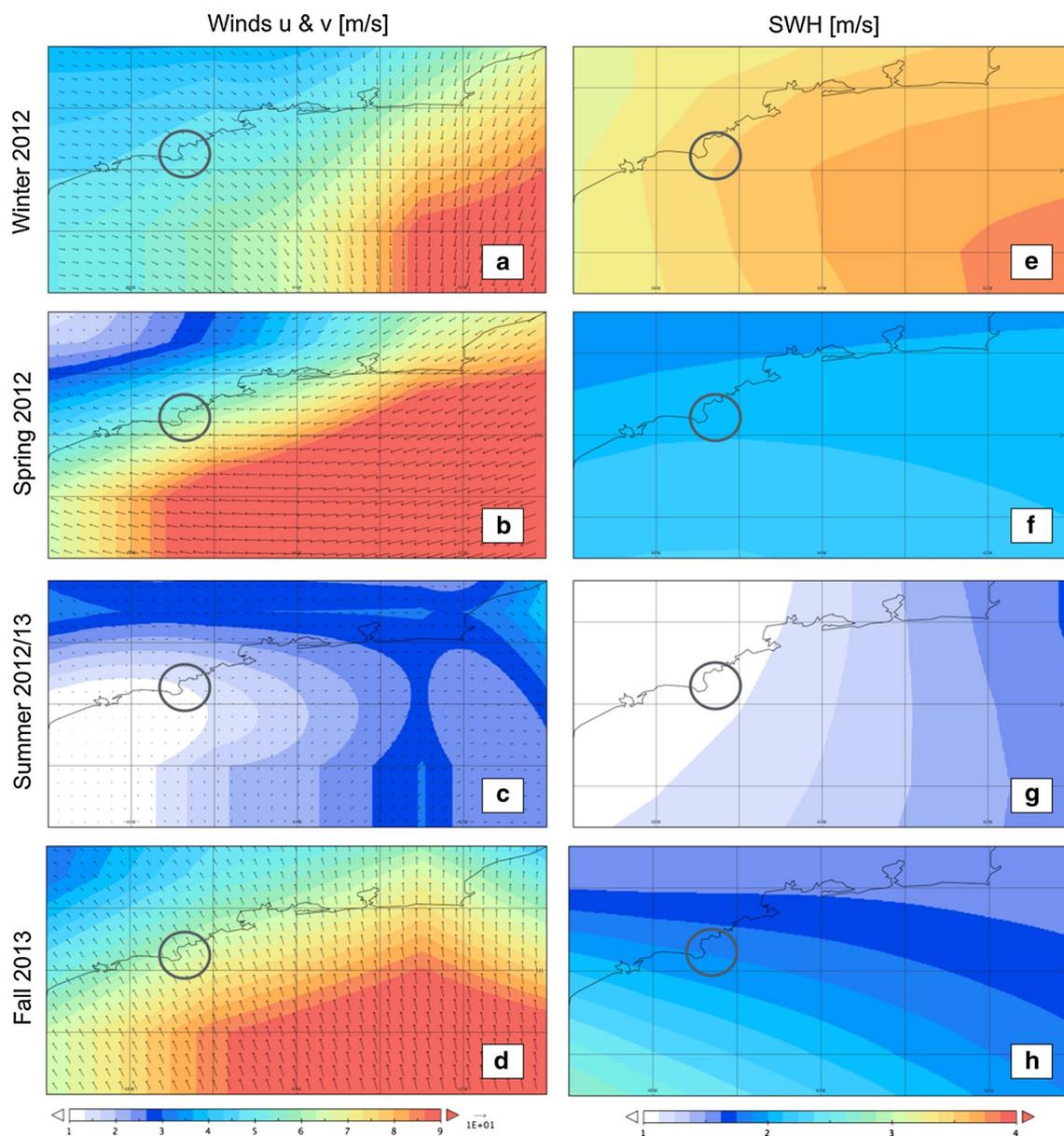


Fig. 2 Seasonal differences in wind (u and v components) (**a**, **b**, **c**, **d**), and waves (significant wave height, SWH) (**e**, **f**, **g**, **h**) in the study region (21 to 26°S and 41° to 46°W). The predominant condition was characterized on specific dates in each season: July 18 for win-

ter 2012, October 8 for spring 2012, December 18 for summer 2012 and May 17 for fall 2013. The color scale represents the gradients of the u , v , and SWH intensities. In panels **a–d**, vectors represent wind direction, wd

associated with an increase in SWH and SSH (Fig. 7e and g), and SWH and SSH reached 2–3 m over the shelf, in addition to elevating Chla levels from 1.5 to 4.5 mg/m^3 (Fig. 7h) and decreasing the SST by 3 $^{\circ}\text{C}$ (Fig. 7i).

Recruitment

Physical forcings, Chla and SST correlated with the observed variation in recruitment over some temporal

scales. Correlations tended to be higher for the recruitment of barnacles ($r \geq 10.61$) than for the mussels (Table 1 and 2) and only significant for the recruitment of mussels at shorter time scales (weeks and days) ($r \geq 0.9$, and $r \geq -0.58$). Overall, considering the spatial scales of the drivers investigated in this study, the local conditions showed stronger correlations than the regional conditions. Net recruitment varied according to the taxa, period of the year and temporal scale of comparison. Specific trends and

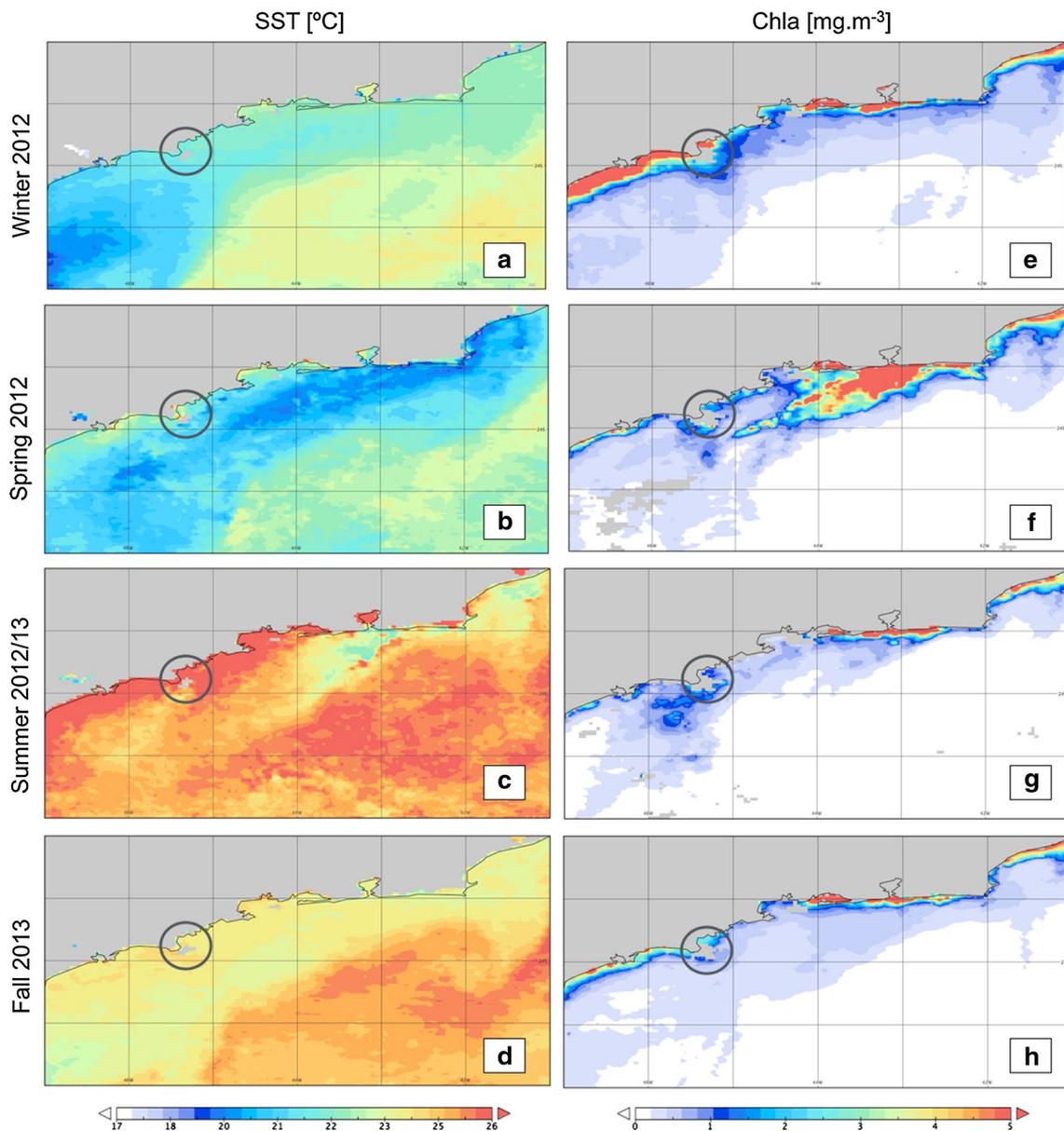


Fig. 3 Seasonal differences in SST (sea surface temperature) (**a, b, c, d**) and Chla (concentration of chlorophyll-*a*) (**a, b, c, d**) (21 to 26°S and 41° to 46°W). The predominant condition was characterized dur-

ing specific periods in each season: July for winter 2012, October for spring 2012, December for summer 2012 and May for fall 2013. The color scale represents the gradients of SST and Chla

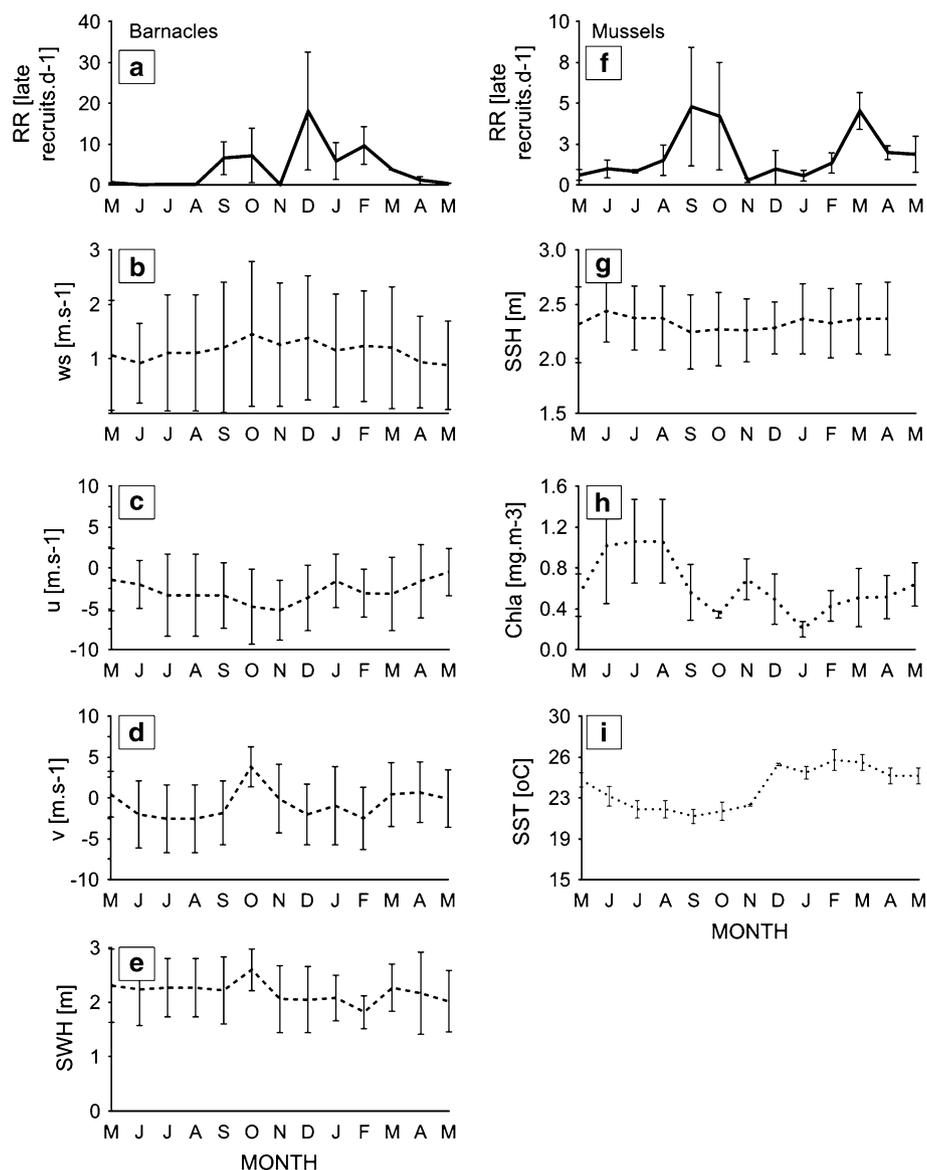
results are detailed in the following text; potential larval transport mechanisms and relevant issues regarding these results are addressed in the Discussion.

Barnacles

Recruitment of barnacles occurred year-round (Fig. 4a). The ws, wd and the number of cold fronts correlated with the observed fluctuations in barnacle recruitment at scales ranging from days to months, as did SST (Table 1). Higher rates were registered in spring (September and October),

summer and the beginning of fall (December to March) (Fig. 4a), when the ws was also highest and dominated by NE–E winds (Fig. 4b, see Electronic Supplementary Material Table S3), whereas fewer cold fronts arrived (see Electronic Supplementary Material Table S3), and local levels of Chla in surface waters were low (Fig. 4h). Maximum recruitment occurred in December (Fig. 4a), when cold fronts were absent in the area (see Electronic Supplementary Material Table S3), Chla levels were minimal (Fig. 3g and Fig. 4h) and the SST was the highest during the study (Fig. 4i). From May to August, recruitment remained close

Fig. 4 Variation in the average monthly recruitment rates (RRs) of barnacles (a) and mussels (f), physical forcings (wind speed, ws (b); zonal wind intensity, u (c); meridional wind intensity, v (d); significant wave height, SWH (e); sea surface height, SSH (g)), Chla (concentration of chlorophyll-*a*) (h) and SST (sea surface temperature) (i) from April 18, 2012, to June 12, 2013. Only the local averages of ws, u, v, SWH, SSH, Chla and SST are presented in the graphs; error bars represent standard deviations (SD); sample size (*n*) varies according to each variable (See ‘Materials and methods’)



to zero (Fig. 4a). In November, when winds from the SW achieved their highest frequency during a strong cold front (see Electronic Supplementary Material Table S3), recruitment was nearly zero (Fig. 4a). A significant temporal synchrony and correlation with recruitment rates were observed for the ws (positive) and wd (negative), number of cold fronts (negative) and Chla (negative) (Table 1). All of the identified correlations occurred at the local scale for the average rates (Table 1).

Barnacle recruitment rates also varied among weeks, with considerable differences observed between consecutive sampling dates (Fig. 5a and 6a). During winter, recruitment was slightly higher during the first 2 weeks but remained nearly zero in the two other biweekly periods sampled (Fig. 5a), when recruitment was only positively correlated with wind direction (Table 1), which was an

opposite trend compared to that observed in monthly and daily trends (Table 1). During summer (Fig. 6a), maximum ($RR \geq 10$ early recruits/d) and minimum ($RR \geq 4$ early recruits/d) recruitment occurred alternately.

Daily recruitment of barnacles occurred immediately after the arrival of a cold front, and the maximal RR reached 4 settlers/day (Fig. 7a), which was synchronous with an increase in ws (Fig. 7b) an increase in SSH (Fig. 7g) and followed by a change in wd from N to S (Fig. 7c and d). Some of these patterns were confirmed by cross-correlation analysis (Table 1). Subsequent changes in wind direction did not result in other recruitment peaks, but the RR decreased with a change in the wd from S to N (Fig. 7c and d). At this scale, significant results of correlation analysis showed that (Table 1): RR was positively correlated with lagged SWH and SST, whereas it

Table 1 Results of the correlation (scales: months and weeks) and cross-correlation analysis (scale: days) to examine temporal synchrony and correlation between recruitment of barnacles and the physical forcings (*ws/wd* wind speed and direction, *u* and *v* velocity of wind, number of cold fronts; *SWH* significant wave height, *SSH* sea surface height), *Chla* and *SST*

	Months		Weeks		Days LAG (<i>r</i>)				<i>p</i>
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	−1	0	1	2	
<i>ws</i>						0.51			0.053
<i>wd</i>	−0.66	0.016*	<i>0.91</i>	≤0.01*	−0.49				0.044
<i>u</i>									
Local	−0.28	0.350	0.58	0.169		−0.02			0.933
Regional	−0.33	0.267	0.51	0.246		0.01			0.989
<i>v</i>									
Local	−0.09	0.761	−0.33	0.139		−0.08			0.774
Regional	−0.12	0.685	−0.25	0.100		−0.04			0.890
Cold fronts									
Local	−0.61	0.022*	0.02	0.966	NA	NA	NA	NA	NA
Total	<i>0.29</i>	0.381	−0.19	0.681	NA	NA	NA	NA	NA
<i>SWH</i>									
Local	−0.24	0.427	−0.08	0.872				0.59	0.011*
Regional	−0.09	0.798	−0.27	0.564		<i>0.27</i>			0.333
<i>SSH</i>	−0.45	0.145	0.58	0.169	0.59				0.032*
<i>Chla</i>									
In situ	NA	NA	NA	NA		−0.41			0.143
Local	−0.62	0.025*	NA	0.160	NA	NA	NA	NA	NA
Regional	−0.32	0.281	<i>0.12</i>	0.822	NA	NA	NA	NA	NA
<i>SST</i>									
In situ	NA	NA	NA	NA		<i>0.31</i>			0.277
Local	<i>0.60</i>	0.036	<i>0.65</i>	0.165				<i>0.59</i>	0.022*
Regional	0.29	0.323	<i>0.72</i>	0.109				0.63	0.011*

Correlations (*) were considered as significant when $p \leq 0.05$ and $\alpha = 0.05$ as determined by the false discovery rate method (See “Materials and methods”). *r* correlation coefficient, *p* probability of error. Results in italics refer to data that were corrected to remove temporal autocorrelation prior to analysis (See “Materials and methods”); NA indicates data were not available

was negatively correlated with lagged *SSH*. For the wind-related variables, the degree of correlation was lower compared to the scale of months, but the detected trends were similar to that registered at the scales of months and weeks (Table 1).

Barnacle NR varied according to the period of the year and the temporal scale of comparison (Fig. 8). When recruitment was compared at the scales of weeks to months (Fig. 8a to d), lower NR was registered in May (Fig. 8a), December (Fig. 8c) and February (Fig. 8d). The NR between weeks and 3-day (Fig. 8e) periods was negative and was close the values observed in May (Fig. 8a). However, NR was positive when weeks were compared to 1-day periods.

Mussels

Recruitment of mussels showed low degrees and statistically insignificant correlation with oceanoclimatic variables and only covaried with wind direction at the scale of weeks and with *SST* at daily scales (Table 2).

Maximum recruitment occurred in September and October (spring) and March (fall), showing two distinct peaks (Fig. 4f). In both periods, *u* and *SST* (local and regional) displayed lower values (Fig. 2b, d, 3b, d, 4c, i). The first recruitment peak (Fig. 4f) coincided with higher regional *Chla* levels (Fig. 2f), together with a more frequent occurrence of the upwelling plume (see Electronic Supplementary Material Table S4). The maximum mussel RR (Fig. 4f) was lower than maximum barnacle RR (Fig. 4a). During the other months, the RRs averaged fewer than 2 late recruits/day (Fig. 4f), similar to the minimum rates found for barnacles (Fig. 4a), and the lowest recruitment was recorded in November (Fig. 4f), like barnacles (Fig. 4a).

In the winter, recruitment at the scale of weeks was close to 1 early recruit/day (Fig. 5f). The lowest values were found in the last weeks of June and beginning of July (Fig. 5f), and recruitment was synchronous with the fluctuation of *ws* (Table 2). During summer (Fig. 6f), the differences in RRs between weeks were higher, although the rates were low, similar to those found during the winter weeks (Fig. 5f).

Table 2 Results of the correlation (scales: months and weeks) and cross-correlation analysis (scale: days) to examine the temporal synchrony and correlation between recruitment of mussels and the physical forcings (*ws/wd* wind speed and direction, *u* and *v* velocity of wind, number of cold fronts, *SWH* significant wave height, *SSH* sea surface height), *Chla* and *SST*

	Months		Weeks		Days LAG (<i>r</i>) 0	<i>p</i>
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>		
<i>ws</i>	0.31	0.311	0.964	≤0.01*	−0.24	0.389
<i>wd</i>	−0.26	0.391	−0.41	0.365	0.01	0.971
<i>u</i>						
Local	−0.24	0.433	−0.19	0.658	0.10	0.717
Regional	−0.28	0.355	−0.21	0.612	0.13	0.643
<i>v</i>						
Local	0.41	0.168	0.12	0.804	−0.06	0.839
Regional	0.43	0.141	0.19	0.675	−0.08	0.769
Cold fronts						
Local	−0.14	0.648	0.28	0.499	NA	NA
Total	0.16	0.534	0.26	0.532	NA	NA
<i>SWH</i>						
Local	0.43	0.143	0.48	0.233	−0.19	0.947
Regional	0.44	0.127	0.41	0.317	−0.08	0.788
<i>SSH</i>	−0.24	0.342	−0.12	0.779	0.31	0.269
<i>Chla</i>						
In situ	NA	NA	NA	NA	0.09	0.065
Local	−0.25	0.414	0.10	0.807	NA	NA
Regional	0.24	0.435	0.46	0.303	NA	NA
<i>SST</i>						
In situ	NA	NA	NA	NA	−0.59	0.027*
Local	0.05	0.911	−0.47	0.286	0.44	0.161
Regional	−0.21	0.500	−0.41	0.365	0.43	0.110

Correlations (*) were considered as significant when $p \leq 0.05$ and $\alpha = 0.05$ as determined by the false discovery rate method (See “Materials and methods”). *r* correlation coefficient, *p* probability of error. Results in italics refer to data that were corrected to remove temporal autocorrelation prior to analysis (See “Materials and methods”); NA indicates data were not available

Recruitment of mussels was highly stochastic when assessed daily, with no prominent recruitment peaks, and it was not influenced by the arrival of a cold front (Fig. 7a). Recruitment rates were negatively correlated with in situ *SST*, with high recruitment rates at lower temperatures (Table 2).

NR was positive in almost all the comparisons (Fig. 9). This trend was stronger during summer months (Fig. 9d and e) and was most intense during the daily samplings (Fig. 9f). The only exception was registered in May 2012, when the NR was 0.27 recruits/d (Fig. 9a).

Discussion

Relationship between physical forcings, *SST* and *Chla* and the importance of the temporal resolution

Our results show potential for oceanographic–meteorological variables (See abbreviations, Table 3) to explain the variation in recruitment detected at different temporal resolutions

for two invertebrate groups. Resolving temporal scales is critical for demarcating among competing ecological processes (Bjørnstad and Grenfell 2001), and temporal resolution is particularly relevant when addressing climate-related processes (Stenseth et al. 2002). The physical environment and pelagic conditions in this study were dynamic, and temporal variation at shorter time scales may be as strong as seasonal variation (e.g., *SST*, Lorenzetti et al. 2009). Most of the observed relationships between recruitment rates and oceanographic–meteorological variables were consistent among the three time scales studied, suggesting that similar oceanographic conditions influence recruitment in the same way at different temporal scales. The magnitude and sign of correlations across temporal scales (months, weeks and days) within each taxonomic group (barnacle or mussel) were similar in most of the cases Tables 1 and 2.

In this regard, there are two issues to be considered. The first is the response time between changes in environmental conditions and the specific response of organisms. For example, differences in *Chla* can be significant at a monthly scale, especially across seasons (Wieters et al.

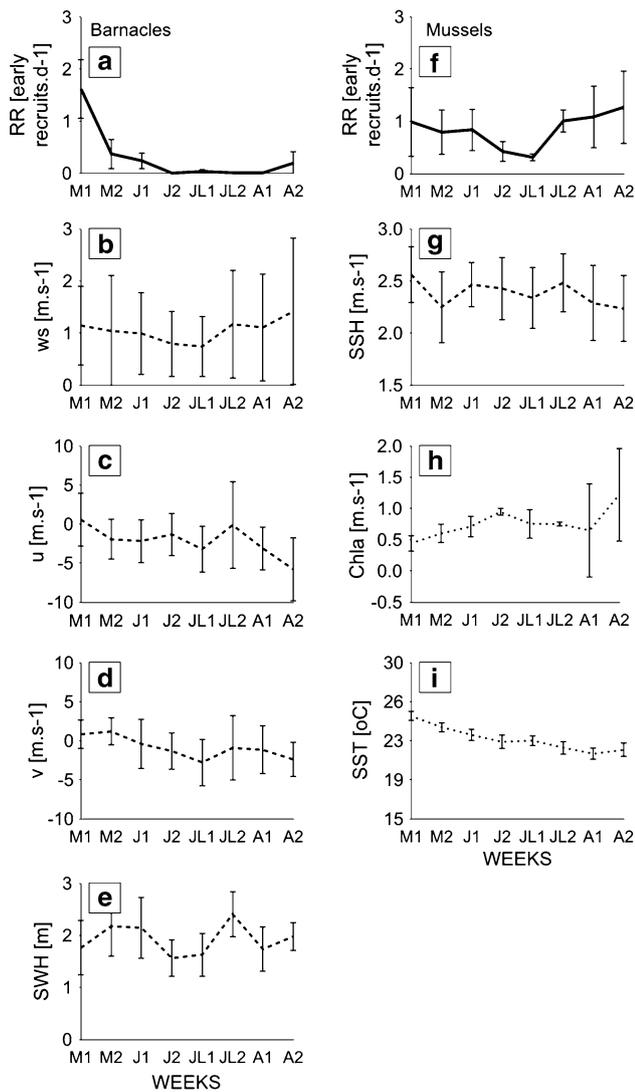


Fig. 5 Variation of the average biweekly recruitment rate (RR) of barnacles (a) and mussels (f), physical forcings (wind speed, ws (b); zonal wind intensity, u (c); meridional wind intensity, v (d); significant wave height, SWH (e); sea surface height, SSH (g)), Chla (concentration of chlorophyll-*a*) (h) and SST (sea surface temperature) (i) during fall and winter 2012 (May, June, July and August). Only the local averages of ws, u, v, SWH, SSH, Chla and SST are presented in the graphs; error bars represent standard deviations (SD); sample size (*n*) varies according to each variable (See ‘Materials and methods’). 1 and 2 represent the two samplings conducted in the same month

2003). These differences can generate responses from both adults and the early life stages of invertebrates, altering the rates of growth and reproduction (Phillips 2002, Narváez et al. 2007). Laboratory experiments show that variation in Chla influences daily survival of larvae and settlers (Marshall et al. 2012). In contrast, in natural environments, the changes in Chla at shorter temporal scales (hours to few days) may not be able to impact the response time of the biological processes of settled consumers (e.g., Coale et al. 1996, Sanford and Menge 2001), or the changes in Chla

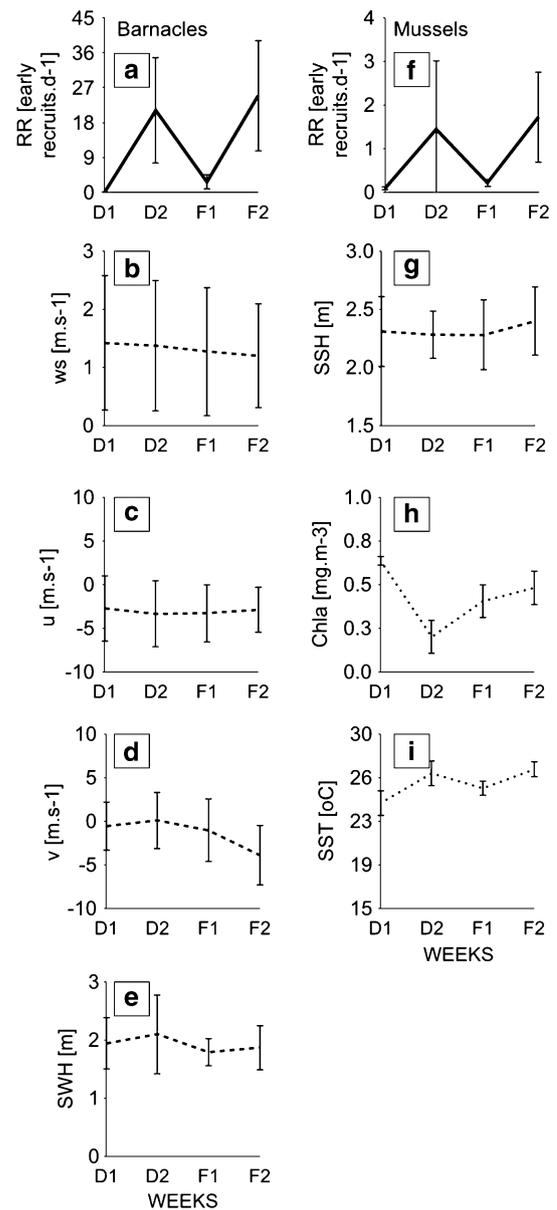
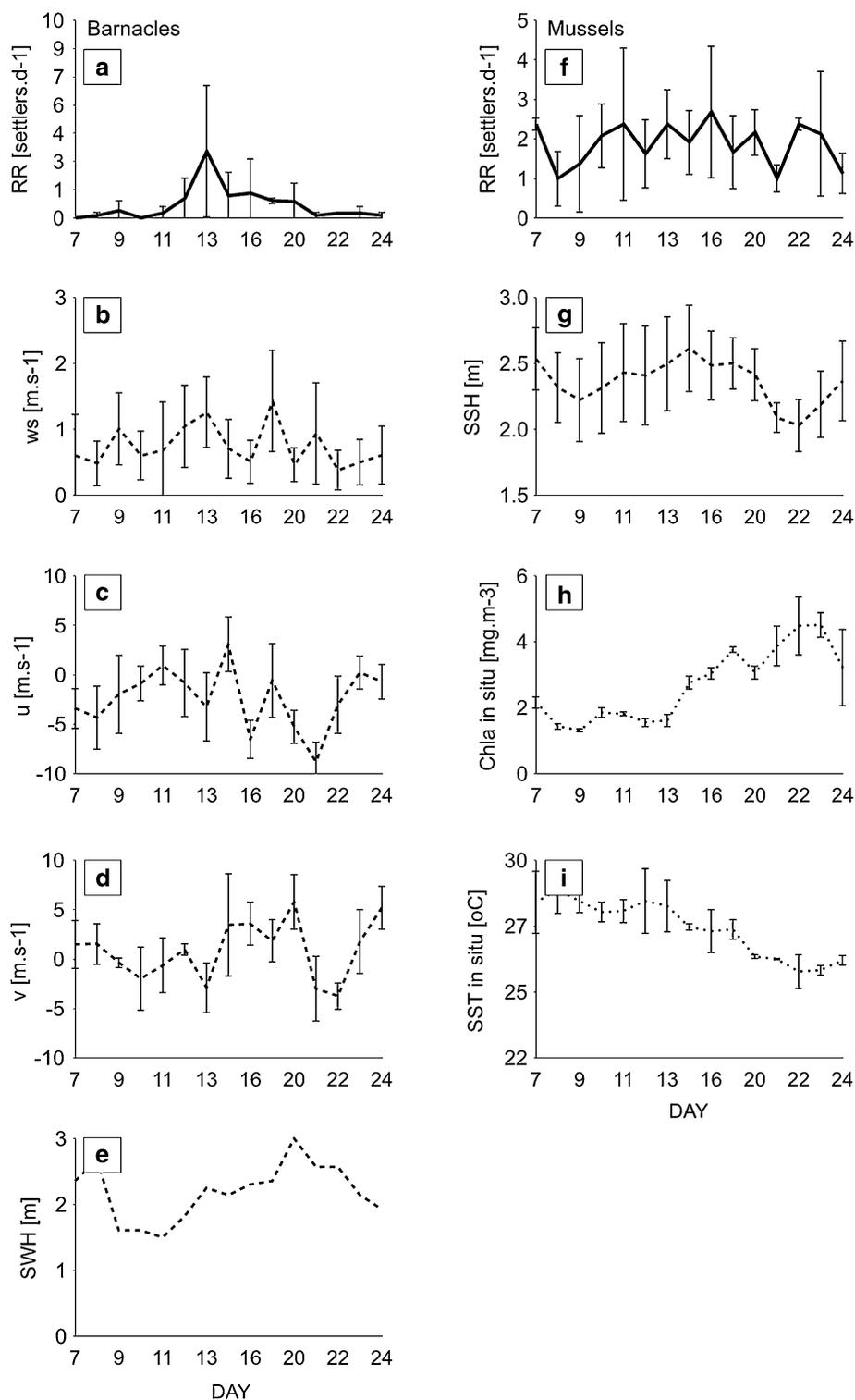


Fig. 6 Variation of the average biweekly recruitment rate (RR) of barnacles (a) and mussels (f), physical forcings (wind speed, ws (b); zonal wind intensity, u (c); meridional wind intensity, v (d); significant wave height, SWH (e); sea surface height, SSH (g)), Chla (concentration of chlorophyll-*a*) (h) and SST (sea surface temperature) (i) during summer 2012/13 (December and February). Only the local averages of ws, u, v, SWH, SSH, Chla and SST are presented in the graphs; error bars represent standard deviations (SD); sample size (*n*) varies according to each variable (See ‘Materials and methods’). 1 and 2 represent the two samplings conducted in the same month

may not be drastic enough to impact larval growth. Moreover, the barnacle larval stage that settles, the cyprid larvae, is non-feeding, and Chla variability lasting a few days would not impact cyprid condition. These factors would reduce the degree of correlation between Chla and settlement rates. Therefore, correspondence between temporal

Fig. 7 Variation in the average daily recruitment rate (RR) of barnacles (a) and mussels (f), physical forcings (wind speed, ws (b); zonal wind intensity, u (c); meridional wind intensity, v (d); significant wave height, SWH (e); sea surface height, SSH (g)), in situ Chla (concentration of chlorophyll-*a*) (h) and in situ SST (sea surface temperature) (i) from March 7, 2013, to March 24, 2013. Only the local averages of ws, u , v , SWH, SSH, Chla and SST are presented in the graphs; *error bars* represent standard deviations (SD); sample size (n) varies according to each variable (See ‘Materials and methods’)



changes in environmental variables and biological cycles can only be identified through estimates obtained using longer time series, such as our monthly rates, or long time series with sampling at shorter intervals, which are difficult to sustain. The second issue is the degree of temporal replication and the coverage of the available dataset of

environmental variables for shorter time scales. Both, biological response time and low temporal replication, might explain differences in correlations from months to weeks. The recruitment estimates at the scale of weeks were not continuous, and most of the coverage took place during winter, leaving important periods of high recruitment out

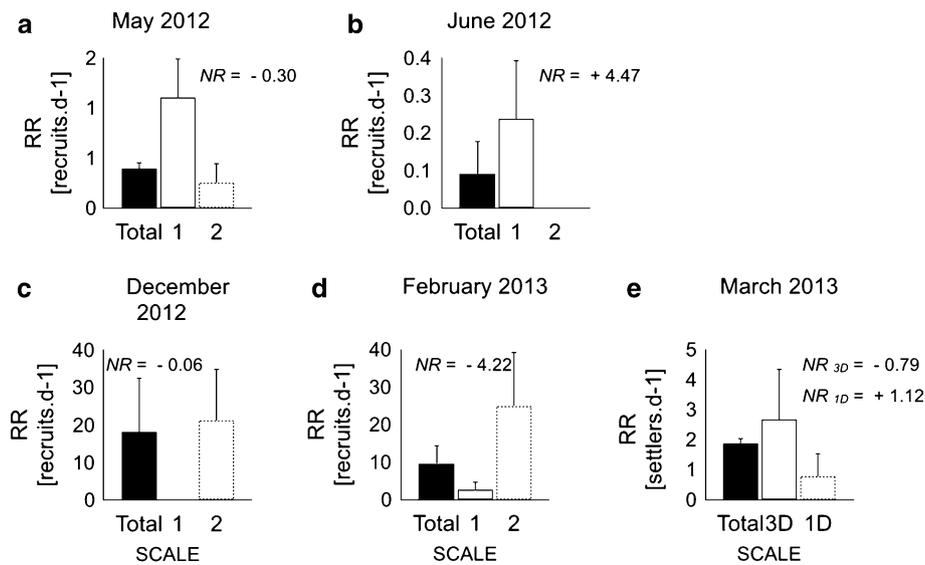


Fig. 8 Comparison of the recruitment rates of barnacles between different temporal scales (NR). Comparisons between the scales of months (Total) and weeks within the month (1, 2) are shown for winter 2012 (May (a) and June (b)) and summer 2012/13 (December (c) and February (d)). Comparisons between the scales of weeks (Total

and 3-day (3D) or 1-day periods (1D) within the weeks are shown for March 2013 (e). $NR = [R_m - (R_1 + R_2)]/T_m$; $NR_{3D} = [R_w - (RR_{3d} \cdot T_w)]/T_w$; $NR_{1D} = [R_w - (RR_{1d} \cdot T_w)]/T_w$. Averages are represented by the columns; error bars represent standard deviations (SD); sample size, $n = 3$ (See 'Materials and methods')

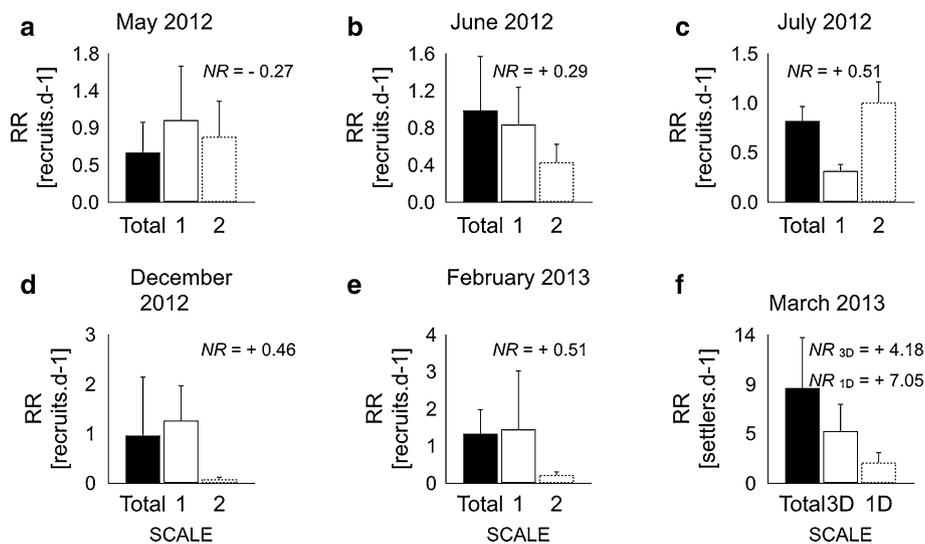


Fig. 9 Comparison of the recruitment rates of mussels between temporal scales (NR). Comparisons between the scales of months (Total) and weeks within the month (1, 2) are shown for winter 2012 (May (a), June (b) and July (c)) and summer 2012/13 (December (d) and February (e)). Comparisons between the scales of weeks (Total

and 3-day (3D) or 1-day periods (1D) within the weeks are shown for March 2013 (f). $NR = [R_m - (R_1 + R_2)]/T_m$; $NR_{3D} = [R_w - (RR_{3d} \cdot T_w)]/T_w$; $NR_{1D} = [R_w - (RR_{1d} \cdot T_w)]/T_w$. Averages are represented by the columns; error bars represent standard deviations (SD); sample size, $n = 3$ (See 'Materials and methods')

of the dataset. The lower recruitment rates might have reduced the power of detecting correlations with the physical forcings, biasing correlations toward the variables showing the greatest differences.

Pelagic variables explaining recruitment rates in different geographic regions can be similar (Navarrete et al.

2008), suggesting a strong benthopelagic coupling, and that similar pelagic processes control the dynamics of intertidal communities. Wind and tidal dynamics drive coastal ocean circulation, which affects larval transport (McQuaid and Phillips 2000; Pineda 2000; Tapia et al. 2004), potentially driving recruitment pulses onshore. SST and Chla

Table 3 List of abbreviations used in this manuscript and the respective meanings

Abbreviation	Meaning
ws	Wind speed
wd	Wind direction
u	Zonal wind U
v	Meridional wind V
SWH	Significant wave height
SSH	Sea surface height
Chla	Chlorophyll- <i>a</i> concentration
SST	Sea surface temperature
RR	Recruitment rate
NR	Net recruitment
r	Correlation coefficient
<i>p</i>	<i>p</i> value

influence adult reproduction (Leslie et al. 2005; Desai et al. 2006; Narváez et al. 2007), and the development of larvae and recruits (Qiu and Qian 1999), and both are influenced by pelagic phenomena potentially driving larval transport (Pineda and López 2002; Narváez et al. 2006, Otero et al. 2009). The zonal and meridional wind (u and z), SST and Chla are important metrics characterizing oceanographic dynamics in coastal environments, and evidence suggests that they can explain variation in recruitment, even under highly stochastic scenarios (McCulloch and Shanks 2003, Menge et al. 2009, Iles et al. 2012). Our results provide evidence that recruitment rates of intertidal species are correlated with these metrics in the different time scales and that measurements of physical forcings could be used to estimate recruitment. Accurate estimates of wind fields, Chla and SST can be obtained from global databases built via remote sensing, and these variables provide global synoptic information about the sea surface and atmospheric variables with high temporal and spatial resolution. Achieving the same resolution for recruitment estimates is impossible. Therefore, a useful tool to predict recruitment rates at the same scale as with the remotely derived variables is the analysis of correlations between these variables and recruitment. These correlations could be incorporated in models of supply-side ecology and rocky shore community dynamics, increasing their power of prediction.

Few studies have compared the temporal trends in settlement and recruitment with oceanographic–meteorological variables, and most of these studies have focused on large-scale upwelling systems (Broitman et al. 2005; Pfaff et al. 2011; Iles et al. 2012). Moreover, most studies that have attempted to relate barnacle and mussel recruitment to pelagic conditions have addressed spatial gradients in recruitment (e.g., Navarrete et al. 2008). In these upwelling systems, reproduction can be timed to correspond to spring

and summer phytoplankton blooms, sometimes caused by upwelling events (Hines 1979). This results in a strong correlation between recruitment and SST (negative) and/or Chla (positive) (Barth et al. 2007) at longer temporal scales, such as decadal cycles (Menge et al. 2011; Iles et al. 2012). Recruitment peaks have also been associated with warm seasons in persistent upwelling areas and were positively correlated with SST (Narváez et al. 2006; Broitman et al. 2008). The previously reported trends for upwelling areas were not reproduced in the present study. We found that barnacle recruitment was positively correlated with wind speed and SST and negatively related to cold front events and Chla. These results indicate that recruitment is more likely to occur when winds are stronger and offshore, when there are fewer cold fronts, when Chla is low, and SST is high. These trends might occur in other systems with similar coastal circulation patterns where upwelling is not the dominant condition. Comparisons with other coastal oceans are needed to increase our understanding of recruitment regulation.

In contrast to other coastal regions, mussel recruitment showed little correlation with most of the oceanic–climatic variables, and only had significant covariation with wind direction at the scale of weeks, and with SST at the daily scale. In upwelling systems, mussel recruitment is associated with variability in adult abundance and fluctuations in primary productivity, upwelling intensity and coastal currents (e.g., Porri et al. 2006; Dudas et al. 2009; Reaugh-Flower et al. 2011, but see Broitman et al. 2005). The wide range of variables covered in this study and the spatiotemporal resolution provided detailed information about the pelagic conditions, hence increasing the probability of finding significant relationship, even with very low recruitment. Thus, the low rates of recruitment found at all scales of the study are the probable causes of the decreased correlation degrees. However, it is also possible that more complex and unaccounted small-scale processes might be involved in the regulation of mussel recruitment patterns (e.g., larval experience, Pechenik 2006; e.g., secondary settlement, Le Corre et al. 2013). Our results suggest that mussel populations at the study area are recruitment limited, which might have important consequences for community dynamics (Roughgarden et al. 1985). Recruitment limitation and small-scale processes should be addressed by future studies.

Significant correlations between barnacle recruitment and oceanographic variables occur in other systems besides upwelling dominated coasts. Therefore, correlations between barnacle recruitment rates and oceanographic variables can be used to enable future forecasts of recruitment from oceanographic variables in non-upwelling systems. Further, our results suggest that the local and regional components are both important for recruitment success and that recruitment of different taxa may be determined by

different processes. If this is true, general global trends of recruitment are unlikely to occur, and local models should consequently be the focus for recruitment forecasting. We speculate that species-specific larval transport mechanisms, and differences in biological and ecological processes, such as larval behavior and mortality rates, influence recruitment in the South Brazilian Bight rocky intertidal system.

Potential larval transport mechanisms

In the present study, barnacle recruitment at Castelhanos Bay was favored when NE winds were strong and frequent, and cold fronts were less predominant in the region. These results do not support our hypothesis that recruitment is higher when cold front systems are frequent and intense. Within the study region, NE winds promote not only offshore advection but also alongshore transport of waters from NE to SE (Fig. 3f, also see Carbonel 2003). These alongshore currents may advect water from the adjacent coastal areas into Castelhanos Bay, in opposition to the circulation caused by cold fronts, which could transport offshore surface 'blue water' into the bay. This phenomenon is possible because Castelhanos Bay is opened to NE allowing the waters coming from the N–NE coastal areas into the bay in favorable conditions. If most larval-rich waters originate from coastal areas along the region, and most settlement and recruitment in the bay shorelines is due to external coastal sources, NE winds are likely to transport larvae to the study area, potentially enhancing recruitment in Castelhanos. In contrast, cold fronts would bring larvae-poor oceanic waters, either from offshore or from southern sandy coastal regions dominated by sandy-dwelling organisms. Although there is no specific information available for the studied sites, data on larval abundance across the continental shelf E of our study areas show that most barnacle larvae are retained in nearshore waters, even during strong NE and upwelling events with offshore waters more likely to exhibit low concentrations of larvae (Yoshinagua et al. 2010).

Daily sampling at Fortaleza Bay indicated that barnacle recruitment peaked 1 day after the arrival of a cold front at the study site. Coastal waters rich in larvae and near the rocky shores along the coast may be transported onshore and cause increases in recruitment due to onshore winds associated with cold fronts, whereas low recruitment may be associated with offshore winds (NE). In contrast, NE winds may transport the larvae away from coastal areas to more distant regions such as Castelhanos Bay, potentially causing recruitment. Studies conducted at sites within the study region have found that supply of competent larvae and recruitment are highest during cold front downwelling events, whereas early larval stages are found under both upwelling and downwelling conditions (Skinner

and Coutinho 2002). Upwelling–downwelling dynamics of larval transport is controversial, and knowledge of these dynamics is far from complete (Roughgarden et al. 1988; Garland et al. 2002; Almeida and Queiroga 2003; Ma and Grassle 2004; Queiroga et al. 2007; Shanks and Shearman 2009; Morgan et al. 2009). Most of the studies have addressed persistent upwelling systems in the Eastern Pacific Ocean, which may not portray the dynamics in other regimes. For example, recent studies on the Benguela current showed that mussel recruitment peaks during the upwelling season, whereas barnacle recruitment does not (Pfaff et al. 2011; see also Porri et al. 2014). Because we did not measure larval supply, larval distributions and water column circulation during this investigation, these potential explanations of the observed recruitment patterns at Fortaleza and Castelhanos are speculative. Furthermore, the daily recruitment results were from one coastal site and might be different from other sites along the main coast. Spatially replicated studies following the passage of cold fronts and alternation with NE winds during the recruitment season should be conducted to adequately test this hypothesis.

Seasonal reproduction in mussels might explain the lack of trends observed between physical forcings and temporal variation of recruitment. Mussel reproduction might be extremely seasonal (van Eken Schurink and Griffiths 1991) compared to that of barnacles, which reproduce year-round, with extended periods of low abundance of competent mussel larvae in the water column. During these periods, even if oceanographic conditions favor larval transport to the shore, recruitment will be low. *Perna perna* reproduces seasonally in the study region, mostly in May, August and October (Mesquita et al. 2001), and this species most likely represented the bulk of larvae that recruited in our study. Focus on reproductive timing may provide a better understanding mussel recruitment variability.

Invertebrate larvae are not evenly distributed in the water column. Their position changes ontogenically (e.g., Tapia et al. 2010) and can be species-specific (Santos et al. 2007). Barnacle cyprids tend to concentrate at deeper layers (Miron et al. 1999) and closer to the bottom (Miron et al. 1995, but see Pineda 2000), especially at sites more distant from shore (Santos et al. 2007; Morgan & Fisher 2010). Mussel larvae also tend to concentrate in lower depths (Rilov et al. 2008) and migrate to surface waters prior to settlement (Graham and Sebens 1996; Dobretsov and Miron 2001). Some conditions or behaviors may uniformly distribute larvae in the water column (e.g., barnacles, Olivier et al. 2000; mussels, McQuaid and Phillips 2000). The vertical position of larvae, together with the ability to sense surrounding environment and maintain their location will influence the transport to settlement sites and rocky shores, affecting timing of recruitment. In

Castelhanos Bay, N–E–NE winds might not only transport larvae from external sources, but also cause a vertical redistribution of barnacle cyprids, increasing their surface abundance, and potentially causing an increase in settlement rates. These mechanisms can help explain the temporal variation of recruitment observed in this study.

Net recruitment

Mortality in post-settlement early life stages is high for sessile organisms inhabiting rocky shores, where the combination of exposure to the air and elevated temperatures can be deadly. In the present study, barnacles exhibited lower NR than mussels, suggesting that barnacles experienced higher post-settlement mortality in time. NR of both types of organisms varied in time but showed different trends, and these taxa might experience different causes of mortality. Barnacles showed the most negative NR in February when the emersion time was long and temperatures were high. Adult barnacles are usually more resistant to emersion compared to mussels in high intertidal zones (Menge and Branch 2001). However, the artificial substrates used for measuring barnacle recruitment can reach high temperatures, do not hold humidity as well as Tuffys, and leave recruits more susceptible to predation. Hence, barnacles on the plates might be subjected to have higher mortality than mussels on Tuffys. Mussels had negative NR in May, when wave exposure was greatest in the study area and might have increased the detachment of mussel recruits (e.g., Crimaldi et al. 2002).

Whereas laboratory experiments are common procedures for measuring specific sources of mortality, field ecological manipulations are frequently employed to understand the mortality caused by predation and competition of sessile adults. Comparing the abundance of settlers and recruits at different temporal scales is a valuable tool for estimating the effect of mortality of settlers and juveniles in field conditions, and this should account for the influence of artificial substrata.

Our study contributes significantly to knowledge on the association between oceanic–climatic variables and recruitment of intertidal invertebrates by showing that climatic fluctuations might have contrasting effects on rocky shore communities. In summary, we showed that the strength of the relationship between recruitment, physical forcing, Chla and SST depends on the temporal scale, with trends varying between different taxonomic groups. Net recruitment and the potential source of mortality could be estimated by comparing recruitment among temporal scales. Wind-driven mesoscale processes might affect onshore abundance of barnacle larvae, causing variation in recruitment; however, these effects could not be detected for mussels at the scales observed in this study.

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