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Wind-driven diurnal temperature variability across a small bay and the spatial pattern of intertidal barnacle settlement

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ABSTRACT

Temperature variability under different wind conditions and its association with the spatial pattern of settlement of three intertidal barnacles – the chthamaloids *Jehlius cirratus* and *Notochthamalus scabrosus*, and the balanoid *Notobalanus flosculus* – were studied across Cartagena Bay, located in the upwelling region of central Chile. During days of strong winds, the diurnal signal in surface temperature at the protected end of the bay (site CTGN) was attenuated and decoupled from the northern sites (ECIM and PCHC) which are directly exposed to wind forcing, suggesting that wind intensity drives shifts in the relative importance of physical transport processes across the bay. Overall, the mean settlement rates of both chthamaloids were higher at PCHC, whereas *N. flosculus* settled at higher rates in CTGN. Under strong wind conditions, settlement rates of both chthamaloids decreased at the northern sites, while the settlement of *N. flosculus* reached minima at all three sites. Moreover, the effect of wind stress on the spatial pattern of settlement across the bay differed between species. A significant and positive correlation between the spatial heterogeneity of settlement and maximum daily wind stress – used as a metric for the intensity of the afternoon sea breeze – was found only for *J. cirratus*. It is concluded that daily changes in wind stress have a strong effect on the spatial pattern of diurnal temperature fluctuations, and on the spatial pattern of barnacle settlement around the bay. Such association emerges from the effect of wind on near-shore circulation and its differential modulation of thermal structure around an open embayment and, by extension, on the patterns of larval transport and onshore delivery to sites located at extremes of the bay, which probably is common in other bays with similar characteristics.

1. Introduction

Over the years, many studies have attempted to link the patterns of larval transport and settlement in marine benthic species with coastal physical processes (Lagos et al., 2008; Pineda, 1991; Pineda and López, 2002; Roughgarden et al., 1988; Shanks, 2009; Vargas et al., 2004; Wing et al., 1995). The interest stems from the fact that patterns of coastal circulation and larval transport can influence the structure and functioning of individual populations (Roughgarden et al., 1988), interacting species (Aiken and Navarrete, 2014; Salomon et al., 2010) and benthic communities (Caro et al., 2010), through their effect on the spatial pattern and timing of larval delivery to near-shore environments. Since planktonic larval stages of benthic invertebrates are small and have limited capabilities for horizontal swimming – relative to the typical speeds of surface currents in the coastal ocean – the cross-shore transport of invertebrate larvae is thought to be strongly modulated by physical processes (e.g. Cudaback et al., 2005; Kaplan and Largier, 2006; Kirincich et al., 2005).

Near-shore circulation is highly complex and variable, both temporally and spatially, due to the combined forcing of various physical processes and their interaction with coastal topography (e.g. Kirincich et al., 2005; Lentz and Fewings, 2012; Sobarzo et al., 2010). Along eastern-boundary regions, circulation on the continental shelf is largely influenced by wind-driven coastal upwelling, which dominates cross-shelf transport of water, its properties, and suspended particles over synoptic timescales. Synoptic variability and the seasonal variation in coastal winds that characterizes most temperate systems, have been the focus of most 'supply-side' studies. However, substantial variability in circulation and transport may result from diurnal fluctuations in wind forcing, i.e. over 24-hour cycles. The sea breeze, perceived in mid to low latitudes as an afternoon intensification of onshore winds, has been identified as one of the most important processes that modulate the thermal structure of the water column and circulation in near shore environments with a regular diurnal periodicity (Bonicelli et al., 2014;

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Dellatorre et al., 2012; Kaplan et al., 2003; Sobarzo et al., 2010; Tapia et al., 2004; Woodson et al., 2007). A number of studies have focused on diurnal variability in cross-shelf transport and settlement patterns (e.g. Jacinto and Cruz, 2008; Kaplan et al., 2003; Tapia et al., 2004), in an attempt to assess the effect of physical processes with a strong diurnal signal on larval transport in coastal environments. Establishing this connection is especially important for the understanding of mechanisms and scales of variability that shape settlement patterns of invertebrate species in subtidal and intertidal environments.

Recently published studies have documented the effects of diurnal fluctuations in wind forcing on local circulation in temperate bays embedded in upwelling regions (e.g. Bonicelli et al., 2014; Woodson et al., 2007). Work centered on small open bays provides a unique opportunity to study the effect that spatial changes in the interaction of wind and coastline configuration may have on nearshore circulation, and the resulting spatial changes in larval transport, onshore larval settlement, and population renewal in many species of coastal invertebrates.

Cartagena Bay is a small south-facing open embayment bay located in the lee (20 km north) of the Punta Toro upwelling center in central Chile (Narváez et al., 2004; Wieters et al., 2003). Diurnal wind variability has a strong influence on temperature variability and circulation around the bay (Kaplan et al., 2003; Narváez et al., 2004; Piñones et al., 2005). Surface waters tend to be warmer and the water column is usually more strongly stratified within this bay (Kaplan et al., 2003; Narváez et al., 2004). A recent study (Bonicelli et al., 2014) showed that patterns of diurnal variability in water-column temperatures may vary substantially across the bay, with a strong diurnal signal at the northern and more exposed end, and persistent stratification at the southern and more protected end, despite the strong sea breeze that develops during the afternoon (see Kaplan et al., 2003; Piñones et al., 2005). This spatial heterogeneity in temporal variability of water-column temperatures, largely induced by differential forcing of diurnal winds, may affect meroplankton distribution by modifying cross-shore transport processes, and ultimately may affect spatial patterns of larval settlement at the shoreline.

A previous study conducted in Cartagena Bay over three consecutive spring–summer seasons (Tapia and Navarrete, 2010) showed inter-annual changes in the persistence of spatial pattern in settlement, and hypothesized that such change could arise from inter-annual variation in coastal wind, through its effect on local circulation and larval supply to intertidal habitats. Here, the same set of daily settlement observations is used together with time series of water temperature and wind stress, to assess whether daily wind variability affects the spatial pattern of settlement of 3 intertidal barnacles (*Jehlius cirratus*, *Notochthamalus scabrosus*, and *Notobalanus flosculus*) around Cartagena Bay. Based on previous work (Bonicelli et al., 2014), it was hypothesized that changes in wind conditions affect settlement patterns by way of their effect on circulation and larval transport around the bay. Such changes in near-shore circulation should be reflected by changes in the pattern of temperature variability around the bay.

2. Material and methods

2.1. Barnacle settlement and study sites

Daily records of larval settlement rates were estimated for three species of intertidal barnacles which are numerically dominant in the mid to low intertidal zone of wave exposed rocky shores around Cartagena Bay: the chthamaloids *J. cirratus* and *N. scabrosus*, and the balanoid *N. flosculus*.

Settlement observations were conducted daily and simultaneously at three sites spanning Cartagena Bay on three consecutive spring to early summer seasons (October–December, 2006–2008), and for an average of 57 consecutive days. Settlement was monitored using 10 × 10 cm Plexiglas plates covered with a gray rubbery surface (Safety-walk, 3M), and attached to the substrate with stainless steel screws (see Tapia and Navarrete, 2010 for more details). Two sites (ECIM, PCHC) were located at the northern end of the bay, whereas a third site (CTGN) was located at the southern end (Fig. 1).

2.2. Environmental data

Wind data for October 2006 through December 2008 were obtained from a meteorological station maintained by the Chilean Navy's DIRECTEMAR at the lighthouse Faro Panul, located 3 km south of the southern end of the bay and at 30 m above sea level (33° 34.898′S, 71° 37.160′W) (Fig. 1). Records of shallow subtidal water temperature were gathered at all three sites using Stowaway TidBit loggers (Onset Computer Corp., USA) that were programmed to record temperature at 5 min intervals. Loggers were installed at 1 m below the Mean Lower Low Water (MLLW) from October 2006 until December 2008 (Fig. 1).

2.3. Data processing and analysis

Wind velocity vectors were rotated according to the wind's principal axis of variability. In this rotated coordinate system, the along-shore component of wind (y) is positive toward the northeast, whereas the cross-shore component (x) is positive toward the southeast (Fig. 1). Wind stress was then calculated following Large and Pond (1981).

Daily maxima for alongshore wind stress (τ_{ym}), recorded over the three consecutive settlement seasons, were used to classify days with temperature and settlement data into three categories according to their frequency distribution (Fig. 2): (1) “strong wind” days when stress was equal or greater than the 75th percentile of the distribution ($\tau_{ym} \geq 0.06$ N m^{-2}), (2) “moderate wind” days when wind stress was between the 25th and 75th percentiles of the distribution (0.01 N/m$^{-2} < \tau_{ym} < 0.06$ N m^{-2}), and (3) “weak wind” days when wind stress was equal or less than the 25th percentile of the distribution ($\tau_{ym} \leq 0.01$ N m^{-2}). To characterize the daily cycle in surface water temperature and its spatial variability as a result of wind changes, the canonical day was computed for each site under different wind conditions. Daily amplitudes in water temperature were also calculated and compared between sites for each wind scenario. Amplitudes were determined via the least-squares fitting of a sinusoidal polynomial to each temperature signal.

To evaluate the effect of wind intensity on the among-site synchrony of settlement, Kendall correlations between settlement rates at pairs of sites were computed for each wind condition (weak, moderate, strong). Positive and significant correlation may reflect synchrony in the timing of settlement across the bay. Only days with 12 or more larvae collected across the three sites were used for this analysis.

In order to evaluate the effect of wind stress on the spatial pattern of settlement, a spatial coefficient of variation (SCV) was computed and used as a proxy for the heterogeneity of barnacle settlement. The SCV was calculated between the settlement rates of the three sites on days with 12 or more settlers collected across the three sites. Since 4 plates were used to monitor settlement at each of the 3 sites, a minimum of 12 settlers corresponds to the count that would be found if settlement was completely homogeneous, i.e. one larva per settlement plate. For each day with settler counts meeting this criterion (118, 128, and 108 days for *J. cirratus*, *N. scabrosus*, and *N. flosculus*, respectively), a daily maximum for alongshore wind stress and the cumulative alongshore wind stress for the period of collector deployment were computed. Spearman's rank correlations between wind statistics and the SCV were then calculated for the three species.

3. Results

Canonical days for water temperatures recorded on days with weak, moderate, and strong wind showed that surface waters cooled

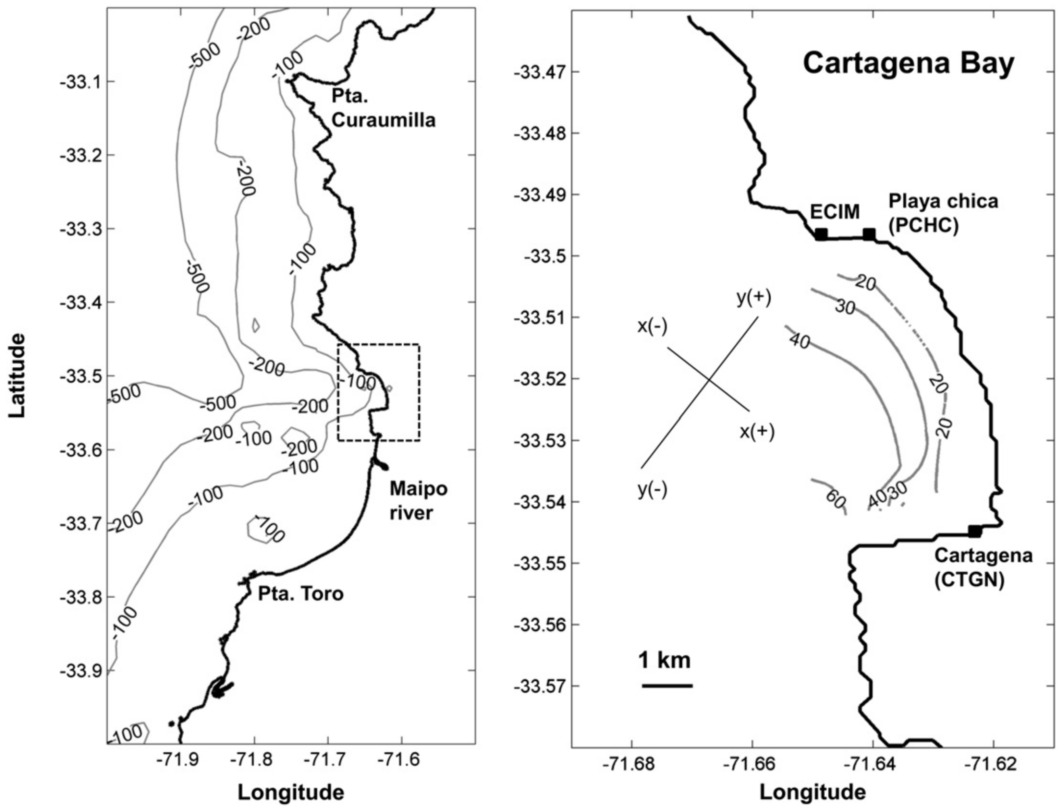

Fig. 1. Location of Cartagena Bay on the coast of central Chile (dashed square, left panel) and the 3 sites where settlement observations were collected (right panel): ECIM (Estación Costera de Investigaciones Marinas), PCHC (Playa Chica), and CTGN (Cartagena). Local bathymetry and the location of Faro Panul meteorological station, along with the coordinate system adopted to rotate wind velocity vectors (black axes), are also shown in the right panel.

throughout the bay as wind intensified, with the lowest mean temperatures at all three sites on days with strong wind conditions (Fig. 3). In general, temperatures were lowest at 8:00 (local time, GMT-4) and then increased to reach maximum values in the afternoon (Fig. 3). While temperature variability had a strong diurnal signal and exhibited greater diurnal amplitude at the northern sites (ECIM and PCHC), it was attenuated under all wind conditions at the southern site (CTGN).

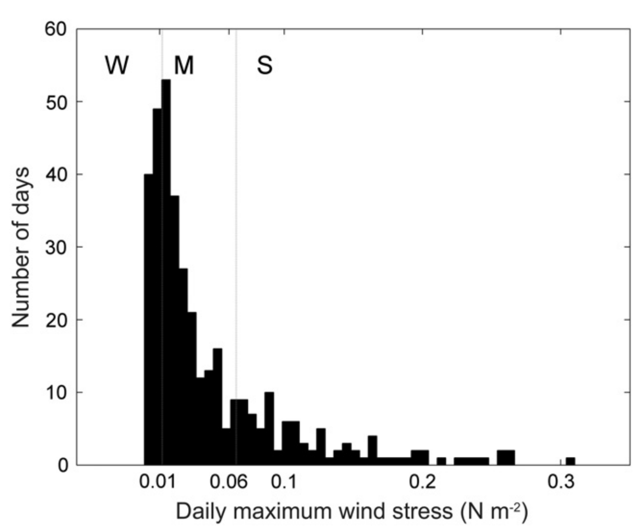

Fig. 2. Frequency distribution for the daily maxima of alongshore wind stress recorded over three spring–summer seasons: October 2006–February 2007, October 2007–February 2008, and October 2008–December 2008. Vertical lines indicate the 25th and 75th percentiles, which were used as criteria to classify wind conditions on a given day as weak (W), moderate (M), or strong (S).

Highest temperatures at CTGN were higher, and were reached at an earlier hour than at both northern sites under all wind conditions (Fig. 3).

Although there was a persistent difference between extremes of the bay in the mean and diurnal variability of temperature under all wind conditions, this difference was accentuated on days with strong wind (Fig. 3). On weak wind days, CTGN was on average 1 °C warmer than ECIM and PCHC during the morning, and then these across-bay differences decreased to 0.5 °C during the afternoon (Fig. 3A). On moderate wind days, between-site differences in temperature were comparable to those observed under weak winds, although afternoon temperatures were more similar across the bay (Fig. 3B). On strong wind days, a diurnal fluctuation in temperature was apparent at both northern sites and it was practically nonexistent at CTGN, with only a slight increase in temperature (0.2 °C) between 13:00 and 16:00 (Fig. 3C). Also, and in contrast with the other wind scenarios, on days with strong winds the late-afternoon temperature at both northern sites was higher than at CTGN (ca. 0.3 °C between 18:00 and 20:00, Fig. 3C). Diurnal fluctuations in temperature were significantly correlated across the bay on days with weak and moderate winds, and were decoupled between the northern sites and CTGN on days with strong winds (Table 1).

Overall settlement rates for both chthamaloid species (*J. cirratus* and *N. scabrosus*) were higher at PCHC, whereas settlement of the balanoid *N. flosculus* was higher at CTGN (Fig. 4). For both chthamaloids, settlement rates were lower at the northern sites on days with strong winds. At PCHC, this drop in settlement was more apparent for *J. cirratus* (Fig. 4B) than for *N. scabrosus* (Fig. 4E). At CTGN, on the other hand, the settlement rates of *J. cirratus* (Fig. 4C) and *N. scabrosus* (Fig. 4F) were similar and apparently unaffected by wind conditions. As for settlement of *N. flosculus*, it appeared that wind stress had no effect on its magnitude or spatial pattern, since the mean settlement rate at all three sites was highest under weak wind conditions than during moderate and strong wind conditions (Fig. 4G, H, I).

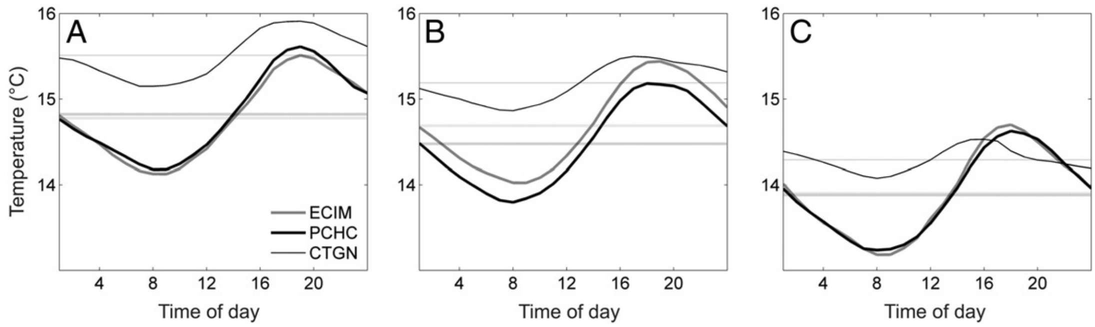

Fig. 3. Canonical days computed from the time series of shoreline temperatures recorded during three consecutive spring–summer seasons at the northern (ECIM: gray line; PCHC: thick black line) and southern (CTGN: thin black line) sites in Cartagena Bay on days with weak (A), moderate (B) and strong (C) wind conditions. Dotted horizontal lines show the mean temperature at each site for each wind condition.

Settlement rates of *J. cirratus* were positively correlated between sites under weak and moderate winds but not between ECIM and CTGN on days with strong wind (Fig. 5A). Among-site correlations for *N. scabrosus* were positive and significant under moderate winds but not during weak winds. On days with strong winds, settlement of *N. scabrosus* was not correlated between CTGN and ECIM (Fig. 5B). Spatial correlations for the balanoid *N. flosculus* were positive and significant among all three sites under the three wind conditions (Fig. 5C), although the correlation between ECIM and CTGN decreased on days with strong wind.

The spatial coefficient of variation (SCV) in settlement, used here as a metric for spatial heterogeneity, was positively correlated with the daily maximum wind stress in *J. cirratus* but not in the other two species (Fig. 6A). The SCV was not significantly correlated with cumulative wind stress for any of the three species (Fig. 6B).

4. Discussion

Results presented here show that spatial differences in thermal variability and the heterogeneity of barnacle settlement around a small bay increase when the wind stress intensifies. In a recent study conducted in this bay, Bonicelli et al. (2014) showed that thermal structure and its high-frequency variability (minutes to hours) differ significantly between northern and southern sites, and suggested that this spatial difference results from the combined effect of upwelling driven circulation, diurnal wind variability and local topography. Here, that work is expanded upon by comparing temperature variability under different wind conditions, and by coupling these changes with the spatial pattern of barnacle settlement around the bay.

Numerous studies conducted over the past decades have focused on establishing which of the many physical processes affecting coastal circulation and larval delivery to intertidal habitats are more important in shaping settlement and recruitment patterns (e.g. Connolly and Roughgarden, 1999; Farrell et al., 1991; Lagos et al., 2005, 2008; Roughgarden et al., 1988). This is an important ecological question that has implications for the understanding of marine population dynamics, as well as for the design and management of marine reserves (Gaines et al., 2003; Largier, 2003; Shanks et al., 2003). Here it has been shown that even across a small bay (6 km) the spatial pattern of barnacle settlement may be heterogeneous and strongly dependent on wind stress variability.

As it has been shown for other bays located in the lee of upwelling centers, stronger upwelling-favorable winds enhance the retention of surface water, and intensify the horizontal gradient of water temperature inside the bay, producing a set of conditions known as "upwelling shadow" (Graham and Largier, 1997). Additionally, in certain bays a strong sea breeze may enhance the onshore transport of warm surface water and its vertical mixing during the afternoon (Kaplan et al., 2003; Piñones et al., 2005; Tapia et al., 2004). At Cartagena Bay, diurnal-scale effects of the sea breeze on surface temperatures appear to be superimposed on synoptic-scale patterns of near-shore circulation and surface water retention (e.g. Bonicelli et al., 2014). Strong upwelling-favorable winds enhance water retention and attenuate the diurnal temperature cycle near the southern, more protected site (CTGN) while the sea breeze enhances the afternoon warming at the northern sites and more exposed to wind forcing (ECIM and PCHC). The fact that across-bay differences in the amplitude of diurnal temperature fluctuations were significant only on days with strong wind (Table 1) supports this interpretation of the data.

In addition to enhanced retention, the attenuation of diurnal temperature cycles at CTGN (Fig. 3C) indicates that strong wind conditions also enhance stratification and stability of the water column at the protected end of the bay. On the other hand, at the exposed end of the bay, the strong diurnal signal in temperature (Fig. 3) reflects stronger advection and a well-mixed water column. These spatial changes in stratification could affect the vertical distribution of larvae in the water column (Daigle and Metaxas, 2011, 2012) and therefore affect their transport and subsequent delivery to intertidal habitats. Additionally, spatial differences in near-shore stratification could produce spatial differences in larval delivery to shore by way of differential conditions for the onshore propagation of nonlinear internal waves; with more frequent internal tidal bore events at sites more strongly stratified (Pineda, 1991, 1995). It has been shown that places with contrasting incidence of internal tidal bores may exhibit large differences in barnacle settlement, due to differential onshore transport of larvae (Pineda and López, 2002). An eventual drop in thermal stratification driven by the diurnal sea breeze should be stronger at ECIM on days with strong wind, and consequently may reduce the onshore delivery of *J. cirratus* larvae (Fig. 4A), while at CTGN the settlement of this species does not seem to respond to changes in maximum wind stress (Fig. 4C). This could be explained by the persistent stratification observed at CTGN even during days with strong wind (Bonicelli et al., 2014). Also, the

Table 1
Among-site correlations (Pearson's coefficient) in the diurnal amplitude of water temperature under conditions of weak, moderate and strong wind stress. Significant correlations are shown in bold.

	ECIM	PCHC	CTGN
Weak winds			
ECIM	1		
PCHC	**0.86**	1	
CTGN	**0.48**	**0.46**	1
Moderate winds			
ECIM	1		
PCHC	**0.88**	1	
CTGN	**0.49**	**0.53**	1
Strong winds			
ECIM	1		
PCHC	**0.89**	1	
CTGN	0.04	0.02	1

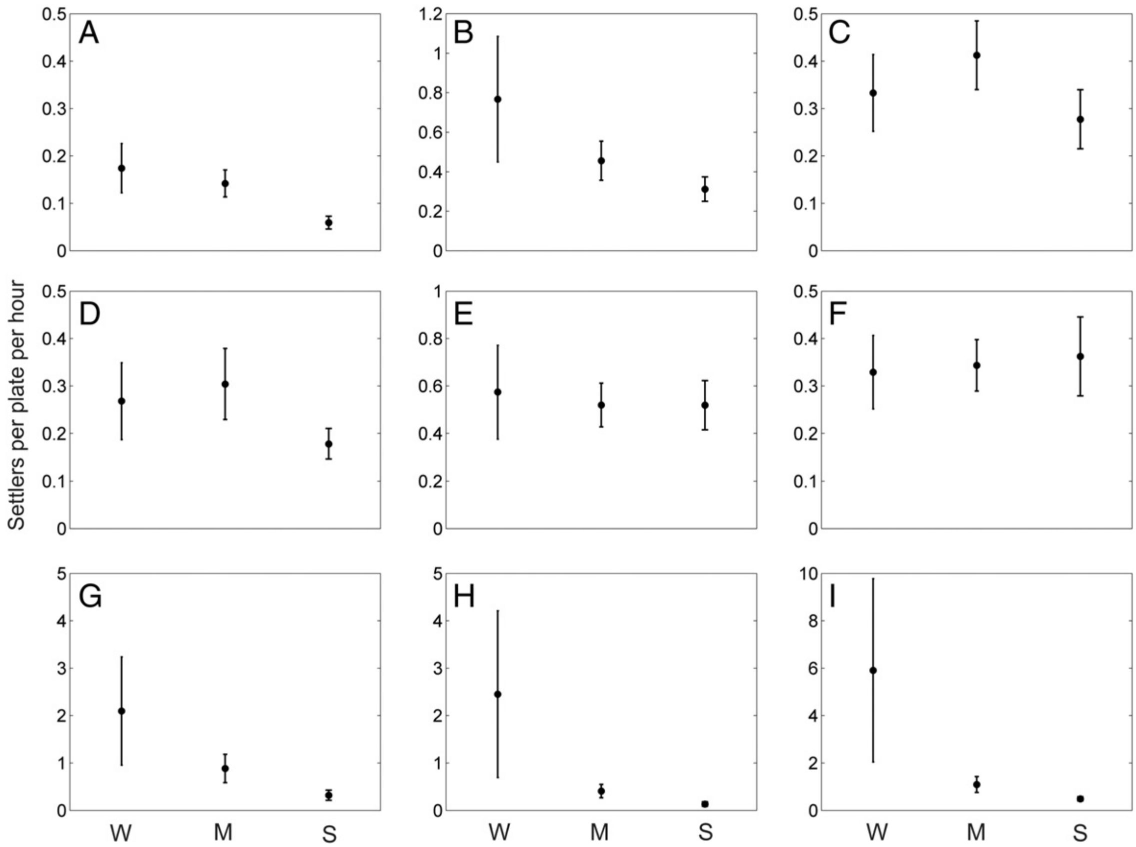

Fig. 4. Mean settlement rates (individuals per plate per hour) for *J. cirratus* (A, B, C), *N. scabrosus* (D, E, F) and *N. flosculus* (G, H, I) under conditions of weak (W), moderate (M), and strong winds (S). Scales on the y axes were adjusted to emphasize the within-species and within-site comparison of settlement rates.

apparent contrast in local stratification/mixing around the bay under strong winds could generate contrasting conditions for the occurrence of physical phenomena that mediate onshore transport, which may alter the timing of larval arrival to intertidal habitats (e.g. Pineda et al., 2010). This may explain the lack of spatial synchrony in the timing of settlement observed for *J. cirratus* on strong wind days (Fig. 5A), and the positive and significant correlation between its spatial pattern of settlement (i.e. SCV) and the maximum daily wind stress (Fig. 6A). It is noteworthy that the SCV of *J. cirratus* was significantly correlated with the daily maximum of alongshore wind stress, but not with cumulative wind stress. This discrepancy may be explained by the fact that, while maximum daily wind stress is a proxy for the intensity of the afternoon sea breeze (Bonicelli et al., 2014), the cumulative wind stress integrates wind variability over the full daily cycle, including the evening and early morning hours with weak or even negative (i.e. southwestward) wind stress. Thus, the computation of cumulative wind stress would attenuate or even mask the signal of the sea breeze, which according to this and previous work is the main driver of circulation and water-column stratification within the bay (Bonicelli et al., 2014).

These results demonstrated that, at least for *J. cirratus*, diurnal wind-driven flows and their interaction with the bay topography would be shaping the pattern of local circulation, larval delivery to intertidal habitats, and larval settlement. However the spatial pattern of settlement in *N. scabrosus* does not appear to respond as directly to wind forcing. While other studies performed in the same region demonstrated that the meso-scale spatial variation of recruitment of *J. cirratus* and *N. scabrosus* resembles the temperature variability induced by coastal upwelling (Lagos et al., 2005, 2008), here it has been found that diurnal variability in wind stress appears to influence the spatial pattern of settlement only for *J. cirratus* but not for *N. scabrosus* (Fig. 6). Based on these results and those obtained by Lagos et al. (2005), it can be concluded that larger-scale physical processes such as coastal upwelling could modulate the meso-scale spatial patterns of recruitment of both chthamaloids, but high-frequency processes operating at smaller spatial

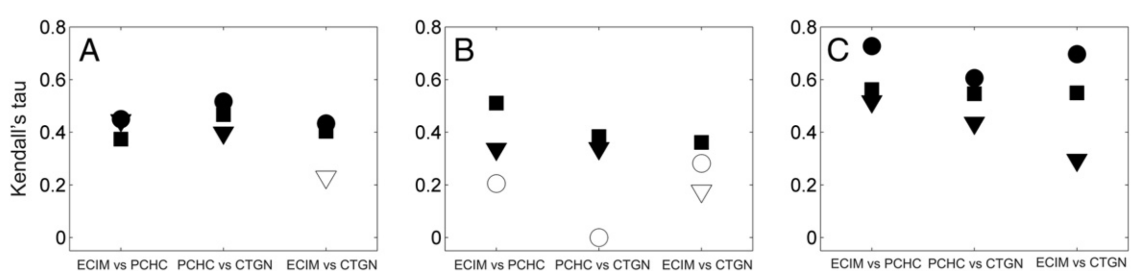

Fig. 5. Kendall correlation coefficients from among-site comparison of settlement rates under weak (circle), moderate (square), and strong (triangle) wind conditions. Filled symbols represent significant correlations with $\alpha = 0.05$.

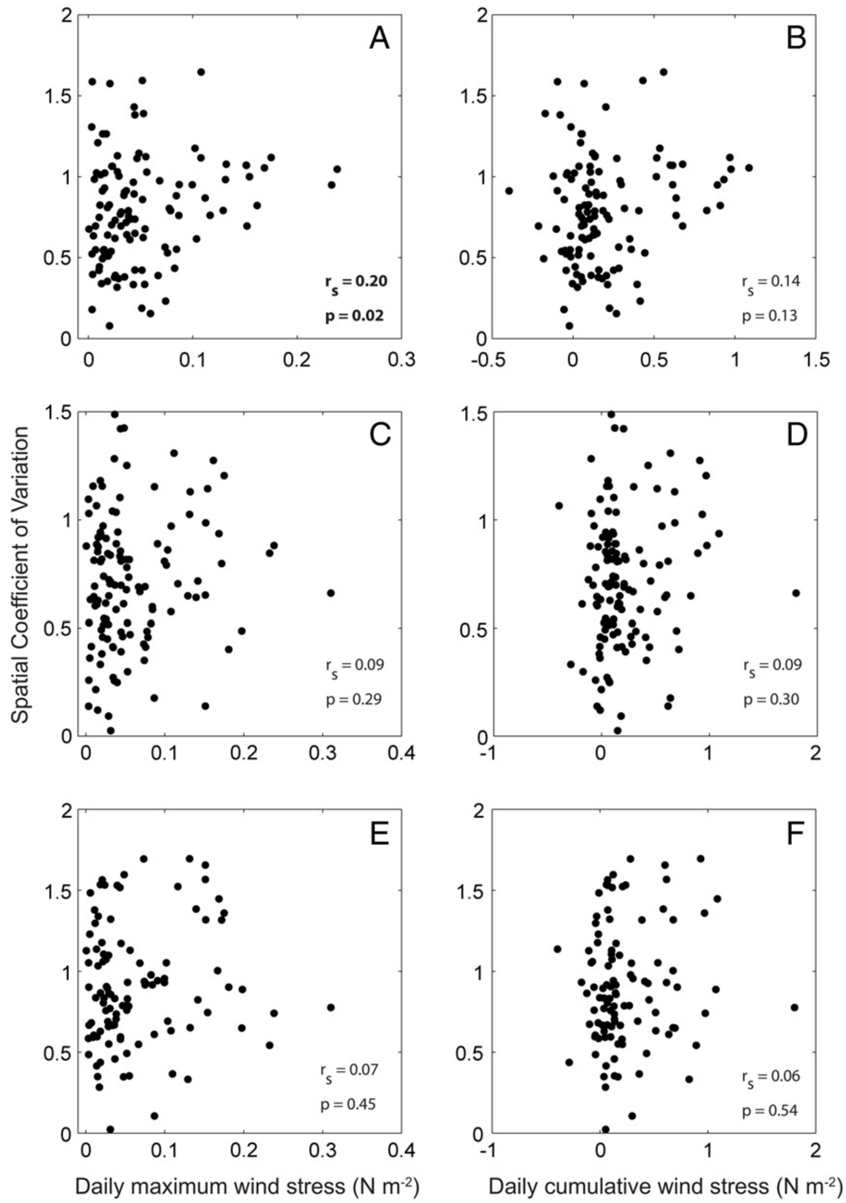

Fig. 6. Scatterplots and Spearman's correlation coefficients computed between settlement heterogeneity and wind intensity in *J. cirratus* (A, B), *N. scabrosus* (C, D), and *N. flosculus* (E, F). Wind intensity was characterized with the daily maximum wind stress (A, C, E), and cumulative wind stress (B, D, F) calculated over the period of collector deployment. Significant correlations are shown in boldface.

scales, such as local circulation driven by diurnal winds, may not have the same effect for both species.

Settlement of the balanoid *N. flosculus* showed positive correlations between sites under all wind conditions (Fig. 5C), although its spatial pattern of settlement does not appear to respond to wind forcing (Fig. 6). This is consistent with the findings of other studies conducted over a larger region that spans Cartagena Bay (Lagos et al., 2005, 2008), where recruitment of *N. flosculus* was not related with mesoscale changes in sea surface temperature, but rather with local topography. Although the spatial pattern of settlement was not affected by changes in wind stress, the total number of larvae settling on the shoreline increased at all sites under weak wind conditions. It is possible that the hydrographic conditions within the bay during days with weak winds enhance the onshore transport of *N. flosculus* larvae. For instance, a more strongly well stratified water column, which is often observed when the wind is weak, could favor the onshore delivery of competent larvae. This could also explain the highest values of settlement rates observed at CTGN, where the stratification is very stable even during days with strong winds (Bonicelli et al., 2014).

In this study, wind and water temperature data were analyzed to make inferences regarding the circulation within Cartagena Bay and its effect on larval transport. Although larval transport was not evaluated directly, settlement rates and their spatial variation were regarded as a sensible proxy for spatial differences in larval transport and onshore delivery. It must be noted, however, that biotic and abiotic conditions unaccounted for in this study, such as larval behavior at the time of settlement (Crisp, 1961; Crisp and Barnes, 1954; Knight-Jones and Stevenson, 1950), potential predators for cyprids in near-shore waters (Gaines and Roughgarden, 1987), and microscale hydrodynamics (Crisp, 1955) may distort or even obscure the relationship between onshore transport and larval settlement (see Rilov et al., 2008). Despite these limitations, it is concluded that daily changes in wind stress have a strong effect on the spatial pattern of diurnal fluctuations in water temperature and on the spatial pattern of barnacle settlement around the bay. It is hypothesized that such association emerges from the effect of wind on local circulation and, by extension, on patterns of larval transport in this and other bays with similar characteristics in upwelling regions.

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