University of São Paulo
Oceanographic Institute

VARIATION IN RECRUITMENT RATES OF ROCKY SHORE INTERTIDAL
INVERTEBRATES IN RESPONSE TO ALTERATIONS IN PHYSICAL FORCINGS,
CHLOROPHYLL-A CONCENTRATION AND TEMPERATURE: THE EFFECT OF
COLD FRONTS

Ana Carolina de Azevedo Mazzuco

Thesis to be presented to the Oceanographic Institute in the University of São Paulo, as
part of the requirements to obtain the title of Doctor in Sciences, Oceanography
Program, Biological Oceanography

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Versão Corrigida

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To my father, Antonio Mazzuco Filho,
who thought me to love the ocean

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“A man who dares to waste one hour of time has not discovered the value of life.”

Charles Darwin

RESUMO

As comunidades marinhas são afetadas por processos oceanográficos que influenciam as interações ecológicas, como as taxas de recrutamento, reguladores essenciais da dinâmica dessas comunidades. Essas relações não são constantes, elas mudam no espaço e no tempo, ou entre taxa. Aqui nós defendemos a tese que processos oceanográficos de origem climática, por influenciarem a abundância larval região de estudo, regulam e estabelecem tendências do assentamento e recrutamento de invertebrados (cirrípedes e bivalves) do entremarés de costas rochosas. Primeiramente, nós investigamos o recrutamento em diferentes escalas de tempo e sua relação com forçantes físicas, concentração de clorofila-a e temperatura da superfície do mar. Em um segundo momento, nós focamos na sincronia e nos contrastes espaciais do recrutamento, e as tendências inter-específicas. Por fim, descrevemos e avaliamos a covariância entre frentes frias, abundância larval e assentamento. Concluimos que há um alto grau de correlação entre recrutamento/assentamento e a variação do campo de ventos, o qual estabelece as tendências temporais. As frentes frias são reguladores importantes do assentamento, mas o recrutamento mais alto está associado a ventos de NE-E. O recrutamento de cirrípedes é mais susceptível às variações ambientais se comparado aos bivalves. O recrutamento regional não é sincrônico no espaço, com diferenças na escala de 100km. Este estudo destaca a importância dos fenômenos oceano-climáticos na previsão de tendências espaço-temporais do recrutamento, mostrando que flutuações climáticas podem ter efeitos contrastantes nas comunidades de costas rochosas.

Palavras-chave: recrutamento, assentamento e suprimento larval; invertebrados do entremarés; fenômenos oceano-climáticos; variação espaço-temporal; costas rochosas.

ABSTRACT

Marine communities are affected by oceanographic processes, which influence ecological interactions, such as recruitment rates, that are essential regulators of community dynamics. These relationships are not constant; they change in space and time or among taxa. We defend the thesis that oceanographic processes of climatic origin influencing larval abundance at the study region, regulate and establish the trends in settlement and recruitment of invertebrates (cirripeds and bivalves) at rocky shore intertidal. We first investigated the recruitment at different temporal scales and its relationships with physical forcings, chlorophyll-a concentration and sea surface temperature. Second, we focused on the spatial synchrony and contrasts of recruitment, and interspecific trends. Third, we described and evaluated the co-variation between cold fronts and the larval abundance and settlement. We concluded that there is a high degree of correlation between recruitment/settlement and the variation of the wind field, which set temporal trends. Cold fronts are important regulators of settlement, but higher recruitment was associated to NE-E winds. Barnacle recruitment is more susceptible to the environmental variations compared to bivalves. Regional recruitment is not spatially synchronic with differences in the scale of 100 km. This study highlights the importance of oceanic-climatic phenomena as predictors of spatio-temporal trends of recruitment showing that climatic fluctuations might have contrasting effects on rocky shore communities.

Keywords: recruitment, settlement and larval supply; intertidal invertebrates; oceanic-meteorological phenomena; spatial-temporal variation; rocky shores.

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GENERAL INTRODUCTION

Marine communities are affected by oceanographic processes of climatic origin, which in turn influence ecological interactions. In particular, recruitment rates are regulated by fluctuations in the pelagic environment as a consequence of their effect on the variation of larval supply. Since larval supply is the main source of new individuals to the populations of sessile marine invertebrates, the mechanisms driving recruitment variation are the bases of ecological models. However, these relationships are not constant, they can change in space and time or among taxa, hereby, the scales of variation must also be considered.

Supply side ecology at rocky shore environments

Most marine organisms have a planktonic larval phase within their life cycle (THORSON, 1950 and 1964). Marine larvae can integrate plankton community during significant periods (LEVIN & BRIDGES, 1995), being subjected to the fluctuations at the pelagic environment. These processes have direct or indirect effects on the biology and ecology of the larvae, consequently impacting the adults. In benthic communities, planktonic larvae are the sources of new individuals to populations. Therefore, the variation of larval abundance in time and space regulate the ecological dynamics of adults, though settlement and recruitment variation. Recruitment rates control the strength of inter-specific interactions, determine the spatio-temporal patterns of adults in intertidal ecosystems and regulate community dynamics (GAINES & ROUGHGARDEN, 1985; BERTNESS *et al.*, 1992; NAVARRETE *et al.* 2008)..

Since Lewin's publication (1986), the supply side ecology has become an important field of marine studies. This author pointed out the conceptual limitations of the previous ecological models of marine community dynamics, including larval supply as an important one. Lewin described the potential consequences of the variation of the number of propagules, and the timing of their arrival, to the structure and dynamics of populations. ROUGHGARDEN *et al.* (1988) is another remarkable work in marine larval ecology. For the first time, it was hypothesized that oceanographic processes occurring at distant areas could directly effect the dynamics of the intertidal communities by influencing larval abundance onshore. These authors suggested the that ocean-larval circulation models should be integrated to improve the ecological models.

Marine larval life cycles are divided in larval release, transport, dispersion and immigration, supply, settlement and recruitment. Larval release happens when the

propagules or larvae are emitted in the environment (MORGAN, 2001). Transport is the movement of larvae changing the geographic position relatively to the parental habitat (MORGAN, 2001). Dispersion or immigration occurs when larvae are transported and settle at a different population (MORGAN, 2001). Larval supply is the amount of larvae that complete the life cycle and reach a population in time (UNDERWOOD & KEOUGH, 2001). Settlement is the supplied larvae which metamorphose to the juvenile stage. Recruitment happens when the settled larvae survive the initial post-settlement period and are counted as members of the population (UNDERWOOD & KEOUGH, 2001). These definitions are applied to most of marine species.

Larval supply is the most pelagic component in the ecology of benthic communities. It is associated to the reproductive biology and to the behavior of adults and propagules in response to specific oceanographic conditions. After release, larvae become part of the plankton, consequently being subjected to the processes intrinsic to the meroplanktonic community. High mortality is expected in this period when larval transport occurs. However, if larvae disperse, competition between adults and propagules and larval mortality by adults consumption are reduced (MORGAN, 1995; LEVIN, 2006). Larvae need to find adequate habitat to live as adults and complete their life cycle. They must keep within a safe distance to return to favorable settlement sites in adequate time. Many species evolved to take advantage of oceanographic features to stay close to or move away from coastal areas. This return is known as “cross-shelf transport” and it reduces population extinction (SHANKS, 1995). Larval supply includes the competent larvae that are able to find the settlement sites.

Settlement is a primary function of larval supply (SUTHERLAND, 1990), however, many other pre and post settlement processes affect the recruitment rates. Factors of biological origin are food concentration, presence of co-specifics, predation, biofilm, larval age, parental and genetic components (CRISP, 1955; LE TOURNEAUX & BOURGET, 1988; MULLINEAUX & BUTMAN, 1991; RODRIGUEZ *et al.*, 1993; SATUITO *et al.*, 1997; HOLM *et al.*, 2000; JENKINS *et al.*, 2005; DESAI *et al.*, 2006); and of abiotic origin, hydrodynamic conditions, substrate type, habitat complexity, humidity, available free space, sensibility to the microclimate, luminosity (THORSON, 1964; TAKI *et al.*, 1980; ECKMAN, 1983; YULE & WALKER, 1984; GAINES & ROUGHGARDEN, 1985; WETHEY, 1986; BUTMAN & GRASSLE, 1992; MULLINEAUX & GARLAND, 1993; O’CONNOR & RICHARDSON, 1994; WALTERS & WETHEY, 1996; MINCHINTON & SCHEIBLING, 1991; JACOBI &

LANGEVIN, 1996; PINEDA & CASWELL, 1997; PEARCE *et al.*, 1998; QIAN, et al. 2000). These processes occur simultaneously, resulting in synergic effects on settlement trends. Therefore, it is challenging to find the factor or set of them which have the stronger effects and will regulate recruitment. In natural systems, the investigation of multiple factors in different temporal and spatial scales can determine the most relevant processes regulating recruitment.

Likewise, larval supply, settlement and recruitment do not always covary (GAINES & BERTNESS, 1992; OLIVER *et al.*, 2000; WIND *et al.*, 2003; JENKINS, 2005; DESAI & ANIL, 2005). So, the investigation of as many phases of the larval cycle as possible helps to build realistic and powerful ecological models. Some studies have investigated the spatio-temporal variation supply and settlement of invertebrate larvae, including different scales (e.g. TAPIA & NAVARRETE, 2010). However, complete larval cycles (emission to recruitment of one group of offsprings) were monitored in laboratory conditions (e.g. GORE, 1977), or in natural environments only for species with short cycles (e.g. ascidians, GROSBERG, 1987). In marine environments, it is very complex to follow larvae from release to recruitment, considering most populations are open and there are an infinite factors involved in spatial-temporal variability. Most studies investigated the processes separately and the connections among them are made a posteriori, what increases the uncertainties and the numerical noise. In this thesis, we investigated the spatio-temporal variability of three larval processes, supply, settlement and recruitment. The study was conducted in natural wave exposed rocky shores. However, in some situations we were able to monitor these processes simultaneously, what allowed us to understand the oceanographic mechanisms driving benthic-pelagic coupling in these shores.

Meteorologic-oceanographic features associated to the variation of recruitment rates, scales of variation

Marine larvae are vulnerable to transport by sea currents from the moment they are released to the water column. Scientists believed that these larvae were transported by ocean currents as inert particles (BAKUN, 1996; LEVIN, 2006). However, these larvae actively respond to changes in pelagic environment. These organisms evolved to directly interact with these currents. They can also migrate vertically. However, larval natatory capacity is limited, consequently, they are not able to move against most horizontal and vertical currents, being passively transported by them. Vertical migration

occurs during emission and with initial larval stages, helping transport and dispersion, reducing predation risks (QUEIROGA *et al.*, 1997). Barnacle first larval stages, for example, are expected to stay at the surface waters as a mechanism to improve dispersion to offshore areas (SANTOS *et al.*, 2007). Latter larval stages also vary their vertical positioning in relation to specific oceanographic conditions, enabling cross shelf transport and maximizing settlement (SHANKS, 1995). Bivalve larvae swim against vertical currents to be retained close to settlement sites (SHANKS & BRINK, 2005).

In this context, if we know the trajectory of the dominant current or feature at the depth that larvae are concentrated, we can determine where larvae will be transported. Likewise, if we know how these currents vary in space and time, we are also able to predict the rates of larval supply along the coast, together with settlement and recruitment rates. Many long term studies covering large spatial areas found spatio-temporal regularities in recruitment trends (NAVARRETE *et al.*, 2008). These patterns are persistent and predictable, allowing the application of ecological data in management and conservation of ecosystems (NAVARRETE *et al.*, 2005).

SHANKS (1995) enumerated the main oceanographic features which transport larvae to the settlement sites: baroclinic currents over the continental shelf; Langmuir cells; currents generated by sea breeze; Eckman transport and other wind driven currents; tidal currents; internal waves and tidal bores; density dependent flow; coastal boundary layer; fronts; and vortex and eddies (PINEDA, 1991; SHANKS, 1995; BAKUN, 1996; LEICHTER *et al.*, 1998; JEFFERY & UNDERWOOD, 2000; TAPIA *et al.*, 2004; QUEIROGA *et al.*, 2007). In coastal areas, wind and tidal generated phenomena might be the most important mechanisms transporting larvae, however, there are only a few evidences corroborating this hypothesis, mostly covering upwelling dominated systems (e.g. WING *et al.*, 2003).

Regarding the variation in time, larval supply, settlement and recruitment vary from hours (GARLAND & ZIMMER, 2002) to decades (MENGE *et al.*, 2009) intrinsically associated to fluctuations of oceanographic conditions. Some authors suggested that studies should focus on shorter temporal scales within the reproductive season (PINEDA *et al.*, 2002). Others highlighted that hourly scale are more adequate to establish the relationship between supply, settlement and pelagic variation (TODD *et al.*, 2006). However, some areas of the coast are not accessible for hourly samplings or even daily campaigns, consequently, only longer recruitment data might be available. Monthly studies have also detected high degrees of correlation between the variation of

ocean-climatic variables and recruitment rates (e.g. ILES *et al.*, 2012), showing that there is a potential to predict recruitment rates in longer temporal scales. Considering the spatial scales, larval processes vary from centimeters (e.g. HILLS & THOMASON, 1996) to hundreds of kilometers (e.g. NAVARRETE *et al.*, 2008). The hydrodynamic regime and pelagic dynamics are important to generate these variations. In scales of km to 100-km recruitment rates are influenced by upwelling intensity (NAVARRETE *et al.*, 2008), hydrodynamic flux (e.g. BERTNESS *et al.*, 1992; ROSS, 2001; RILOV *et al.*, 2008) and morphology of the coast (MORGAN *et al.*, 2011). In this study, we investigated both, spatial and temporal variation of recruitment, including settlement and larval supply when possible. But, differently from other studies, we met different scales of variability simultaneously. With this approach, we could determine if the regulatory mechanisms persist independent of the scales.

The biological models

Cirripeds and bivalves are important components of the intertidal community. They are numerous and they occupy all zones of the intertidal (MENGE & BRANCH, 2001), consequently, variation of their abundance and distribution influence the entire community. Cirriped and bivalve larvae are commonly found in the meroplankton (e.g. HIGHFIELD *et al.*, 2010), where they are transported by oceanographic features (PINEDA *et al.*, 2007), which sets settlement and recruitment trends (e.g. MCCULLOCH & SHANKS, 2003). Cirriped and bivalve larvae may have contrasting responses to the same environmental fluctuations, as a result, they show different spatio-temporal trends of larval supply (MCCULLOCH & SHANKS, 2003) and recruitment (ILES *et al.*, 2012). In this study, we included both taxa to test if the oceanographic regulators of recruitment were similar. Adding biological components increases the prediction power of the results to the community level.

At the study region, we mostly find at the rocky shore intertidal: three species of cirripeds, *Chthamalus bisinuatus*, *Tetraclita stalactifera* and *Megabalanus coccopoma*; and three of bivalves, *Brachidontes solisianus*, *Isognomon bicolor* and *Perna perna* (COUTINHO & ZALMON, 2009). These six species were included in the investigations within this thesis. Adults of *C. bisinuatus* are more abundant and dominate the upper mid-littoral zone, *T. stalactifera* and *I. bicolor* are more successful at the lower mid-littoral, while *P. perna* and *M. coccopoma* are concentrated at the upper subtidal.

Data about the reproductive cycles and larval dynamics of these species are punctual and scarce for the study region. Cirripeds might reproduce year around, however, there are evidences that they show different reproduction periods depending on the taxa and latitudinal location. *T. stalactifera* show maximum breeding in summer months (North part of the study region, SKINNER *et al.*, 2011). Bivalves reproduce seasonally: *Perna perna*, mostly in May, August and October, when maxima occur (LUNETTA, 1969; MESQUITA *et al.*, 2001; FERREIRA and MAGALHÃES, 2004). Barnacle species might show rhythmic larval release, as identified for *C. bisinuatus*, mostly coinciding with neap tides, when the speed of tidal currents is the lowest (South part of the study region, BUENO *et al.*, 2010). Recruits are found along the entire intertidal with maximum abundances at the zones occupied by their adults (CHRISTOFOLETTI *et al.*, unpublished data). *C. bisinuatus* and *T. stalactifera* show higher densities of later stage larvae and settlement rates in autumn and winter, while densities of first larval stages were lower (North part of the study region, SKINNER & COUTINHO, 2002; SKINNER *et al.*, 2011). *Perna perna* settles in higher rates in October (BORDON *et al.*, 2011). Because of these differences among species, we compared recruitment inter-specific resolution.

Cold fronts at the Southeastern Coast of Brazil

In meteorology, a front is defined as the boundary between 2 air masses of different characteristics, such as density. A cold front is the boundary between a cold air mass advancing over a warm air mass. The South and Southern coast of Brazil are periodically influenced by meteorological cold fronts, generated by low pressure centers moving from Antarctica to South America along the coast line and propagating from SW to NE. They take 2 days to cross the South Brazilian Bight with an average speed of 500 km per day (STECH & LORENZETTI, 1992). In the region that precedes the front (the warm sector), the wind blows from NE with a mean velocity of 5 m/s, rotating counterclockwise to NW when the front approaches. Immediately after the passage of the front, the wind blows from SW (in the cold sector) (8 m/s average), rotating to SE and returning to NE after 1 day.

When cold fronts move over the ocean, they modify the interactions in marine boundary systems, atmosphere and the ocean, and the water column and the sea floor. These swells drastically impact the atmospheric and pelagic environment by changing the speed and direction of the main winds (CARBONEL, 2003) (Fig A1), elevating

wave and sea level heights (PIANCA *et al.*, 2010), causing vertical mixing of the water column, altering sea surface temperatures and the concentration of chlorophyll-a (PALMA & MATANO, 2009). A new cold front occurs every 3 to 10 days, approximately 3 to 6 per month year round, varying seasonally in frequency and intensity. These fronts are important phenomena driving local and regional ocean circulation. Generally, during cold fronts, surface waters are driven onshore and surface currents move from SW to NE.

Figure A1. The schema illustrates the expected conditions of wind direction (upper boxes), wave and sea level heights (lower boxes) before, during, and after a cold front.

Besides the importance of these meteorological-oceanographic phenomena to the region, the effect of cold fronts on the benthic and very nearshore systems is almost unknown. The strong winds and high wave conditions complicate samplings during these events, in particular, at wave exposed and open ocean sites. Succession patterns and ecological consequences are either barely known, or unpublished. Consequently, it is almost impossible to formulate efficient population and community ecological models without generating more information about these cold front effects. One study (GALLUCCI & NETO, 2004) showed that the passage of cold fronts, a short-term event, affects the entire shallow intertidal and sub-littoral ecosystems, i.e. both pelagic and benthic compartments. In the pelagic system, fronts change the seston, nutrient and chlorophyll-a concentrations, by phytoplankton retention, resuspension and accumulation near the coast. In the benthic system, sediment features and the benthic fauna are affected by the fronts. In the coastal areas of strong upwelling influence, larval abundance and settlement rates of barnacles and bivalves are also influenced by the cold

front events, varying temporally in stage and inter-specific (SKINNER & COUTINHO, 2002; LÓPES *et al.*, 2008; MAZZUCO *et al.*, 2008).

Hypotheses

In this research, we first (Chapter 1) investigated the variability of recruitment of intertidal barnacles and mussels at different temporal scales and its relationships with physical forcings (wind velocity and direction, wave height and sea surface height), chlorophyll-a concentration and sea surface temperature. 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 environmental conditions were favorable for larval metamorphosis and juvenile growth during the post settlement period. This hypothesis was tested by evaluating changes in recruitment rates at monthly, weekly, and daily temporal scales in response to fluctuations in physical forcings. 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 rises. Since larval development and recruitment are affected by the concentration of chlorophyll-a in the water and sea temperature, the relationships between recruitment rates and these variables 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 of oceanographically favorable conditions for the onset of recruitment.

Second (Chapter 2), we focused on the spatial variability of recruitment rates of the intertidal barnacles and mussels. Our aim was to identify the relative importance of local and regional contributions to the variation of recruitment of rocky shore intertidal invertebrates. We compared the temporal synchrony of monthly recruitment on two coastal islands, assessing spatial variation among sites (km) and between islands (100km). Species-specific resolution was included, as well as information about the adult population. Gradients in the surface pelagic environment were described. Since these islands are located at the same oceanographic region and supposedly subjected to similar temporal variation in pelagic conditions, we expected recruitment to be synchronic across sites within and between islands. Since there are spatial gradients of the effects of cold fronts and upwellings, we expected similar rates of recruitment within islands but different rates between them. Also, we expected recruitment to be positively correlated to adult abundance.

Third (Chapter 3), we described and evaluated the co-variation between cold fronts, larval supply and settlement. Here, we tested the influence of cold fronts at small temporal scales on the abundance of larvae at the very nearshore and on the settlement rates of intertidal barnacles and mussels. We sampled larvae and settlers during cold front events while characterizing the atmospheric and pelagic conditions at three different sites within the same region testing the spatial consistency of the trends. We hypothesized that advancing cold fronts transport the larval pool to the coastal shores, increasing the abundance of post-larvae and the settlement rates. Therefore, post-larvae abundance and settlement would be better correlated to wind speed and direction than are the best descriptor of cold front. Considering cold fronts as a main driver of nearshore perturbations, we expected that spatial variability among sites would be minimal due to the overwhelming influence of this synoptic event. Since cold fronts vertically mix the water column nearshore, we expect larvae to behave as passive particles, and, consequently, both barnacle and mussel would show similar temporal trends.

1. CHAPTER I: Temporal variation in intertidal community recruitment and its relationships to physical forcings, chlorophyll-a concentration and sea surface temperature.

1.1 Abstract

We investigated the recruitment of intertidal barnacles and mussels at three temporal scales (months, weeks and days), and its relationships with physical forcings, chlorophyll-a concentration (Chla) and sea surface temperature (SST), at both a local (km) and a regional (10-100km) 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 co-varied 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.

Key words: recruitment; rocky shores; intertidal invertebrates; oceanic-meteorological variables; temporal scales.

1.2 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 intra- and inter-specific interactions (ROUGHGARDEN *et al.*, 1988; CALEY *et al.*, 1996; KINLAN & 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.*, 2008; JACINTO & CRUZ, 2008; LATHLEAN *et al.*, 2010; GYORY & 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 & 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 & TODD, 1998; gregarious behavior, KNIGHT-JONES & STEVENSON, 1950) and abiotic factors (e.g., substrate heterogeneity, BERS & WAHL, 2004; hydrodynamic characteristics, ECKMAN *et al.*, 1990; meso-scale 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; MENGE *et al.*, 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 & HAWKINS, 2003; MCQUAID & LINDSAY, 2000; HUNT & 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, large scale currents) are rarely considered in recruitment studies (but see PINEDA & LÓPEZ, 2002). Correlations between recruitment rates and oceanographic variables depend on the temporal frequency of recruitment measurements (TAPIA & 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 & 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 & BRINK, 2005) and in tolerance of recruits to environmental stress (WETHEY *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 & SEBENS, 1996), have different swimming capabilities (YOUNG, 1995), and hence are exposed to different currents and transport mechanisms (MCCULLOCH & SHANKS, 2003). In addition, the seasonality and frequency of reproduction in both groups is 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; LORENZZETTI *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 & LORENZZETTI, 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 & 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 & LORENZZETTI, 1992; GALLUCCI & NETO, 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 & PEARSE, 1995; PHILLIPS, 2002; THIYAGARAJAN *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 of oceanographically favorable conditions for the onset of recruitment.

1.3 Aims

The aims of this chapter were to investigate the recruitment of intertidal cirripeds and bivalves at different temporal scales (months, weeks and days) and its relationships with physical forcings, chlorophyll-a concentration and sea surface temperature at both a local and regional resolution.

1.4 Study Area

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. 1.1). 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 are 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 & LORENZZETTI, 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 & ZALMON, 2009), mainly due to differences in wave exposure, geomorphology, pelagic productivity and anthropogenic impacts (CHRISTOFOLETTI *et al.*, 2011).

To investigate variation at the scale of months or weeks, three sites located 5 km apart in Castelhanos Bay (Fig. 1.1) 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. 1.1). 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.

Figure 1.1. 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 (center); study sites for the investigations performed at the scales of months and weeks (Castelhanos Bay) (lower left), and at the scale of days (Fortaleza Bay).

1.5 Materials and Methods

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 was 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, and 2.5° latitude x 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 x 1° longitude. 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. 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 & 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 (WELSCHEMEYER, 1994). Natural fluorescence was measured in 3 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, U.S.A.). Chlorophyll extraction was carried out 6 times during the sampling campaign. For this purpose, 3 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 x 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 (RR) 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 x 8 cm x 0.2 cm) covered with Safety Walk® 3M anti-slip tape, which provides adequate rugosity to

stimulate barnacle settlement. Tuffys are traps made of a multi-filament plastic mesh (typically used for dish-washing; S.O.S. Tuffy®), and provide a complex substrate for settling mussel larvae. All substrates were placed at the mid-intertidal zone about 5 meters 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 & 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 (KEOGH & 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 vs. weeks, and weeks vs. days. Considerations of this analysis includes, first, that recruitment is greater when more free space is available for settlement, and the settlement substrate saturates (MINCHINTON & SCHEIBLING, 1993; but see PINEDA & 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 & KENNY, 1991; PINEDA, 2000); and fourth, a potential reduction of 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 (RR) 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 days intervals. Barnacles and mussel recruitment was 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 was a total of 10 biweekly sampling events: 6 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 2 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 6 to 24 March 2013 according to the following design: 8 replicates of each substrate were replaced daily (total of 15 sampling events), 4 replicates of each substrate were replaced every 3 days (total of 5 sampling events), and 4 replicates of each substrate remained in place from 6 to 24 March (1 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 ws [m.s⁻¹] and wind direction wd [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, 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: (i) regional trends over time were described from graphs made for representative periods of time at scales of months, weeks and days; (ii) ws and wd were categorized according to the origin, speed and percentage of time the wind assumed a determined orientation (%); and (iii) 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 & ROHLF, 2003). The series were considered synchronous when $r \geq |0.5|$. 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 Attachments Table S1): scale of months, number of cold fronts (total), SWH (regional), SST (local); scale of weeks, wd, 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 & LÓPEZ, 2002) (see Attachments 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 periods [recruits. d^{-1}], and T_w is the total sampling time in this period, with units days [d].

Note that the scale of weeks refer 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.

1.6 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. 1.2a to Fig. 1.2d). In winter, the intensity of the wind velocity field was higher than in summer

(4 to 7 m/s) (Fig. 1.2a), and gradually increased from western to eastern areas near the Cabo Frio upwelling center (Fig. 1.2c). 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. 1.2b). Spatial variation was greater in summer (Fig. 1.2c) than in winter (Fig. 1.2a), 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. 1.2d). Cold fronts reached the study region most frequently in late fall (May and June), but they were also present in October (Fig. 1.2, see Attachments 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 Attachments 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 Attachments 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 Attachments Table S3). In December and March, winds from the E reached their maximum frequency and cold fronts were absent in the study region (see Attachments 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. 1.4c). 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. 1.4d).

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. 1.2e to Fig. 1.2h). In spring and fall, SWH were similar, but the spatial gradient was from N to S (Fig. 1.2f and Fig. 1.2h). Within the study area, wave height varied from 1.5 to 2.5 m, with maxima in October and minima in February (Fig. 1.2e to Fig. 1.2h, Fig. 1.4e). Maximum sea surface height SSH was in June, and minimum levels were observed in spring (September) and the beginning of summer (January) (Fig. 1.4g).

Figure 1.2. 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 winter 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.

Figure 1.3. 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 during 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.

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. 1.7b). The cold fronts were associated with an increase in SWH and SSH (Fig. 1.7e and Fig. 1.7g), and SWH and SSH reached 2-3 m over the shelf, in addition to elevating Chla levels from 1.5 to 4.5 mg/m³ (Fig. 1.7h) and decreasing the SST by 3°C (Fig. 1.7i).

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 ($r \geq |0.6|$) than for the mussels (Table 1.1 and 1.2), 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 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. 1.4a). 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 1.1). Higher rates were registered in spring (September and October), summer and the beginning of fall (December to March) (Fig. 1.4a), when the ws was also highest and dominated by NE-E winds (Fig. 1.4b, see Attachments Table S3), whereas fewer cold fronts arrived (see Attachments Table S3), and local levels of Chla in surface waters were low (Fig. 1.4h). Maximum recruitment occurred in December (Fig. 1.4a), when cold fronts were absent in the area (see Attachments Table S3), Chla levels were minimal (Fig. 1.3g and Fig. 1.4h) and the SST was the highest during the study (Fig. 1.4i). From May to August, recruitment remained close to zero (Fig. 1.4a). In November, when winds from the SW achieved their highest frequency during a strong cold front (see Attachments Table S3), recruitment was nearly zero (Fig. 1.4a). A significant temporal synchrony and

correlation with recruitment rates was observed for the ws (positive) and wd (negative), number of cold fronts (negative) and Chla (negative) (Table 1.1). All of the identified correlations occurred at the local scale for the average rates (Table 1.1).

Figure 1.4. Variation in the average monthly recruitment rates (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) from April 18th, 2012, to June 12th, 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).

Table 1.1 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 (wind speed and direction, ws/wd; velocity of wind, u and v; number of cold fronts; significant wave height, SWH; sea surface height, SSH), Chla and SST. 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 shaded in gray refer to data that were corrected to remove temporal autocorrelation prior to analysis (See Materials and Methods); NA indicates data were not available

	MONTHS		WEEKS		DAYS				<i>p</i>
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	LAG (<i>r</i>)				
					-1	0	1	2	
ws	0.69	0.010*	0.12	0.532	0.51				0.053
wd	-0.66	0.016*	0.91	≤ 0.01*	-0.49				0.044
u									
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
v									
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	0.29	0.381	-0.19	0.681	NA	NA	NA	NA	NA
SWH									
local	-0.24	0.427	-0.08	0.872				0.59	0.011*
regional	-0.09	0.798	-0.27	0.564		0.27			0.333
SSH	-0.45	0.145	0.58	0.169	0.59				0.032*
Chla									
<i>in situ</i>	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	0.12	0.822	NA	NA	NA	NA	NA
SST									
<i>in situ</i>	NA	NA	NA	NA		0.31			0.277
local	0.60	0.036	0.65	0.165				0.59	0.022*
regional	0.29	0.323	0.72	0.109				0.63	0.011*

Figure 1.5. Variation of the average bi-weekly recruitment (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.

Barnacle recruitment rates also varied among weeks, with considerable differences observed between consecutive sampling dates (Fig. 1.5a and 1.6a). During winter, recruitment was slightly higher during the first 2 weeks but remained nearly zero in the two other biweekly periods sampled (Fig. 1.5a), when recruitment was only positively correlated to wind direction (Table 1.1) which was an opposite trend compared to that observed in monthly and daily trends (Table 1.1). During summer (Fig. 1.6a), 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. 1.7a), which was synchronous with an increase in ws (Fig. 1.7b), an increase in SSH (Fig. 1.7g) and followed by a change in wd from N to S (Fig. 1.7c and 1.7d). Some of these patterns were confirmed by cross-correlation analysis (Table 1.1). 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. 1.7c and 1.7d). At this scale, significant results of correlation analysis showed that (Table 1.1): RR was positively correlated with lagged SWH and SST, whereas it 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 1.1).

Barnacle NR varied according to the period of the year and the temporal scale of comparison (Fig. 1.8). When recruitment was compared at the scales of weeks to months (Fig. 1.8a to 1.8d), lower NR was registered in May (Fig. 1.8a), December (Fig. 1.8c) and February (Fig. 1.8d). The NR between weeks and 3-day (Fig. 1.8e) periods was negative and was close the values observed in May (Fig. 1.8a). However, NR was positive when weeks were compared to 1-day periods.

Bivalves

Recruitment of mussels showed low degrees and statistically insignificant correlation with oceano-climatic variables, and only co-varied with wind direction at the scale of weeks, and with SST at daily scales (Table 1.2).

Maximum recruitment occurred in September and October (spring) and March (fall), showing two distinct peaks (Fig. 1.4f). In both periods, u and SST (local and

regional) displayed lower values (Fig. 1.2b, 1.2d, 1.3b, 1.3d, 1.4c, 1.4i). The first recruitment peak (Fig. 1.4f) coincided with higher regional Chla levels (Fig. 1.2f), together with a more frequent occurrence of the upwelling plume (see Attachments Table S4). The maximum mussel RR (Fig. 1.4f) was lower than maximum barnacle RR (Fig. 1.4a). During the other months, the RRs averaged fewer than 2 late recruits/day (Fig. 1.4f), similar to the minimum rates found for barnacles (Fig. 1.4a), and the lowest recruitment was recorded in November (Fig. 1.4f), like barnacles (Fig. 1.4a).

Table 1.2 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 (wind speed and direction, ws/wd; velocity of wind, u and v; number of cold fronts; significant wave height, SWH; sea surface height, SSH), Chla and SST. 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 shaded in gray refer to data that were corrected to remove temporal autocorrelation prior to analysis (See Materials and Methods); NA indicates data were not available.

	MONTHS		WEEKS		DAYS	
	r	p	r	p	LAG (r)	p
					0	
ws	0.31	0.311	0.964	≤ 0.01*	-0.24	0.389
wd	-0.26	0.391	-0.41	0.365	0.01	0.971
u						
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
v						
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
SWH						
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
SSH	-0.24	0.342	-0.12	0.779	0.31	0.269
Chla						
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
SST						
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

In the winter, recruitment at the scale of weeks was close to 1 early recruit/day (Fig. 1.5f). The lowest values were found in the last weeks of June and beginning of July (Fig. 1.5f), and recruitment was synchronous with the fluctuation of ws (Table 1.2). During summer (Fig. 1.6f), the differences in RRs between weeks were higher, although the rates were low, similar to those found during the winter weeks (Fig. 1.5f).

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. 1.7a). Recruitment rates were negatively correlated with in situ SST, with high recruitment rates at lower temperatures (Table 1.2).

NR was positive in almost all the comparisons (Fig. 1.9). This trend was stronger during summer months (Fig. 1.9d and 1.9e) and was most intense during the daily samplings (Fig. 1.9f). The only exception was registered in May 2012, when the NR was 0.27 recruits/d (Fig. 1.9a).

Figure 1.6. Variation of the average bi-weekly recruitment (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.

Figure 1.7. Variation in the average daily recruitment (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 to 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).

Figure 1.8. 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).

Figure 1.9. 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).

1.7 Discussion

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

Our results show potential for oceanographic-meteorological variables 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 & 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, LORENZZETTI *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.

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.*, 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 influence 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 & MENGE, 2001), or the changes in Chla 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 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 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 benthic-pelagic 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 & PHILLIPS, 2000; PINEDA, 2000; Tapia *et al.*, 2004), potentially driving recruitment pulses onshore. SST and Chla influence adult reproduction (LESLIE *et al.*, 2005; DESAI *et al.*, 2006; NARVÁEZ *et al.*, 2007), and the development of larvae and recruits (QIU & QIAN, 1999), and both are influenced by pelagic phenomena potentially driving larval transport (PINEDA & 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 & SHANKS, 2003; MENGE *et al.*, 2009; ILES *et al.*, 2012). Our results provide evidence that recruitment rates of intertidal species are correlated to 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 to warm seasons in persistent upwelling areas, and were positively correlated to 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 co-variation 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 spatio-temporal 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. 6.3f, 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 one 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 & 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 & QUEIROGA, 2003; MA & GRASSLE, 2004; QUEIROGA *et al.*, 2007; SHANKS & 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 EKKON SCHURINK & 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 specie-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, 1999), 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 & SEBENS 1996, DOBRETISOV & MIRON 2001). Some conditions or behaviors may uniformly distribute larvae in the water column (e.g. barnacles, OLIVIER *et al.*, 2000; mussels, MCQUAID & 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 & 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 have to 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 depend 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 synoptic 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.

1.18 Attachments

Table S1. Results of the regression analysis assessing the temporal autocorrelation of the physical forcings (wind speed and direction, ws/wd; velocity of wind, u and v; number of cold fronts; significant wave height, SWH; sea surface height, SSH), Chla (chlorophyll-a concentration) and SST (sea surface temperature). (*) represent statistically significant results ($r^2 \geq 0.5$; $p \leq 0.05$).

		MONTHS		WEEKS		DAYS	
		<i>p</i>	<i>R</i> ²	<i>p</i>	<i>R</i> ²	<i>p</i>	<i>R</i> ²
ws		0.924	≤ 0.01	0.370	0.13	0.538	0.02
wd		0.385	0.07	0.037*	0.54	0.771	≤ 0.01
u							
	local	0.647	0.02	0.064	0.46	0.647	0.02
	regional	0.709	0.01	0.067	0.45	0.535	0.03
v							
	local	0.488	0.04	0.022*	0.61	0.526	0.03
	regional	0.637	0.02	0.025*	0.59	0.315	0.08
cold fronts							
	local	0.328	0.09	0.654	0.04	NA	NA
	total	0.041*	0.33	0.081	0.42	NA	NA
SWH							
	local	0.087	0.24	0.959	≤ 0.01	0.202	0.12
	regional	0.049*	0.31	0.749	0.02	0.046*	0.27
SSH		0.788	≤ 0.01	0.187	0.27	0.129	0.17
Chla							
	<i>in situ</i>	NA	NA	NA	NA	≤ 0.01 *	0.75
	local	0.068	0.27	0.054	0.48	NA	NA
	regional	0.114	0.21	0.042*	0.52	NA	NA
SST							
	<i>in situ</i>	NA	NA	NA	NA	≤ 0.01 *	0.91
	local	0.050*	0.30	≤ 0.01 *	0.89	0.053	0.26
	regional	0.061	0.28	≤ 0.01 *	0.91	0.054	0.26

Table S2. Results of the regression analysis assessing if the correction technique was efficient to remove temporal autocorrelation of the autocorrelated variables (see Table S1).

	MONTHS		WEEKS		DAYS	
	<i>p</i>	R ²	<i>p</i>	R ²	<i>p</i>	R ²
wd			0.391	0.15		
v						
local			0.928	≤ 0.01		
regional			0.638	0.04		
cold fronts						
total	0.973	≤ 0.01				
SWH						
regional	0.914	≤ 0.01			0.742	≤ 0.01
Chla						
<i>in situ</i>					0.882	≤ 0.01
regional			0.501	0.09		
SST						
<i>in situ</i>					0.788	≤ 0.01
local	0.828	≤ 0.01	0.114	0.42	0.087	0.22
regional			0.085	0.47		

Table S3. Characterization of the relative frequency of the wind origin (%) and speed and the frequency of cold fronts from April 2012 and June 2013. Mx: wind direction in which the maximal velocity was registered. E: events.

		Frequency					Cold fronts	
		mx	SW	SE	E	NE	i	T
E1	April-May	E, NE	5-10	< 5	15	5-10	3	6
E2	June	SW, NE	5-10	< 5	10-15	10-15	3	7
E3	July	E	5-10	< 5	10-15	15-20	3	9
E4	August	SW, NE	5-10	< 5	20-25	15	2	9
E5	September	SW, SE, E, NE	5-10	< 5	20-25	10	0	5
E6	October	E, NE	5-10	< 5	20-25	10-15	3	7
E7	November	E	10	> 5	25	10-15	1	3
E8	December	NE	5-10	< 5	25-30	5-10	0	9
E9	January	W, NW, NE, E	5-10	< 5	15-20	5-10	1	2
E10	February	SW, W, NW, NE, E	5-10	< 5	25-30	5-10	0	4
E11	March	E, NE	10	< 5	20-25	10	1	4
E12	April	E, NE	5-10	< 5	20-25	10	1	3
E13	May-June	SW	5	< 5	15-20	> 10	4	5

Table S4. Characterization of the relative frequency of occurrence of upwelling plumes. Mx: maximum average chlorophyll-a concentration inside the plume [mg.m⁻³]. i: number of images where fronts occurred; t: total number of images available for the period. * Indicates the periods when the Cabo Frio upwelling plume reached the study area.

		Upwelling		
		i/t	Mx	
E1	April-May	1/5	2.5-10	
E2	June	0/3	-	
E3	July	0/4	-	*
E4	August	2/4	>30	*
E5	September	2/4	>30	*
E6	October	3/4	10-30	*
E7	November	3/4	>30	
E8	December	1/6	2.5-10	
E9	January	0/3	-	
E10	February	2/4	2.5-10	
E11	March	0/3	-	
E12	April	0/4	-	
E13	May-June	1/5	10-30	

2. CHAPTER II: Inter-specific variation of recruitment in intertidal rocky shores: consistency of spatial and temporal trends

2.1. Abstract

Distant populations can be regulated by the same set of processes at the same time, resulting in similar patterns of distribution and abundance of organisms. In this study, we assessed the spatio-temporal synchrony of recruitment of intertidal barnacles and bivalves within the same oceanographic region. We compared the inter-specific variability of recruitment rates among sites (kms) and between coastal islands (100 kms), evaluating the relation to adult abundance. Recruitment was affected by local and regional processes. Recruitment was not synchronic on the islands, varying in: length of the recruitment seasons; number and timing of recruitment maxima; site synchrony; total recruitment; and correlation to adult abundance. However, some spatial coincidences were registered suggesting that large scale processes can also control recruitment across the region. Not all species recruited at the same time and in the same rate, suggesting inter-specific competition among recruits is reduced. This work evidences that local and regional processes have similar power when regulating recruitment temporal variation, affecting community to species levels.

Keywords: recruitment; rocky shores; intertidal invertebrates; spatio-temporal variation; species-specific trends.

2.2. Introduction

Community dynamics are regulated by local, regional and larger scale processes, which affect populations in varying intensities and frequencies. When local processes are strong, the variability among adjacent populations and communities increase (e.g. recruitment of barnacles, GIL et al., 2010). On the other hand, when there is spatio-temporal synchrony in the distribution and abundance of organisms among populations, it indicates that these communities are controlled by a similar set processes, acting regionally at the same time and intensity. Therefore, identifying ecological variability at the population level is a tool to evaluate the strength of local and regional processes as regulators of the community dynamics (MCCULLOCH & SHANKS, 2003; WOODSON et al., 2012). Moreover, determining spatio-temporal synchrony can establish the degrees of which different populations are inter-connected (BECKER et al., 2007).

In sessile marine organisms, adult populations are connected by their larval stages. Primarily, if adult populations have similar reproductive cycles and timing, larvae will be present during the same periods in different locations of the coast, in a shared larval pool. Also, larvae will become ready to settle (e.g. competent) relatively together along the coast. However, oceanographic features can prevent larvae from settling simultaneously along the coast, resulting in spatial contrasts in recruitment rates, from cm to 100-km (RITTSCHOF et al., 2007; RILOV et al., 2008). Environmental conditions affect either larval supply or settlement, or both at the same time. There are many geographic barriers for larval transport (e.g. NAVARRETE et al., 2008), and larvae may accumulate in determinate sites (MORGAN et al., 2009). Besides, along shore differences in the incidence of some oceanographic features, such as upwelling plumes, generate pelagic gradients that affect reproduction of adults (ZARDI et al., 2007) and settler development (PRZESLAWSKI et al., 2005), resulting in spatial variation of recruitment (MENGE et al., 2013). Investigating temporal variability of recruitment rates in different sites in a regional scale can identify the oceanographic features which regulate larval supply, and thus, connect sessile marine populations.

The movement of meteorological low pressure centers over the ocean have huge impacts on the pelagic environment. In some coastal zones, these meteorological features are common and periodical, as well as their impacts on coastal communities. In the South Atlantic Ocean, these systems are known as cold fronts. Cold fronts occur approximately every 3 to 10 days, causing above average changes in wind direction and velocity, also, generating swells and strong onshore currents, and elevating sea surface height (CARBONEL, 2003; LORENZZETTI et al., 2009; PIANCA et al., 2010; NIETO-FERREIRA et al., 2012). Events vary in intensity and effect range (GALLUCCI & NETTO, 2004; AMORIN et al., 2012). Although, cold fronts disturb local pelagic conditions synoptically and reduce local contrasts in the water column (e.g. WALKER et al., 2005), their effects are attenuated or intensified by coastal geomorphology, resulting in spatial variability. These perturbations of the pelagic and benthic environment might affect reproduction, larval supply and settlement. Cold fronts have the potential to create spatio-temporal gradients or synchrony in recruitment rates, depending in which level they reduce local variability.

In order to assess the relatively importance of pelagic processes in regulating spatio-temporal variability through out recruitment, and determine the degree of connectivity among coastal populations, we compared time series of local and regional recruitment rates of intertidal invertebrates. We expected that species would recruit in synchrony among sites (km) along the region (100km), as a consequence of the regional effect of cold fronts. However, we hypothesized that there were differences in magnitude of recruitment rates, as an effect of persistent local environmental gradients.

Since reproductive timing is a function of favorable environmental conditions (HINES, 1978), and different species of larvae have different responses to changes in pelagic environment (e.g. water flow, CRISP et al., 1955; temperature tolerance, HOEGH-GULDBERG & PEARSE, 1995; attaching capacity, STANCY & FELLER, 1986), we included species specific resolution in our study. We compared recruitment trends among cirripeds and bivalve species to compare the connectivity in the population and community levels. Likewise, another important effect of spatio-temporal variability of larval supply and settlement rates at the community level is the power to determine the strength of pre or post recruitment processes as regulators of ecological dynamics (NAVARRETE et al., 2008). We also evaluated the degree of benthic-pelagic coupling by comparing adult abundances to recruitment rates.

2.3 Aims

The aim of this study was to identify the relative importance of local and regional pelagic contributions to the variation of recruitment rates of rocky shore intertidal invertebrates.

2.4 Study Area

This study was carried out in rocky shores on the oceanic and wave exposed side of two coastal islands located in the Southeastern Brazilian Bight, São Sebastião Island (South island) and Grande Island (North island), distant 130 km apart (Figure 7.1). Three sites were chosen on each island. Sites have similar wave exposure, geomorphological features, depths (20 m isobaths), anthropomorphic pressure and accessibility. Sites on the South island are located inside a bay, and they are oriented to the E (Figure 7.1), while sites on the North island are oriented to the SE (Figure 7.1).

Figure 7.1. Location of: the studied region at the Southeastern cost of Brazil (left); the studied South and North islands within the region (upper right); the sites within each island (lower right).

The spatio-temporal gradients in the pelagic environment at the study region are influenced by meteorological cold fronts and upwelling intrusions. Meteorological cold fronts are generated by low pressure centers moving from SW to NE promoting: cyclonic circulation of the surface waters (STECH & LORENZZETTI, 1992) and onshore transport (CASTELÃO et al., 2004; ASSIREU et al., 2003; PALMA & MATANO, 2009; MATANO et al., 2010); increase in wave action (PIANCA et al., 2004); variation of chlorophyll-a concentration (GALLUCCI & NETTO, 2004) and temperatures (PALMA & MATANO, 2009; CIOTTI et al., 2010; MATANO et al., 2010). Cold fronts occur approximately every 7 days with varying intensity and duration (CPTEC: Centro de Previsão do Tempo e Estudos Climáticos, INPE (Instituto Nacional de Pesquisas Espaciais), available at www.cptec.inpe.br/prevnum/). Upwelling intrusions are sporadic at the studied sites, with unknown frequency and intensity. They are caused by wind driven Ekman transport of surface waters (VALENTIN, 1984), coastal vortices and eddies (CALADO et al., 2010). Upwelling events result in sub-

superficial inputs of nutrients, drops in sea surface temperatures, and further increase in chlorophyll-a concentration (VALENTIN, 1984).

2.5 Materials and Methods

Recruitment

Recruitment rates (RR) of barnacles and mussels were monthly sampled (30 to 60 days) from May 2012 to June 2013. Recruitment was measured on artificial substrates, plates for barnacles (*Chthamalus bisinuatus*; *Tetracita stalactifera*; *Megabalanus coccopoma*; spat, first barnacle settlers which could not be identified as species) and Tuffys for mussels (*Brachidontes solisianus*; *Isognomon bicolor*; *Perna perna*; *Mytilidae*, first mussel settlers from Mytilidace family which could not be identified as species). Plates are flat PVC squares (8 cm x 8 cm x 0.2 cm) covered with Safety Walk® 3M anti-slip tape, which provides adequate rugosity to stimulate barnacle settlement. Tuffys are traps made of a multi-filament plastic mesh (typically used for dish-washing; S.O.S. Tuffly®), and provide a complex substrate for settling mussel larvae. All substrates (4 to 10 replicates) were placed at the mid-intertidal zone along the rocky shore about 5 meters apart. Plates and Tuffys were secured to the rocks with stainless steel screws and washers. At the end of each sampling period, the artificial 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.

Abundance of Adults

We estimated the frequency of adults at the intertidal communities of each site using the method of quadrants. The samples were obtained along the surface of each dominance zone: Upper-Midshore, for *C. bisinuatus* and *B. solisianus*; Lower-Midshore, for *T. stalactifera* and *I. bicolor*; Sub-litoral, for *M. coccopoma* and *P. perna*. Quadrants of 25 cm (n = 4) were photographed and the images processed in the laboratory. The species were identified and counted on the images using a grid of 100 intersections.

Conditions of the surface waters

We used temperature (*SST*) and chlorophyll-a concentration (*Chla*) to describe regional and local spatio-temporal variability of the pelagic conditions. Estimates of *Chla* and *SST* were obtained by remote sensing from GIOVANNI database (ACKER & LEPTOUKH, 2007), which generates these estimates using radiometers on the MODIS-Acqua satellite at temporal and spatial resolutions of 8 days and 4 km. We estimated monthly *SST* and *Chla*, by averaging the available estimates during each sampling period (month), for specific areas of the shelf surrounding the islands (North Island: 23° to 25°S / 46° to 44.5°W; South Island: 23° to 25°S / 46° to 44.5°W). Regional variation was described averaging all the available estimates of *Chla* and *SST* from May 2012 to June 2013.

Data Analysis

The ecological variables were: monthly recruitment rate *RR* [recruits/day]; and accumulated recruitment (*AR*) [recruits/trap], calculated by summing the average recruitment per trap per month.

Correlation analyses tested if *RR* were synchronic among sites and between islands (Sokal and Rohlf 1995). Time series were considered synchronic when $r \geq |0.5|$.

2-way analyses of variance (ANOVA) assessed the spatial variation of monthly *RR* among sites and between islands. ANOVA design: factor 1, island, with two levels South and North; factor 2, site, nested and random, with two levels (sites) (UNDERWOOD, 1997). Analyses were performed separately for barnacles and mussels. To reduce the probability of Type II error, we only included the data when *RR* was high on both islands simultaneously, February for barnacles and October for mussels. Therefore, ANOVA were performed including data of only two sites, sites 1 and 2 on North island, and sites 2 and 3 on South islands. ANOVA were balanced with 4 randomly chosen replicates (UNDERWOOD, 1997), the minimum number available at both sites. Normality and homogeneity of variances were respected.

Periods of maxima and minima *RR* were compared among species to evaluate inter-specific variation of recruitment trends.

Regression analysis described the relationship between adult abundances and *AR* (SOKAL and ROHLF, 1995).

Monthly temperatures (*SST*) and chlorophyll-a concentrations (*Chla*) were compared between islands by cross correlation analysis (SOKAL and ROHLF, 1995) to assess the temporal synchrony. The series were considered synchronic when $r \geq |0.5|$. We assumed $\alpha = 0.05$, and determined the significant p-values. We used R-project (R Development Core Team 2005), ODV (SCHLITZER, 2013) and Panoply 3.1.8 (SCHMUNK, 2013) softwares for statistical analyses and as graphical tools.

2.6 Results

Figure 7.2. Regional (a,b) and local (c,d) contrasts of sea surface temperature SST and chlorophyll-a concentration Chla during the studied period (May 2012 to June 2013), total (a,b) and monthly averages (c,d). sd: standard deviation.

Contrasts in Chla and SST

Total *Chla* and *SST* were similar at both islands (Fig. 2.2a and 2.2b), however, monthly averages of *Chla* and *SST* differed between them (Fig. 2.2c and 2.2d). On the South island, *Chla* maxima happened in the winter and in November, but on the North island, it happened two months later, in August until the end of fall (Fig. 2.2c). On both islands, the lowest *Chla* was registered in January (Fig. 2.2c), with significant correlations when lag 0 ($r = 0.55$ $p \leq 0.01$) and lag 2 ($r = 0.54$ $p \leq 0.01$). *SST* was also correlated between islands ($r = 0.98$ $p \leq 0.01$). The lowest *SST* were registered from June to November (Fig. 2.2d).

Spatio-temporal variation in recruitment

Periods of maximum and minimum recruitment differed between islands, for mussels and barnacles (Fig. 2.3). On South island, barnacle recruitment rates RR were higher in the spring and summer months (average = 7.9 recruits/d). RR were near zero from the end of fall to winter months (Fig. 2.3a). On the North island, the highest RR of barnacle were registered in February (averages = 7.74 recruits/d) (Fig. 2.3b). Mussels recruited in higher rates in spring 2012 and fall 2013 on the South Island (Fig. 2.3c), but from fall 2012 to January 2013 on the South island (Fig. 2.3d). In November 2012, all RR were close to null on both islands (Fig. 2.3a, 2.3b, 2.3c, 2.3d).

Recruitment at the North island sites were more synchronic than at the sites on the South Island, for all barnacle and mussels species (Fig. 2.3, Table 2.1). On South island, the sites located at the mouth of the bay showed the highest degrees of correlation for barnacle (S1 and S3, $r = 0.92$), with the highest RR at S3 (Fig. 2.3a, Table 2.1). However, RR of mussels were synchronic only at S1 and S2 ($r = 0.88$) (Fig. 2.3c, Table 2.1). On the North island, RR at the three sites were highly correlated for barnacles and mussels (Fig. 2.3b and 2.3d, Table 2.1). Time-lagged series were not significantly correlated (Table 2.1). According to ANOVA results (Table 2.2), among site contrasts were responsible for the most amount of variation in recruitment.

Figure 7.3. Spatio-temporal variation of the RR[recruits/d] of barnacles and mussels on the South (upper) and North (lower) islands, from May 2012 to June 2013. Dots and error bars represent the averages and standard deviations, respectively. The colors separate the sites: blue, S1; green, S2; and yellow, S3.

Inter-specific trends

On both islands, recruitment of barnacle *C. bisinuatus* overlapped in time, with the highest RR during summer (Fig. 2.4a and 2.4b). *T. stalactifera* also recruited in summer, however, on the South island, maximum RR happened one month before the maximum RR on the North island (Fig. 2.4c and 2.4d). Within each island, recruitment of *C. bisinuatus* and *T. stalactifera* were synchronic at the three sites (Fig. 2.4a, 2.4b, 2.4c and 2.4d; Table 2.1). Recruitment of *M. coccopoma* was not synchronic between islands, with peaks in October on the South island (Fig. 2.4e) and in February on the North island (Fig. 2.4f). Recruitment of spats was maximum in the spring and in the summer on the North island (Fig. 2.4h), but only in the summer on the South island (Fig. 2.4f).

On the North island, *P. perna* and other Mytilidae mostly recruited from May to October 2012 (Fig. 2.5f and 2.5h). On the South island, however, maxima RR occurred in September (Mytilidae) and October (*P. perna*), with a second increase in March (Fig. 2.5e and 2.5g). *I. bicolor* recruited with the highest RR from February to June 2013 on the South island (Fig. 2.5c) and from March to June 2013 on the North island (Fig. 2.5d). RR of *B. solisianus* were the lowest from the studied species with also the highest relative standard deviations. Recruitment of Mytilidae and *I. bicolor* were synchronic at the three sites on the South island (Fig. 2.5c and 2.5g), but they recruited during the same period only at the most distant sites on the North Island (Fig. 2.5d and 2.5h). The recruitment of Mytilidae was correlated between paired sites when the time lags were included (sites 1 and 2: lag 1 $r = 0.71$; sites 2 and 3: lag -1 $r = 0.76$) (Table 2.1).

On South island, accumulated recruitment AR was similar between islands but differed among sites for most of the species (Fig. 2.6). S2 received the highest amounts of recruits of barnacles, and of *C. bisinuatus* and *T. stalactifera* (Fig. 2.6a and 2.6c). Recruits of *M. coccopoma* and barnacle spats were more abundant at S3 (Fig. 2.6e and 2.6g). On the North island, AR was less different among sites than on the South island (Fig. 2.6). S1 received the highest number of recruits of barnacles (Fig. 2.6). AR of *M. coccopoma* was found in greater numbers on the South island, an exception compared to the trends of the other species. Mussel recruitment was 10 to 200 times greater on the North island compared to the South island (Fig. 2.7). S3 received the most amount of recruits of mussels (Fig. 2.7), and *P. perna* and Mytilidae were the most abundant (Fig. 2.7f and 2.7h).

Figure 7.4: Inter-specific contrasts in the temporal variation of recruitment rates (RR) of mussels on South (upper) and North (lower) islands. From May 2012 to June 2013, dots and error bars represent the average and standard deviations, respectively, for the separate life sites: green, S1; blue, S2; and yellow, S3.

Figure 7.6. Inter-specific contrasts in the temporal variation of accumulated recruitment AR [recruits/trap] of barnacles on South (superior) and North (inferior) islands, from May 2012 to June 2013. Dots and error bars represent the averages and standard deviations, respectively. The colors separate the sites: blue, S1; green, S2; and yellow, S3.

Figure 7.7. Inter-specific contrasts in the temporal variation of accumulated recruitment AR [recruits/trap] of mussels on the South (superior) and North (inferior) islands, from May 2012 to June 2013. Dots and error bars represent the averages and standard deviations, respectively. The colors separate the sites: blue, S1; green, S2; and yellow, S3.

Table 2.1 Results of the cross correlation analysis to assess the temporal synchrony of recruitment rates among sites within each island (South and North). The sites were compared in pairs, sites 1 and 2 (1-2), sites 1 and 3 (1-3), sites 2 and 3 (2-3), including total recruitment (barnacles and mussels) and specie specific (*C. bisinuatus*, *T. stalactifera*, *M. coccopoma*, spat, *B. solisianus*, *I. bicolor*, *P. perna*, Mytilidade). r: correlation coefficient. ns: non significant results.

Sites	r					
	South			North		
	1-2	1-3	2-3	1-2	1-3	2-3
BARNACLES	ns	0,92	0,64	0,96	0,86	0,92
<i>C. bisinuatus</i>	0,76	0,85	0,61	0,85	0,75	0,89
<i>T. stalactifera</i>	0,96	0,96	0,86	0,86	0,91	0,72
<i>M. coccopoma</i>	ns	0,98	ns	ns	0,93	ns
Spat	ns	0,99	ns	0,99	0,64	ns
MUSSELS	0,88	ns	ns	0,77	0,93	0,68
<i>B. solisianus</i>	ns	ns	0,69	ns	ns	ns
<i>I. bicolor</i>	0,86	0,87	0,61	ns	0,72	ns
<i>P. perna</i>	0,74	ns	ns	ns	ns	ns
Mytilidade	0,75	0,61	0,67	ns	0,94	ns

Table 2.2. Results of the 2-way analysis of variance comparing contrasts of recruitment rates between islands (South and North) and sites (sites 1 and 2 on North island, and sites 2 and 3 on South islands). df: degrees of freedom. F: F-statistic. p: p-value, * if ≤ 0.01 .

Sites	df	BARNACLES		MUSSELS	
		F	p	F	p
ISLAND	1	9,00	0,204	0,36	0,656
SITE	1	12,68	0.003*	1,88	0,195
ISLAND*SITE	1	1,48	0,246	35,3	< 0.001*
Residual	12				

Abundances of Recruits vs. Adult

Accumulated recruitment AR was proportional to the abundance of adults. Sites on the South island showed the lowest degrees of correlation ($R^2 < 0.34$) (Fig 2.8). On the North island, correlation was detected at S1 and S3 ($R^2 = 0.81$) (Fig 2.8). AR varied between barnacles and mussel species, also, with different trends between islands (Fig 2.9).

Figure 7.8. Relation between the frequency of adults Freq (%) and accumulated recruitment AR [recruits/trap] of barnacles and mussels at the sites (S1,S2,S3) within each island, South (upper) and North (lower). R^2 : coefficient of determination.; $n = 4-6$.

Figure 7.9. Relation between the frequency of adults Freq (%) and accumulated recruitment AR [recruits/trap] of barnacles (upper) and mussels (lower) within each island, South (dashed line) and North (full line). R^2 : coefficient of determination: $n = 9$.

2.7 Discussion

Our results showed a balance between local and regional regulation of recruitment variability. Recruitment of intertidal organisms was not synchronic in the scale of 100 km. The length of the recruitment seasons, the number and timing of recruitment peaks varied between islands. Likewise, site (scale of km) and inter-specific differences were also important sources of variation, affecting the magnitude of recruitment rates and the temporal trends, reinforcing the importance of local variability for ecological dynamics. However, regional coincidences of recruitment were detected, including spatio-temporal and inter-specific trends, suggesting that large scale processes are also involved in community regulation.

In the scale of 100 km, recruitment variation was related to fluctuations in pelagic conditions, which persisted at the species specific level. At least one species of barnacle and mussel have shown delayed recruitment seasons between islands. Most species of barnacles recruited earlier in the season on the South island, where the highest concentrations of chlorophyll-a also happened before (winter). For some species, such as the barnacle *M. coccopoma*, the delay (number of months) between recruitment peaks and chlorophyll-a concentration maxima was the same. The coastal waters of the study region are relatively oligotrophic (GAETA et al., 1999; GIANESELLA et al., 1999). Phytoplankton blooms are rapidly consumed and chlorophyll-a depleted (MCMANUS et al., 2007). Since food (e.g. phytoplankton) is a limited resource for intertidal filter feeders (e.g. barnacles and mussels) at the studied sites, it could regulate reproduction and/or the development and survival of larvae and settlers. Positive relationships between reproduction and recruitment are known for temperate barnacles (KENDALL & BEDFORD, 1987), which are associated to fluctuations of food concentration in the water column.

Mussels recruited earlier on the North island. Maximum recruitment rates happened in the winter, when average sea surface temperatures were approximately 1°C higher. Mussels are very sensitive to temperature fluctuations. Differences of sea surface temperature, in the same magnitude as observed in the study area, can cause variation of recruitment rates, either affecting reproductive timing, larval development or settler survival. In temperate and upwelling systems, mussel recruitment is benefited by temperature drops (YOUNG et al., 1996; REAUGH-FLOWER et al., 2011), and settlement is coupled with reproduction (MCQUAID & PHILLIPS, 2006). At the other sites close to the South island, for example, *P. perna* (one of the mussels species) reproduces and settles at maximum rates during the same period, fall (LUNETTA, 1969; FERREIRA & MAGALHÃES, 2004; BORDON et al., 2011), what partially agrees with the trends observed in our study. Although the reproductive cycles of intertidal barnacles and mussels are not described for the studied sites, our results suggests that they might be locally controlled, therefore, intertidal dynamics are primarily regulated by local sources.

Periods of recruitment and the degree of site synchrony also varied at the scale of 100km. More species recruited simultaneously on the South island, where the studied sites are located inside a bay. First, this result suggests that recruitment synchrony depends on coastal morphology. Moreover, recruitment is probably driven by the same

environmental conditions and/or larval transport mechanism. Besides, the degree of population connectivity varies between islands, likewise, are probably more vulnerable to stochastic changes in the pelagic environment and also the genetic flux of larvae from other populations.

Within the same taxonomic group, barnacles or mussels, the recruitment of most species did not coincide. This can be an evolutive mechanism to reduce inter-specific competition at the settlement, increasing the survival of the first life stages. For example, *M. coccopoma* and *P. perna* occupy the lower levels of the intertidal. They recruited in synchrony on the South island but in different months on the North island. At the first situation, the recruits of the different species will not compete for space and food, however, they will at the second situation. The previous trend was different among islands, suggesting that the ecological dynamics of these intertidal communities might also differ. So, competition is more important on the North island. Furthermore, when many species recruit simultaneously and in high levels, the strength of inter-specific relationships is higher in setting adult patterns (GAINES & ROUGHGARDEN, 1985; NILSEN & NAVARRETE, 2004). On the South island, since recruitment might be a limited processes, the abundance and distribution of recruits should determine adult patterns (CONNELL, 1985).

Our study found different trends of recruitment between barnacles and mussels. Opposite trends were identified between islands. Also, barnacles showed higher site synchrony compared to mussels. Previous studies found different degrees of correlation of recruitment and environmental variables between barnacles and mussels, and also, in the effect of cold fronts in recruitment (MAZZUCO et al., 2015). Barnacles and mussels are components of the same community, also, both are sessile and filter-feeders, and are supposedly subjected to similar environmental conditions. However, barnacles and mussels may show different spatio-temporal trends of recruitment (e.g. BROITMAN et al., 2008; ILES et al., 2010), what indicates that different factors might be involved in the regulation of population dynamics of these groups. Likewise, barnacles and mussels may not reproduce simultaneously (e.g. HINES, 1975), producing variations in larval supply and recruitment.

Comparing sites, accumulated recruitment did not converge. This means that these populations received different amounts of recruits during the sampling period. For some species, this difference reached 100%, and tendencies varied between islands. Since all studied sites have similar community profiles, coastal morphology is probably

the most important component regulating this recruitment variation by affecting larval distribution and abundance. On the South island, for example, the site at the center of the bay received the most amount of recruits. Central bay areas may present the highest rates of larval supply and recruitment when favorable conditions allow offshore waters to penetrate (MCCULLOCH & SHANKS 2003). If larvae come from outside the bay, this site might be receiving allochthonous water more frequently, consequently, resulting in higher recruitment. On the other hand, on the North island, inter-specific trends were highly variable but magnitudes were less different among sites. Sites on the North island are more open to coastal currents coming from other sites compared to bay sites on the South island. This means that North island sites should present more local fluctuations of pelagic origin, such as variations in larval supply. On the other hand, benthic post-settlement conditions were responsible to neutralize local variability, converting in lower among site differences of recruitment rates.

On the North island, we expected that unlimited recruitment would cause a disagreement with trends in adult abundance (CONNELL, 1985). However, on this island we registered a significant correlations between recruitment and the frequency of adults. The additional amount of recruits found at the North island did not saturate the community, and post-settlement processes were not able to cause variation between settlement and adult trend. Constant space availability might reduce competition among recruits of sessile species. The two sites at the north island where we detected this trend might be more wave exposed than the others, where waves can open new spaces by removing encrusting organisms. This result suggest that pelagic processes, such as waves action, can influence the level of recruitment limitation by affecting the benthic conditions.

Process occurring simultaneously across the region might have prevented recruitment at the studied sites during specific periods. On both islands, most taxa showed nearly null recruitment rates during the winter, when cold fronts are frequent and intense (PIANCA et al., 2010), and in November, when temperature oscillations on the intertidal are common (see FLORES et al., 2015). Recruitment does not occur when competent larvae is absent onshore (MINCHINTON & SCHEIBLING, 1991), either caused by reduced larval production by adults (MCQUAID & PHILLIPS, 2006), high larval mortality (PINEDA et al.; 2002) or dispersion by ocean currents (HERBERT et al., 2009). Settlement can also be prevented by hydrodynamic regime (e.g turbulence and waves, VEDAS et al., 1990; FUCHS & DIBACCO, 2011). Besides, when post-

settlement mortality is high, recruitment is reduced (RAIMONDI, 1991). The studied rocky shores are drastically affected by cold fronts and temperature oscillations, both being able to impede settlement or reduce recruitment by post-settlement effects. Cold fronts may drive larvae to deeper areas, in a similar scenario of what happens in downwelling situations (GARLAND & ZIMMER, 2002) when they bring oceanic waters to shore. Also, larvae may not settle or be removed from the rocks by wave action caused by the front swells. The alternation of cold upwelling waters and high sun radiation can produce extreme temperature oscillations at the intertidal, killing adults (HARLEY, 2008) and settlers (SHANKS et al., 2009).

In our region, recruitment is regulated by a balance between local and regional processes. Recruitment is not synchronic along the region (scale: 100kms), varying in: the length of the recruitment seasons; the number and timing of recruitment maxima; site synchrony and total recruitment (scale: km); and the correlation with adult abundance. Inter-specific differences affected the magnitude of recruitment rates and the temporal trends, suggesting that recruits experiences reduced competition. However, spatial coincidences in recruitment trends suggest that regional processes are also involved in population regulation.

3. CHAPTER III: The influence of cold fronts on larval supply and settlement: case studies of subtropical rocky shores showing daily variability

3.1 Abstract

In this study we evidenced that meteorological cold fronts (CF) significantly influence the abundance of larvae at very nearshore and the settlement rates of intertidal organisms overcoming the spatial variability. We hypothesized that: (i) CF bring larval pool to shore, increasing the abundance of post-larvae and the settlement rates, in correlation to the descriptors of CF; (ii) barnacles and mussels show the same temporal and correlation trends in relation to CF; (iii) which are applicable at the regional scale. We sampled larvae and settlers before, during and after CF at three sites within the same region, monitoring atmospheric and pelagic conditions. According to our results, CF had a higher influence in settlement than in larval abundance, which was stronger for barnacles than mussels. The initial larval stages were mostly found between CF, but the abundance of these larvae were not synchronic to the abundance of post-larvae or settlement rates. Higher rates of barnacle settlement occurred one day before and/or at the first day of the CF. Settlement of mussels occurred independently of the presence of CF, or to the abundance of their post-larvae, which were higher during non-CF periods. Wind speed and direction presented the highest degrees of correlation with post-larval abundance and settlement, suggesting that those processes are wind driven at the study region. We detected important local particularities that might be a consequence of spatial variation at the coastal environment. This study highlights that climatic fluctuations have important but contrasting effects on rocky shore communities.

Keywords: larval supply; larval settlement; invertebrates; intertidal environment; atmospheric fronts; temporal variations.

3.2 Introduction

Nearshore physical transport processes affect larval dispersion and settlement and will regulate many marine benthic communities. Once in the pelagic environment, larvae will be displaced by currents (SHANKS, 1995) and can advect away from favorable settling sites (MCEDWARD, 1997; TAPIA & PINEDA, 2007; COWEN & SPONAUGLE, 2009), potentially increasing the chances of dispersion and mortality rates. The concentration of invertebrate larvae in a given water mass depend on the intensity and direction of costal currents from their sources (LEICHTER *et al.*, 1998;

MCCULLOCH & SHANKS, 2003; GYORY & PINEDA, 2011; MENGE & MENGE, 2013). Larvae can disperse to long distances (STRATHMANN & STRATHMANN, 2007), although most of the larvae from coastal organisms are retained within the continental shelf borders (EPIFANIO & GARVINE, 2001; MA & GRASSLE, 2004; YOSHINAGUA *et al.*, 2010; MORIARTY & O'Brien, 2013). While the role of larval behavior, especially for larvae retention at the coast, has been reported (DOBRETISOV & MIRON, 2001; SHANKS & BRINK, 2005), larval survival and settlement rates dependent on the physical processes and will also affect the adult populations.

Physical processes in the ocean are influenced by changes in meteorological conditions. For instance, the frequent passage of meteorological cold fronts over the Southeastern Coast of South America can drastically impact the atmospheric and physical pelagic environment by changing the speed and direction of the main winds and superficial ocean currents (CARBONEL, 2003). During cold front events, both the wind field and the wave swell are from SW-S-SE (CARBONEL, 2003; PIANCA *et al.*, 2010), causing elevation in wave action and sea level height (PIANCA *et al.*, 2010). As a consequence, coastal waters show enhanced vertical mixing and changes in sea surface temperature and the concentration of chlorophyll-a (e.g., PALMA & MATANO, 2009). Passages of cold fronts, in the very nearshore can promote the exchange of waters from coastal bays and the inner continental shelf, potentially affecting reproduction and larval transport mechanisms of some marine invertebrates. Therefore, it is reasonable to assume that the passage of cold fronts might influence settlement rates of marine invertebrates. However, very little is known about the effect of these events on supply side ecology of many marine organisms.

Among several factors influencing larval settlement, a basic premise is that settlement will only occur when competent larvae (PINEDA, 2000) are present at the settlement site, assuming a supply side in pulses to the shore. In previously studied marine systems, competent invertebrate larvae are driven to shore sites by specific features and conditions, which are responsible for regulating settlement pulses of intertidal organisms, such as Lagmuir cells and internal waves (SHANKS, 1995). Studies on rocky shore intertidal communities at coastal upwelling regimes show wind, sea surface temperature (SST) and chlorophyll-a concentration (Chla) correlation with recruitment (RANGE & PAULA, 2001; MENGE *et al.*, 2009; MENGE *et al.*, 2011, ILES *et al.*, 2012). Several oceanographic phenomena influence on changes in sea surface that may affect the transport of larvae, settlement and recruitment (JENKINS &

HAWKINS, 2003; MCQUAID & LINDSAY, 2000; HUNT & SSCHEIBLING, 1996). In addition to the pulses delivering to the shore, changes in sea surface height may influence the recruitment rates thorough less specific mechanism that influence sea level (i.e., storms, large scale currents), which are rarely considered in recruitment studies (but see PINEDA & LÓPEZ, 2002). Considering the importance of cold fronts changing the physical dynamics, we believe they can overlap the other features, deeply influencing the coastal environment. Therefore, we hypothesized that cold fronts would bring the larval pool to potential settlement sites, causing settlement pulses at the intertidal.

Ecological processes vary in a range of different spatial-temporal scales. When considering spatial scale, settlement rates vary in magnitude and synchrony from centimeters to hundreds of kilometers (ROBERTS *et al.*, 1991, NAVARRETE *et al.*, 2008). However, it is reasonable to assume that similar processes at sites with comparable physicochemical characteristics will regulate settlement rates. It is expected that events that act in meso and large scales would overwhelm local particularities, enhancing similarities among shores in these scales. For example, in upwelling systems, settlement rates measured at regional scales reflect the spatial variability in both upwelling intensity and frequency (NAVARRETE *et al.*, 2008). Therefore, we hypothesized that during cold front passages over the region, local characteristics are of less importance during the events, influencing distinct sites in a similar manner.

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). Due to the stochasticity in meteorological and oceanographic processes, it is crucial to consider temporal resolution to improve the understanding of recruitment dynamics. MAZZUCO *et al.* (in press) showed that recruitment on rocky shores varied in relation to the oceano-meteorological features over different time scales, where some small temporal scale variation was observed. Some factors are known to influence settlement at a daily scale, as larval abundance (e.g. PINEDA *et al.*, 2002) and fluctuations of coastal oceanographic processes, such as tidal bores (e.g. PINEDA & LÓPEZ, 2002). Cold fronts is one short term event, varying over the scale of days, that might influence settlement. However, daily variation of intertidal larval abundance and cold fronts have not been investigated simultaneously, neither the potential effect on settlement. If cumulative effects of daily settlement are important driving population

trends, patterns at large spatio-temporal scales may differ as a result of the effect of cold fronts in settlement.

One approach to observe the influence of cold fronts on settlement rates of marine invertebrates is to follow the frequency of cold front passages themselves at a given shore, while concurrently monitoring both larval abundances and settlement rates. In this type of field study, some limitations should be considered as important sources of variation. First, cold front events occur independently of the presence of competent larvae in the adjacent waters, consequently, the degree of correlation is vulnerable to the temporal patterns of reproduction. Also, in natural systems, oceanographic features are simultaneous and interact, presenting synergic effects (e.g. MCCLLOCH & SHANKS, 2003). Third, in the studied system, cold fronts vary in frequency, intensity and duration (STECH & LORENZETTI, 1992; PIANCA *et al.*, 2010), adding an extra source of variation for the temporal benthic-pelagic dynamics, which can be reflected in changes of settlement rates. So, replication of independent cold front events is crucial to reduce these confounding effects by increasing the probability of registering larvae and settlement and capturing the influence of strong and weak cold fronts.

3.3 Aims

Here, we tested the influence of cold fronts at small temporal scales on the abundance of larvae at the very nearshore and on the settlement rates of intertidal barnacles and mussels. Studies conducted at a northern site (about 350 km distant) found that barnacle larval supply and settlement might increase when cold fronts are present (SKINNER & COUTINHO, 2002) and in association to wind changes (LOPEZ & COUTINHO 2008). However, in a previous study, we found a different result, barnacle recruitment was negatively related to cold front events in a monthly scale, more likely to occur when winds are stronger and offshore, when there are fewer cold fronts, when Chla is low, and SST is high (MAZZUCO *et al.*, in press). Mussel recruitment showed little correlation with the changes in the pelagic and meteorological environment. These differences are explained by the circulation patterns at the coastal island where this study was conducted and by seasonality which may favor reproduction during periods when cold fronts are less frequent and weaker. Therefore, we hypothesized that advancing cold fronts transport larval pool to the coastal shores in SE Brazil, increasing the abundance of post-larvae and their settlement rates. If this first hypothesis is true, we can further hypothesize that post-larvae abundance and settlement will be better

correlated to wind speed and direction that are the best descriptor of cold front (see MAZZUCO *et al.*, in press). And, considering cold fronts as a main driver we also expect that spatial variability among sites will be minimal due to the overwhelming influence of this synoptic event. Besides, since cold fronts will vertically mix the water column near shore, during these events, we expect larvae to behave as passive particles, consequently, both barnacle and mussel will show similar temporal trends. To test these, we sampled larvae and settlers during cold front events while characterizing the atmospheric and pelagic conditions. The case studies were conducted at three different sites within the same region (Latitude: 21° to 26°S; Longitude: 41° to 46° W) testing the spatial consistency of the trends.

3.4 Materials and Methods

The study was conducted at three sampling sites where settlement rates and larval abundance of intertidal barnacles and mussels were measured daily. At each site observations were made over different time periods (Fig. 3.1). Site/time period combinations are hereafter referred to as Case studies: Case 1, Sonar (22°59'16.8"S; 42°1'1.1"W), at Arraial do Cabo-RJ, from October 22 to November 6, 2012; Case 2, Bravinha (23°30'19,6"S; 45°10'18,3"W), at Ubatuba-SP, from March 5 to 26, 2013; and Case 3, Baleero (23°49'44.6"S; 45°25'25.1"W), at São Sebastião-SP, from November 6 to 30, 2013. Accordingly, the sites corresponding to each of the Cases will be named Site 1, Site 2 and Site 3. The duration of sampling differed between Cases (7 days for Case 1; 17 days for Case 2; and 21 days for Case 3) due to logistical constraints. All three sites are subjected to random passages of cold front systems, which in this work were characterized according to wind speed and direction (ws and wd) and significant wave height (SWH). In addition, chlorophyll-a concentration (Chla) and sea surface temperature (SST) were monitored in situ twice a day. The three sites are highly exposed to the effects of meteorological cold fronts, but each site has specific characteristics regarding recruitment rates of the two intertidal biological models, barnacles and mussels, the influence of upwelling plumes and wave exposure. Site 1 was under constant influence of cold nutrient rich waters from upwelling events, and it is the most exposed to wave action. Site 2 is located inside a shallow bay and Site 3 is located at the southern border of a coastal channel. Site 2 and 3 are episodically affected by intrusions of upwelled cold nutrient rich waters and by wave action due to the cold fronts.

Figure 3.1. Location of the study sites and shores (lower maps) within the Cabo Frio Upwelling region.

Sampling Methods

Larval abundance of intertidal barnacles (nauplii and cyprids) and mussels (D larvae and Veliger) were monitored twice a day (morning and afternoon) onshore. Larvae were sampled by concentrating 150 L of sea water collected from the rocky shore using a 15L bucket in 20µm plankton mesh. The sample was preserved in ethyl alcohol solution (70%), until analysis. In the laboratory, larvae were identified and counted under a stereomicroscope (Zeiss Discovery v.08). During Case 2, we also sampled larval abundance in the surrounding areas of the site by boat in three moments. At each moment, nine vertical tows (see Fig. 3.5) from bottom to surface were collected in three consecutive transects parallel to the mouth of the bay, using a plankton mesh (20µm; 30 cm mouth width; 70 cm length). Each survey was undertaken at the diurnal high tide over a period of one hour.

Settlement was measured in the mid intertidal zone (dominated by the barnacle *Tetraclita stalactifera*) using artificial surfaces, plates for barnacles (all Cirripedia) and tuffys for mussels (all Bivalvia). Plates were made of PVC squares (8cm x 8cm x 0,2cm) covered with Safety Walk® 3M anti-slip tape which provides adequate rugosity to promote larval settlement. Tuffys are traps made of a multi-filament plastic mesh (typically used as dish-washing sponges; S.O.S. Tuffly®), providing a complex substrate for settling mussel larvae. Plates and tuffys were secured to the rock with stainless steel screws and washers. Every morning, after approximately 24h, plates and tuffys were

replaced with new ones. During some periods high wave action did not allow daily sampling. In these situations, plates and tuffys could not be replaced, and they sampled continuously up to 3 days. In Case 1, settlement was measured every 2 m measured in one area of the shore. During Case 2 and 3, settlement was also measured every 2 m, but in two 50 m-separate adjacent areas of the shore. Plates and tuffys that had been on the rocks were transported to the laboratory and frozen at -20°C until being processed (minimum freezing time: 1 day). In the laboratory, barnacle settlers on the plates were counted using the stereomicroscope. Tuffys were washed in fresh water, and settlers 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 the stereomicroscope.

Cold fronts (CF) were described using wind direction (wd, degrees) and wave height (SWH, meters). CF were considered to be influencing the site when wd changed to SW-S-SE and persisted through at least one day causing SWH to increase (GALLUCCI & NETTO, 2004; PIANCA *et al.*, 2010). As wind speed (ws, ms-1) showed considerable correlation to recruitment in our previous study (Mazzuco *et al.* 2015), we included this variable in the analysis. Additional information about in situ water column (chlorophyll-a concentration Chla, mgm-3; and sea surface temperature SST, °C) was used to describe the conditions of the pelagic environment during the study period and for comparisons with settlement and larval abundance.

Wind speed and direction (ws and wd) were measured by the oceanic-meteorological stations of: Institute of Marine Studies Almirante Paulo Moreira IEAPM-Brazilian Navy (located at the Cabo Frio Island, close to Sonar shore), for Case 1; the Agronomic Institute of Campinas (located in São Sebastião Channel, close to Castelhanos Bay), for Case 2; and the Marine Biology Center CEBIMar-USP (located at Baleeiro shore), for Case 3. Measurements of ws and wd were averaged over the previous 24h for comparisons with settlement data (plates and tuffys sampled continuously for 24h), and over the previous 6h for comparisons with larval abundance (arbitrary as the representation of the wind regime previous to the collection of larval abundance).

SWH 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 x 1° longitude. Local estimates were

averaged for a specific area of the platform for each Case 1, 2 and 3, respectively: 22°S to 24°S, 41°W to 43°W; 22°S to 25°S, 44°W to 46°W; and 23°S to 25°S, 47°W to 45°W.

SST was registered locally through averaging measurements conducted twice per day, simultaneously to the larval samplings, using a portable hand-held temperature system (YSI Model 30). Chla estimates were obtained together with SST measurements. Measurements of the natural fluorescence of sea water were used to estimate Chla values according to the fluorescence of extracted chlorophyll-a from particulate matter. Natural fluorescence was measured in 3 samples of 20 ml 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, U.S.A.). For calibrating natural fluorescence measurements, we performed chlorophyll extraction 6 times during the sampling campaign. For this purpose, 3 samples of 500 ml of surface sea water were filtered through GF/F glass fiber filters (0.7 μ m, Whatman®). Filters and the retained material were extracted in a 90% acetone solution for 48 h, and after extraction, fluorescence was measured using the same fluorometer.

Data Analysis

The first hypothesis, Cold fronts bring larvae to the shore, increasing the abundance of post-larvae and the settlement rates, was tested by describing temporal and spatial trends in larval abundance (larvae.day-1) and settlement rates SR (settlars.day-1) during the case studies. To assess if cold front samples were more similar than the other samples, we conducted principal components analysis (PCA) for each case and biological model.

To test the second hypothesis, Post-larvae abundance and settlement will be better correlated to the best descriptor of cold front, wind speed and direction), we analyzed the correlation between larval abundance, settlement and variables used to describe the CF and the environmental conditions during the studies (ws, m/s; wd degrees; SWH m; Chla mg.m-3; SST °C). Cross correlation analysis (CCA) was conducted, including time-lag comparisons. We assumed $\alpha = 0.05$, however, because of the multiple paired comparisons in our analysis, we reviewed the significant p-values by using the false discovery rate method (GARCIA, 2004; VERHOEVEN *et al.*, 2005; PIKE, 2011). Temporal autocorrelation was assessed previously to CCAs by comparing each variable versus time with a simple regression analysis. Variables were considered

autocorrelated when $p \leq 0.05$ and results are exposed in Table SI (Supplementary Material). We removed the autocorrelation using the differences between the averages of consecutive periods (e.g., PINEDA & LÓPEZ, 2002) (Table SII - (Supplementary Material), which were used to conduct the final analysis for those variables. Results of the PCA were also used to understand the variable responsible for similarity of the samples.

Separate descriptions and analyses were conducted for barnacles and mussels, comparing both biological models for the test of the hypothesis that Barnacles and mussels will show similar temporal and correlation trends.

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.

3.5 Results

Cold fronts (CF) influenced settlement of the biological models more clearly than larval abundance, and significant correlations were frequently registered with wind speed. Although Case studies were at different sites and time, bringing variability on the overall pattern for spatial consistence or similarity between biological models, some patterns and trends were observed, being Case 2 and 3 the most similar. Barnacles and mussels did not show the same trends in relation to the CF, also, neither larval stages nor settlement were coincident in time. In summary, nauplii was found in higher abundances during CF at Case 1, between CF in Case 2 and 3. Cyprids were found in very low abundances, usually when CF were not influencing the sites. Higher rates of barnacle settlement occurred one day before and/or at the first day of the CF. Mussel D-larvae and post larvae were more frequently registered in non CF periods. Settlement of mussels occurred independent of the presence of the CF. Case-specific conditions and variations are detailed in the following text.

Figure 3.2. Daily variation of the cold front descriptors of the pelagic and meteorological conditions during Case 1 (upper), Case 2 (middle), Case 3 (lower): wind speed and direction, ws (bars) and wd (arrows); and significant wave height SWH (lines). Cold front events are highlighted by the shaded areas in the graph.

Case 1

One CF was registered during the studied period, when SWH was higher than 1.7 m and the main wd was from SO-SE (Fig. 3.2). Before and after the CF, ws was the highest ($|ws| > 3.4 \text{ ms}^{-1}$) prevailing from E and SWH was lower than 1.5 m (Fig. 3.2).

Higher abundance of cyprids and barnacle settlers were registered before the CF, decreasing when CF arrived at the site (Fig. 3.3). Nauplii were positively influenced by the CF, presenting low abundance before and after the CF, with higher densities at the shore during the CF (Fig. 3.3). Both mussel larval stages were negatively affected by CF. Higher abundances were registered before the CF, decreasing approximately two days prior to the arrival of the CF (Fig. 3.3). On the other hand, mussel settlement slightly increased during the CF, followed by a decrease two days after the end of the CF (Fig. 3.3).

Figure 3.3. Case 1 - Temporal variation of larval abundance, 1st larval stages (dashed line) and post-larvae (full line), and settlement (bars) of barnacles and bivalves before, during and after a cold front. This sampling occurred from October 30 to November 6, 2012. Cold front events is highlighted by the shaded area in the graph.

Settlement rates were not significantly correlated to the abundance of any of the larval stages for neither barnacles (1st stages: $R^2 = 0.03$, $p = 0.816$; Post-larvae: $R^2 = 0.10$, $p = 0.683$) nor mussels (1st stages: $R^2 = 0.61$, $p = 0.219$; Post-larvae: $R^2 = 0.07$, $p = 0.728$).

Significant statistical results were not found for the correlation between settlement and the cold front descriptors; however, the degree of correlation registered was above 0.7 for the comparison SWH and settlement of barnacles and mussels (Table 3.1 and 3.2). Larval abundance was correlated to the cold front descriptors: the abundance of nauplii was positively related to Chla and SST (Table 3.1); cyprid abundance was positively related to ws and wd (Table 3.1); the abundance of D-Larva

was positively related to *ws* and negatively related to *wd* (Table 3.2); the abundance of post-larva was positively related to *ws* (Table 3.2).

Case 2

During this sampling period, three CF were observed at the site, causing SWH to rise higher than 2 m (Fig. 3.2). Although there were intervals when CF were not influencing the site, prevailing *wd* was from SE. *ws* was lower than registered in Case 1, with averages $< 1 \text{ ms}^{-1}$ (Fig. 3.2). The second CF showed the highest *ws* averages (0.9 ms^{-1}) while the third CF showed the highest SWH averages (2.6 ms^{-1}) (Fig. 3.2).

The temporal variation of nauplii and cyprids were not significantly correlated ($R^2 = 0.01$; $p = 0.649$) and nauplii were found in higher abundances than cyprids. Cyprids were found in low abundance over time, reaching maxima before the second CF (Fig. 3.5). Nauplii showed two peaks not directly related to the cold fronts, one was found 1 day before the second CF and the other 3 days after the third CF (Fig. 3.4).

Barnacle settlement presented higher rates during CF events in both areas (Fig. 3.4). Maximum rates at the area 1 were observed when the second CF arrived, decreasing as time progressed and the third CF affected the site, while at area 2 it started one day before than area 1 ($r = 0.69$, $p \leq 0.001$) (Fig. 3.4). Settlement was not correlated to the abundance of nauplii in both areas (A1: $R^2 \geq 0.01$, $p = 0.812$; A2: $R^2 = 0.03$, $p = 0.501$), but a local scale variability was observed regarding the relation between settlement and cyprids abundance. In this case, at area 1, settlement peaked after 3 days of the increase in cyprids abundance (Lag -3: $r = 0.59$, $R^2 = 0.5$; $p = 0.003$), whereas no correlation was observed at area 2 ($R^2 = 0.13$, $p = 0.182$) (Fig. 3.4).

Mussel larval stages showed different trends over time. D larvae were more abundant between the first and second CF, while mussel post larvae did not show the same trend ($R^2 = 0.05$, $p = 0.426$), when periods of higher densities occurred independent of the presence CF (Fig. 3.4). Settlement at area 2 started before area 1 (Fig. 3.4), with one-day inverse correlation (Lag -1 day: $r = -0.55$, $p = 0.034$). Settlement of mussels showed similar patterns to those described for barnacle. settlement at area 2 started 1 day before area 1 (Lag -1 day: $r = -0.55$, $p = 0.034$). Also, at area 1, SR increased during the second CF (Fig. 3.4), but it was not significantly related to the amount of D larvae ($R^2 = 0.19$, $p = 0.099$) or post-larvae ($R^2 = 0.01$; $p = 0.6915$). SR at area 2 increased after the first CF and during the third CF (Fig. 3.4), one

day lagged of the abundance of D larvae (Lag -1: $r = 0.53$, $R^2 \leq 0.32$, $p = 0.035$) but uncorrelated to the abundance of post-larvae ($R^2 \leq 0.01$, $p = 0.853$).

Figure 3.4. Case 2 - Temporal variation of larval abundance, 1st larval stages (dashed line) and post-larvae (full line), and settlement (bars) of barnacles and bivalves during and between three cold front periods. Settlement was measured in two areas at the same shore, area 1 (dark bars) and area 2 (light bars). This sampling occurred from March 6 to 24, 2013. Cold front events are highlighted by the shaded areas in the graph.

Regarding larval abundance within the Bay surveyed at this Case (Fig. 3.5), there was identified a variability during the different CF conditions. Barnacle showed a greater variation compared to mussels, whose trends were more persistent. Before the CF, a greater amount of larvae were found inside the bay and larval concentration decreased as it approached the mouth of the bay. Nauplii were found in higher concentrations than cyprids, which were present at the more centered stations. During the CF, larvae were unevenly distributed inside the bay. The concentration of nauplii decreased and of cyprids increased. After the CF, cyprids were not registered by the tows, but the abundance of nauplii was also high, especially towards the mouth of the

bay. For mussels, the amount of post-larvae was always lower than the amount of D-larva, and larva was distributed homogeneously inside the bay independent of CF presence. The concentration of larvae was similar among the samplings.

For barnacles, only settlement at area 2 was significantly correlated to the descriptors of cold fronts: positively to ws and SST, and negatively to wd (Table 3.1). Nauplii abundance was positively correlated to lagged ws and Chla (Table 3.1). Post-larval abundance was positively correlated to wd and lagged ws (Table 3.1). For mussels, settlement was also positively correlated to ws (at area 2) and negatively correlated to wd (at area 1, with two days lag) (Table 3.2). D larvae was positively correlated to ws, but a negative trend was found when comparing ws with the abundance of mussel post larvae (Table 3.2).

Figure 3.5. Case 2 - Abundances of barnacle (superior) and bivalve (inferior) larvae at Fortaleza Bay during three random situations associated do events of cold fronts CF (from left to right): before a CF; during a CF; after a CF. Circles: diameters represent relative averages of larval abundance; black part represent the relative amount of 1st stage larvae; and white part represent the relative amount of post larvae.

Case 3

Five CF events influenced the site during this last sampling (Fig. 3.2). The first CF caused the highest SWH averages = 2.7 m (Fig. 3.2). When CF were present, ws were the lowest and wd were from SO-S-SE (Fig. 3.2). Strong NE winds, were registered between CF that reached the highest ws observed during the entire study (Fig. 3.2).

Peaks of nauplii, when present, were observed before CF (Fig. 3.6). They were found in the beginning of the sampling between the first and the second CF (days 10 and 11), with another smaller increase in the abundance approximately nine days after those first two peaks (days 19 to 21), it also happened before another CF (Fig. 3.6). Cyprid abundance fluctuated independently of the variation of nauplii ($R^2 = 0.01$, $p = 0.525$) or the presence of CF at the site (Fig. 3.6). Barnacle settlement occurred at the beginning of CF, with maximum settlement at area 2 was registered about ten days after the nauplii maxima (Lag -10: $R^2 = 0.81$, $p \leq 0.001$) one day before the CF, in two situations (Fig. 3.6). SR at area 1 were close to zero (Fig. 3.6), lower than area 2 but with one day lag correlation (Lag 1: $r = 0.83$, $p \geq 0.001$).

Mussel larval stages showed similar temporal variation ($R^2 = 0.10$, $p = 0.036$; Lag 1: $R^2 = 0.17$; $p = 0.005$), in general, higher abundances were found between CF periods (Fig. 3.6). SR of mussels showed low variation over time, with maximum rates at area 1 occurring during the second CF (Fig. 3.6). SR of mussels were correlated at area 1 and 2 ($r = 0.66$; $p = 0.001$). Settlement was correlated to the abundance of post-larvae (A1: $R^2 = 0.34$, $p = 0.005$; A2: $R^2 = 0.28$, $p = 0.014$), but it was not to D larvae abundance (A1: $R^2 = 0.10$, $p = 0.152$; A2: $R^2 = 0.04$, $p = 0.382$).

For barnacles, nauplii abundance was positively correlated to ws (Table 3.1). Barnacle SR was positive related to the variation of ws/wd/SST, with peaks occurring after 7 and 5 days to the increase in wd, wd and SST (Table 3.1). The relation to SST was significant in different temporal lags between areas. For mussels, post larvae were positive related to ws and SST, with one and two days lag. SR was negative related to ws, with one day lag (Table 3.2). A negative correlation between mussel SR and SWH was significant only at area 2 (Table 3.2).

Figure 3.6. Case 3 - Temporal variation of larval abundance, 1st larval stages (dashed line) and post-larvae (full line), and settlement (bars) of barnacles and bivalves during and between three cold front periods. Settlement was measured in two areas at the same shore, area 1 (dark bars) and area 2 (light bars). This sampling occurred from November 6 to 30, 2013. Cold front events are highlighted by the shaded areas in the graph.

Table 3.2. Bivalves - Results of the cross correlation analysis comparing the daily variation of the cold front descriptors (ws, wd, SWH, Chla and SST) with the fluctuation of larval abundance (1st stages and post-settlement) and settlement rates of bivalves, for Case 1, 2 and 3. When the analysis identified significant correlations for time lagged series, the results are equivalent to the comparison with lagged series. Terms: r is the correlation coefficient; lag is the time lag which the results are exposed. Significant results * ($p \geq 0.01$) are written in bold.

	1 st stages									Post-larvae									Settlement														
	Case 1			Case 2			Case 3			Case 1			Case 2			Case 3			Case 1			Case 2			Case 3								
	Case 1			Case 2			Case 3			Case 1			Case 2			Case 3			Case 1			Case 2			Case 3								
	r	lag		r	lag		r	lag		r	lag		r	lag		r	lag		r	lag		r	lag		r	lag							
ws	0.93*	0		0.49*	0		-0.02	0		0.86*	0		-0.37*	1		0.37*	1		-0.29	0		-0.21	0		0.54*	1		-0.47*	-1		-0.55*	-1	
wd	-0.67*	0		-0.07	0		0.02	0		0.52	0		-0.05	0		-0.27	0		NA	0		-0.47*	2		-0.21	0		-0.23	0		0.09	0	
SWH	-0.69	0		-0.21	0		-0.06	0		-0.48	0		0.04	0		-0.56	-3		0.78	0		0.35	0		-0.63*	-3		-0.12	0		-0.47*	-2	
Chla	-0.28	0		0.19	0		0.37*	-8		-0.29	0		0.26	0		-0.13	0		0.63	0		-0.54*	-2		-0.21	0		-0.12	0		-0.08	0	
SST	-0.02	0		0.03	0		0.47*	1		0.06	0		-0.55*	7		0.36*	2		NA	0		-0.35	0		-0.52	0		0.29	0		0.32	0	

3.6 Discussion

Our results showed that cold fronts affect the temporal variation of larval abundance and settlement of rocky shore barnacles and mussels. Changes in wave action, sea surface height and sea surface temperature, follow a predictable sequence when influenced by cold fronts, with relatively repetition over time every event. As marine organisms are able to sense and respond to pelagic and atmospheric cues (e.g. KOEHL, 2007; JONES *et al.*, 2009), as well as, take advantage of specific conditions to return to settlement sites (e.g. internal tidal bores, PINEDA & LÓPEZ, 2002) or settle (e.g. turbulence, RITTSCHOF *et al.*, 2007), it is possible that the species living at the study region have evolved to use cold fronts as settlement drivers. Results on settlement presented more clearly the influence of cold fronts than those of larval abundance. However, it is important to highlight that larval abundance is more variable and, thus, results are frequently less precise. We assume this limitation to increase the precision for the larval abundance variable, as our main focus was to evaluate the cold front influence in a daily scale and the challenge for this approach and design and logistic limitation prevented us from increasing replicates of larval abundance.

Because cold fronts pile surface waters onshore at the study region (STECH & LORENZZETTI, 1992, LIMA *et al.*, 1996, AMORIM *et al.*, 2012), we have initially hypothesized that the larval pool would respond to the passage of the front by approaching the settlement sites, consequently, increasing the abundance of post-larvae and the settlement rates. Barnacle settlement rates were the highest simultaneously on the three sites when the front arrived at the shore, meaning that only barnacles agreed with this first hypothesis. Therefore, we conclude that CF are promoting the settlement of barnacles.

The primary factor driving settlement is the increase of the amount of competent post-larvae at the settlement site (PINEDA, 2000). However, in the present study, the abundance of barnacle post-larvae was not synchronic to the variation of settlement rates. Cyprids were found in very low abundances and, in general, during periods that were not influenced by CF. It is possible that post-larvae were located at deeper areas of the water column (SANTOS *et al.*, 2007, TAPIA *et al.*, 2010) and sampling procedures could not assess them, resulting in low correlation. Besides, other processes, such as turbulence (SCHLICHTING, 1979; RITTSCHOG *et al.*, 2007), could be stimulating settlement during low larval situations. During CF, wave breaking is more frequent and

intense, consequently, there are more turbulent flux than during non CF conditions, therefore, it is reasonable to consider this positive influence for barnacle settlers.

The first hypothesis could not be applied to the settlement of mussels, which occurred independently of the presence of CF, or to the abundance their post-larvae, which were higher during non CF periods. In short term scales (days), mussels settle in association to spring tides (PORRI *et al.*, 2008), onshore winds (YOUNG *et al.*, 1996), internal tidal bores (VARGAS *et al.*, 2004) and deep layer onshore currents during downwelling (DUDAS *et al.*, 2009). Mussel larvae are able to migrate vertically migrate and be retained close to shore (e.g. GARRISON & MORGAN, 1999), but their abundance is also influenced by the fluctuation of pelagic conditions (GARLAND *et al.*, 2002). In our study, we did not identify a determinate condition that could have caused mussels to settle. Besides the lack of significant temporal correlation, the maxima settlement coincided with peaks of post-larval abundance onshore in cases 2 and 3, which means that settlement variation must be associated to some mechanism used by larvae to go back to shore. There are many possible features that have not been explored to these species, especially at the study region, such as tides or Langmuir cells. Specie-specific contributions within this variation may also be masking the results and relation with CF. For example, two very abundant taxa, *P. perna* and *B. solisianus*, are from Mitilidae family, this means that their larvae are relatively similar and can be easily confounded as first settlers. Future studies with specific sampling design are needed to better explain temporal trends of larval supply and settlement of mussels at the region.

We also hypothesized that the effects of CF would be strong enough to overcome the taxonomic specificities; consequently, cirripeds and mussels would present similar temporal trends of settlement and larval abundance. However, cirripeds and mussels did not vary in similarity according to the presence or absence of CF, rejecting our third hypothesis. Both taxa occupy the intertidal zone (COUTINHO & ZALMON, 2009). Their larvae have similar capacities to respond to changes in the pelagic environment (e.g. vertical migrate, GARRISON & MORGAN, 1999; SANTOS *et al.*, 2007). Although, they can use similar mechanisms to return to settlement sites, many are the cases where cirripeds and mussels show different spatio-temporal trends of settlement and larval supply (e.g. MCCULLOCH & SHANKS, 2003).

The initial larval stages of both taxa mostly occurred between CFs and the variation of their abundances were not synchronic to either the abundance of post-larvae

or settlement rates. In open marine populations, larval emission and settlement are independent processes (PINEDA *et al.*, 2009). Although, when local larval retention occurs, there are more probability for self-settlement, consequently, higher degrees of temporal correlation between peaks of first stage larvae abundances and settlement events are expected. Simultaneous sampling of all larval stages and settlement measurements are not so common as most of the studies have focused on one of life cycle periods. The available studies for cirripeds and mussels have found contrasting results, high (HOFFMANN *et al.*, 2012) and low correlation (PORRI *et al.*, 2006) between supply and settlement. At the study sites, the lack of correlation suggests that local settlement may contribute less to the total settlement. If this hypothesis is confirmed, these populations have continuous genetic flux, what guarantees high genetic diversity (see PINEDA *et al.*, 2007). On the other hand, the success of these populations may be vulnerable to external larval pools and even to determinate source populations (HANSKI & GILPIN, 1997).

The CF descriptors that presented the highest degrees of correlation with post-larval abundance and settlement were wind speed and direction, being also the most frequently significant. This result corroborated our second hypothesis, however, trends were very case specific and complex to interpret. Wind speed and direction are very good descriptors of the pelagic conditions at the studied coast, specially regarding the main sea current direction (AMORIN *et al.*, 2012). Wave action is an adequate variable to represent the intensity of cold fronts. We represented wave action with daily averages of significant wave height from remote sensing. The limitations of this variable could have affected the correlation with the ecological variables. Wave force might be a better representative of wave action and must be more correlated to local larval supply and settlement. Tidal regime is also very important locally (PEREIRA *et al.*, 2007), although, depending on the wind regime, it can overcome or potentiate the effects caused by tides. Chlorophyll-a concentration can indicate specific water masses intrusions or even vertical mixing of the water column (CIOTTI *et al.*, 2010). But, the fluctuation of chlorophyll-a concentration also depends on phytoplankton reproduction, growth and mortality, three biological processes that may happen at different scales that invertebrate larvae can respond, not affecting present larval abundance or settlement rates. At subtropical zones, sea surface temperature is regulated by solar radiation, especially during summer months when our studies were conducted. Upwelling inputs

are also present, however, they can happen at the subsurface (e.g. CARBONEL, 2003), not reflecting direct changes at the superficial temperature.

Our findings suggest that larval abundance and settlement are regulated by wind driven processes. As it was discussed previously in this manuscript, for barnacles, it might be related to the approach of CF at the region, but for bivalves, other wind driven processes may be more important. In general, larval abundance and settlement was positive related to wind speed, suggesting that stronger winds bring more larvae and increase settlement rates of barnacles and mussels. Wind direction was positive or negative related depending on the processes, taxa and depending on the study case. Because of these results, the specific meteorological-oceanographic feature that causes settlement to occur at the study region is still uncertain. At the daily scale, a lot of variation and stochasticity is incorporated at the biological and physical measurements, resulting in lower correlation degrees.

In a world of changing environments and climate (e.g. MENGE *et al.*, 2009, MEEHL *et al.*, 2004), there is an urgent need to increase the power of predicting ecological processes regulating biological stocks, such as recruitment for marine intertidal invertebrates. Because it is logistically challenging to measure recruitment over large coastal areas, there is a clear benefit to developing techniques to estimate recruitment using environmental data. For rocky shores, correlations between recruitment and environmental variables that allow the development of robust models have been established only for upwelling regions (e.g. ILES *et al.*, 2012). This view should be expanded for coasts where other oceanographic features are dominant.

Each study case showed important particularities. Comparing the three cases, case 1 was the most divergent. Case 1 study site was the most distant. It also subject to stronger and more frequent upwelling events. Likewise, at this site, coastal geomorphology intensifies the effects of CF and of the South Atlantic High Pressure Center, affecting the studied variables (RODRIGUES & LORENZZETTI, 2001). It is expected that these differences influence biological processes, such as barnacle settlement and larval abundance. However, the lack of replication of cold front events could have influenced the trends in Case 1. Local dynamics are important source of variation for larval ecology of intertidal invertebrates (BURROWS *et al.*, 2010). Besides that, similar trends were found, suggesting that processes with regional influence, such as cold fronts, have great degree participation for regulating of larval abundance and settlement. These results raise the importance of regional processes as

predictors of intertidal dynamics and stock regulation, and they might be used as forecast tools.

According to our results, cold fronts affect settlement and larval abundance of intertidal organisms. These effects change ontogenetically and between taxonomic groups. Although larval abundance was not correlated to settlement, correlations between settlement and wind regime suggest a wind driven regulation of those processes at the study region. Local particularities are important sources of variation, and they might be a consequence of spatial variability at the coastal environment. This study highlights that climatic fluctuations have important but contrasting effects on rocky shore communities. Also, raising the importance of regional processes as predictors of intertidal dynamics and stock regulation, and forecast tools.

8.7 Attachments

Table SI. Results of the regression analysis assessing the temporal autocorrelation of ws, wd, SWH, Chla and SST. Numbers in bold represent statistically significant results ($R^2 \geq 0.5$; $p \leq 0.05$).

	Case 1		Case 2		Case 3	
	R^2	p	R^2	p	R^2	p
ws	0.17	0.168	0.03	0.538	≤ 0.01	0.807
wd	0.54	0.004	≤ 0.01	0.771	0.02	0.339
SWH	≤ 0.01	0.937	0.07	0.260	≤ 0.01	0.887
Chla	≤ 0.01	0.782	0.75	≤ 0.001	≤ 0.01	0.961
SST	0.39	0.015	0.91	≤ 0.001	≤ 0.01	0.665

Table SII. Results of the regression analysis assessing if the correction technique was efficient to remove temporal autocorrelation of the autocorrelated variables (Table SI). Numbers in bold represent statistically significant results ($R^2 \geq 0.5$; $p \leq 0.05$).

	Case 1		Case 2		Case 3	
	R^2	p	R^2	p	R^2	p
ws	-	-	-	-	-	-
wd	0.01	0.702	-	-	-	-
SWH	-	-	-	-	-	-
Chla	-	-	≤ 0.01	0.986	-	-
SST	≤ 0.01	0.115	≤ 0.01	0.826	-	-

FINAL CONSIDERATIONS:

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. Cold fronts affect the settlement and larval abundances. In our region, recruitment is regulated by a balance between local and regional processes. Local particularities are important sources of variation, and they might be a consequence of spatial variability at the coastal environment. Also, raising the importance of regional processes as predictors of intertidal dynamics and stock regulation, and forecast tools.

The main limitations of this study are the uncertainties about the reproduction cycles of the biological models and the scales of larval supply measurements. There is not information about the reproduction cycles of all the species of barnacles and mussels included in this study. We were not able to measure reproduction output of the studied barnacles and mussels, consequently, we did not detect the influence of reproduction on the spatio-temporal trends of larval supply and the recruitment. Likewise, we did not estimate larval supply in all spatial and temporal scales that we measure settlement and recruitment. Hence, we can not distinguish between larval supply and post-settlement processes as the regulators of recruitment variation in the longer time scales.

However, we overcame the logistic difficulties of sampling in wave impacted sites in order to understand the influence of cold fronts where their effect are the highest. The spatio-temporal resolution covered in this study is praiseworthy. Also, the efforts of weekly and daily samples allowed us to monitor the influence of separate cold front events. With specie-specific variability and the use of two biological models, we could infer about two ecological levels, population and community.

Our results raised questions regarding the oceanographic mechanisms regulating the variation of mussel recruitment, which could not be identified in this study. Also, since cold fronts influence the coastal areas from the study region (South Brazilian Bight) to the southeast American shores, it would be interesting to investigate if the trends of barnacle recruitment are the same across this litoral. The post-settlement factors influencing recruitment variation are also unknown neither the effect of cold fronts on post-settlement survival. Future studies incorporating these views would improve the ecological models of rocky shore communities.

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Articles

Chapter 1. (Published)

Temporal variation in intertidal community recruitment and its relationships to physical forcings, chlorophyll-a concentration and sea surface temperature. (2015) Mazzuco, A.C.A.; Pineda, J.; Starczak, V. C.; Christofolletti, R.A.; Ciotti, A.M. *Marine Biology*, 162: 1705-1725.

Chapter 3. (Submitted)

The influence of cold fronts on larval supply and settlement: case studies of subtropical rocky shores showing daily variability (2015, under review) Mazzuco, A.C.A.; Christofolletti, R.A.; Ciotti, A.M. *Estuarine, Coastal and Shelf Science*