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# Ten years of monitoring recruitment of the edible stalked barnacle *Pollicipes pollicipes*: linking to oceanographic variability

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## Abstract

Understanding recruitment patterns of an exploited species is essential to predict changes in population dynamics and to improve its management and conservation. Temporal variability in recruitment of the edible stalked barnacle *Pollicipes pollicipes* was analyzed over a decade (consecutive annual recruitment seasons from 2007 to 2016) at a cape area located in the Canary-Iberia Current Upwelling System (Cape of Sines, Southwestern Portugal), in terms of (1) the timing and length of the main recruitment season and (2) the variation in monthly and annual recruitment intensity and its relationship with several oceanographic variables. A longer recruitment season was detected, corresponding to approximately 9–10 months (June through either March or April of the following year, as in 2012, 2015, and 2016) in recent years, while a shorter recruitment season was detected between 2007 and 2010 (< 5 months, September–January in 2007 and July–December in 2010). Mean annual recruitment from 2012 to 2016 was about four times higher (ca. 43 recruits adult$^{-1}$) than in the first 5 yr of the 10-yr period (ca. 12 recruits adult$^{-1}$). Correlation analyses between monthly recruitment and oceanographic variables revealed a significant positive correlation with sea surface temperature and a negative correlation with upwelling index. Results indicate a trend toward a longer recruitment season and a higher recruitment intensity in recent years (2012–2016), and a clear association between recruitment of *P. pollicipes* and both relaxation of upwelling and seawater warming.

Resolving interannual and intraannual variation in recruitment and the underlying mechanisms responsible for the observed patterns can be a valuable tool to predict major changes in population dynamics of marine species, and to solve crucial problems in the management and conservation of exploited species (Pineda et al. 2009). However, this is a challenging issue, as recruitment is a complex process in the sense that it is determined by many factors operating and interacting on multiple temporal and spatial scales (Connell 1985; Pineda et al. 2009). For sessile invertebrate species with a two-phase life cycle (planktonic larvae vs. benthic adults and juveniles), recruitment is generally defined as the number of settled individuals per unit area that survive after an arbitrary period of time (Pineda et al. 2010). In general, observations done at a daily scale are considered as settlement, while observations at a weekly or monthly scale are considered as recruitment (Connell 1985; Shanks 2009a). Consequently, recruitment might be affected by presettlement (larval pool dynamics and larval transport processes) and postsettlement processes (biological interactions, disturbances, larval experience, and larval production) (Pineda et al. 2009). Moreover, larval supply and settlement, as well as settlement and recruitment might not be correlated (Shanks 2009a; Pineda et al. 2010), which enhances difficulties to identify the main processes affecting recruitment.

Intertidal acorn barnacles have been extensively used as model organisms for studying recruitment in many parts of the world due to their high abundance and the accessibility of rocky shores where they occur, but most studies are shorter than a decade (less than 2 yr—e.g., Roughgarden et al. 1991; O'Riordan et al. 2004; Lagos et al. 2005; 5–8 yr—e.g., Roughgarden et al. 1988; Broitman et al. 2008; Pfaff et al. 2011; but *see* Kendall et al. 1985 for annual recruitment during 13 yr; Menge et al. 2011 for monthly recruitment during 20 yr; Scrosati and Ellrich 2016 for annual recruitment during 12 yr). According to Kendall et al. (1985), studies during periods shorter than a decade may not be long enough to fully understand the processes of recruitment.

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Several studies performed in the California Current Upwelling System have investigated the relation between acorn barnacle recruitment and upwelling, suggesting that larvae are carried away from shore during upwelling and transported shoreward during downwelling or upwelling relaxation (Roughgarden et al. 1988; Farrell et al. 1991; Roughgarden et al. 1991), and that reversals of upwelling-driven alongshore currents (Dudas et al. 2009) and upwelling fronts colliding with the shore (Woodson et al. 2012) may enhance larval transport and settlement. Furthermore, the intermittency of upwelling (alternation between upwelling and downwelling events on scales of days to weeks) was suggested to explain geographical variability of barnacle recruitment (Menge and Menge 2013). Internal waves (Shanks 1983), internal tidal bores (Pineda 1991), sea breeze (Tapia et al. 2004), and processes related to the surf zone hydrodynamics (Morgan et al. 2017; Shanks and Morgan 2018) have also been proposed as mechanisms for explaining the onshore transport of larvae in the Pacific coast of North America. Studies in other major upwelling systems have also revealed a relationship between barnacle recruitment and upwelling: Lagos et al. (2005) and Navarrete et al. (2008) in the Peruvian-Chilean Coastal Upwelling System; and Pfaff et al. (2011, 2015) in the Benguela Current Upwelling System. Evidence for this association was partially supported on the other world's major coastal upwelling system—the Canary-Iberia Current Upwelling System (Queiroga et al. 2007).

In contrast to intertidal acorn barnacles, temporal variation in settlement and recruitment of intertidal stalked barnacles has been much less studied. Studies on daily settlement of the stalked barnacle *Pollicipes polymerus* suggested that internal tidal bores were responsible for onshore transport of larvae (Pineda 1991, 1994). Recruitment studies with longer sampling intervals (3–15 d) did not find any consistent association between recruitment of *Pollicipes* spp. and oceanographic transport processes (Pavón 2003; Dudas et al. 2009) or found only limited evidence of a possible relationship with upwelling (Cruz 2000; Macho 2006). Cruz et al. (2010) found spatial correlation in recruitment between sites that were ca. 40 km distant, suggesting that physical transport processes of stalked barnacle larvae were acting at this spatial scales.

Three species of the stalked barnacle genus *Pollicipes* are abundant along three major coastal upwelling regions: *P. polymerus*—Western North America; *Pollicipes elegans*—Western North, Central, and South America; and *Pollicipes pollicipes*—Southwestern Europe and Northwestern Africa (Barnes 1996). These species are mostly intertidal and occur in very exposed shores within these regions, are exploited by humans, and can be important economic fishery resources, as it is the case of *P. pollicipes* in Portugal and Spain (Molares and Freire 2003; Cruz et al. 2015). Total catches of *P. pollicipes* in Portugal and Galicia (Northwest Spain) reached 101 and 334 t yr$^{-1}$ with a mean annual value of 1,203,298 € and 8,966,324 €, respectively (official data for the period 2015–2019, Docapesca 2020; https://www.pescadegalicia.gal/estadisticas/, last accessed 23 October 2020).

Recruitment of *P. pollicipes* is intense on conspecifics and has been mostly studied by counting cyprid larvae and juveniles on adult conspecifics (Cruz et al. 2010). Mateus (2017) measured recruitment of *P. pollicipes* on conspecifics and on a recently developed artificial substrate (Cruz et al. 2018) and compared the relationship among different recruitment indices, showing that the number of cyprids plus juveniles with maximal rostrocarinal distance (RC) < 1 mm counted on conspecifics might be a good proxy of monthly recruitment in this species.

In the present study, we described the intra and interannual patterns of the monthly recruitment of *P. pollicipes* on conspecifics over 10 yr at a cape area in Southwestern (SW) Portugal, in the Canary-Iberia Current Upwelling System, and analyzed these patterns in relation to variability of several oceanographic variables. Specifically, we examined whether the recruitment of *P. pollicipes* was influenced by upwelling, by hypothesizing a significant correlation between the intensity of recruitment and the upwelling index (UI) or sea surface temperature (SST) or both.

## Materials

This study was carried out in the southwestern coast of Portugal, at the Cape of Sines (37°57′46″N, 8°53′10″W), a wave-exposed rocky headland, where *P. pollicipes* occurs in abundance along shallow subtidal and intertidal zones and is collected for human consumption (Sousa et al. 2013). The Cape of Sines region is under persistent upwelling-favorable wind conditions during summer months (Lamas et al. 2017).

Over 10 yr, from July 2007 to March 2017, 20–50 adult individuals of *P. pollicipes* with RC > 15 mm, were collected during low tide from the middle to upper intertidal distribution of *P. pollicipes* (1.5–3 m above mean low water springs), approximately fortnightly, depending on sea conditions. On each sampling date, individuals were haphazardly sampled from barnacle clumps along a stretch of ca. 100 m of the intertidal rocky shore. Barnacles were collected with the help of a chisel and care was taken to not cause any damage to barnacle peduncles. Samples were frozen until further analysis.

Adult individuals from clumps were separated, the number of cyprids and juveniles with RC < 1 mm attached to each adult barnacle (Fig. 1) was measured using a dissecting microscope with a calibrated eyepiece, and the mean number of recruits (cyprids plus juveniles with RC < 1 mm) per adult barnacle (IR1, sensu Cruz et al. 2010) was calculated for each sampling date. On average, cyprids represented 8% ± 1.2% and juveniles represented 92% ± 1.2% of IR1. The index of recruitment IR1 reflects recruitment that occurred mainly during the last month before sampling (Mateus 2017), and will thus be considered as monthly recruitment, hereafter. In each year, the main recruitment season (IR1 > 3; Cruz et al. 2010) was defined and its duration (months) was calculated. The length of the main

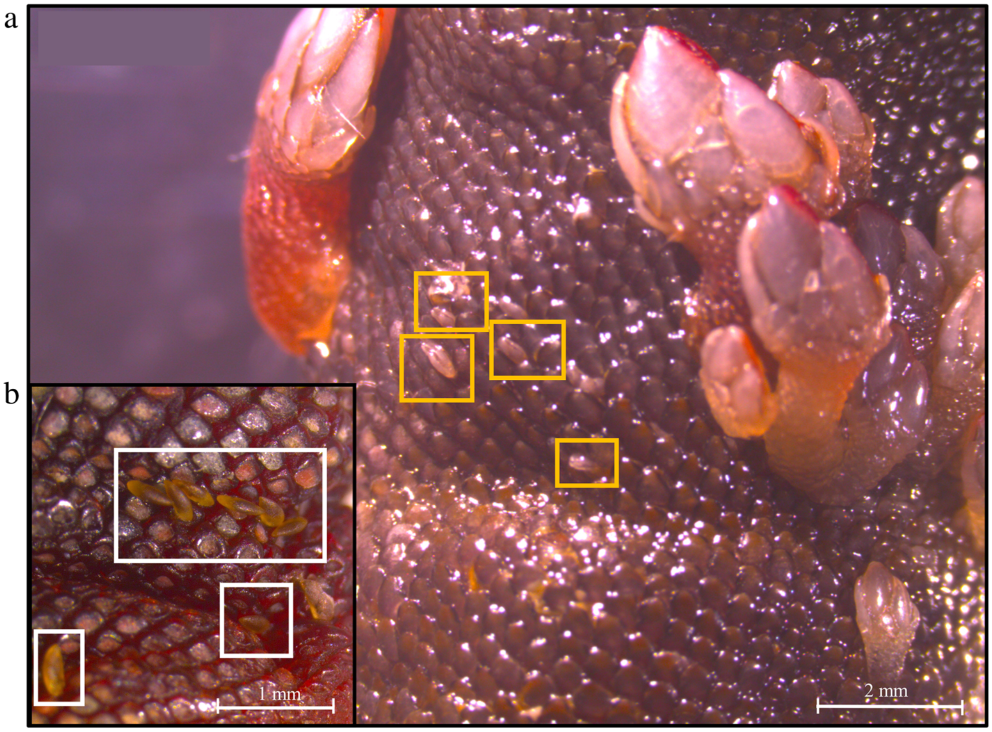

**Fig 1.** Details of a peduncle of an adult *Pollicipes pollicipes* with several (**a**) juveniles (RC < 1 mm; yellow boxes) and (**b**) cyprids (white boxes).

recruitment season was obtained from linear interpolation of dates of two consecutive IR1 data points that crossed the value of 3 (i.e., *see* Fig. 2a). In the case of 2008, the end and consequently the length of the main recruitment season, could not be defined due to rough seas that prevented sampling during autumn and winter. As sampling had a fortnightly periodicity and IR1 recruitment index reflects monthly recruitment, there might be a possible lack of independence in IR1 between two consecutive sampling dates. Consequently, for correlation purposes and to avoid non-independence of data, we eliminated IR1 data points that had less than ca. 30 d between two consecutive sampling dates.

Mean annual recruitment (annual recruitment hereafter) was estimated for each year, after calculating monthly means and without removing any data points. Both variables, monthly and annual recruitment, were obtained only for the months of July to October. This period was chosen considering that, in most years, these 4 months were included in the main recruitment season, and that June had still null or very low levels of recruitment. Moreover, in most years, cyprids were only detected from July to October (results not shown), which is an unequivocal sign of arrival of larvae and settlement.

Oceanographic variables were obtained for the period from 01 June to 31 October, every year from 2007 to 2016. A 6-h UI time series for Sines region was provided by the Instituto Español de Oceanografía (www.indicedeafloramiento.ieo.es, last accessed 07 May 2020), which is calculated using sea level pressure data from the WXMAP (Global and Regional Weather Prediction Charts) atmospheric model provided by the US Navy Fleet Numerical Meteorology and Oceanography Center. Significant wave height and averaged wave period measured every 10 min were obtained from an oceanographic buoy located near the Cape of Sines (37°55.3′N, 8°55.7′W). SST was provided by the Operational Sea Surface Temperature and Ice Analysis global SST reprocessed product, which provides daily gap-free maps of Foundation SST at $0.05^\circ \times 0.05^\circ$ horizontal resolution, using in situ and satellite data from both infra red and microwave radiometers. These SST products have a temporal time step of 1 d. Measurements of chlorophyll *a* (Chl *a*) derived from satellite data (Ocean Color Climate Change Initiative) were used in this study. European Space Agency produces "climate-grade" Essential Climate Variables based on satellite data; merger of the sensors Sea-viewing Wide Field-of-view Sensor, Visible Infrared Imaging Radiometer Suite, Medium Resolution Imaging Spectrometer, and Moderate Resolution Imaging Spectroradiometer instrument aboard the Aqua satellite. We used the Level 4 standard daily mapped image. Daily mean values were computed for the physical variables, including UI, wave height, and wave period.

To investigate if long-term temporal recruitment patterns reflect variability in any of the studied physical variables, we performed Spearman correlation analysis between monthly recruitment and each physical variable (UI, wave height and wave period, SST, and Chl *a*) for the whole 10-yr period (July

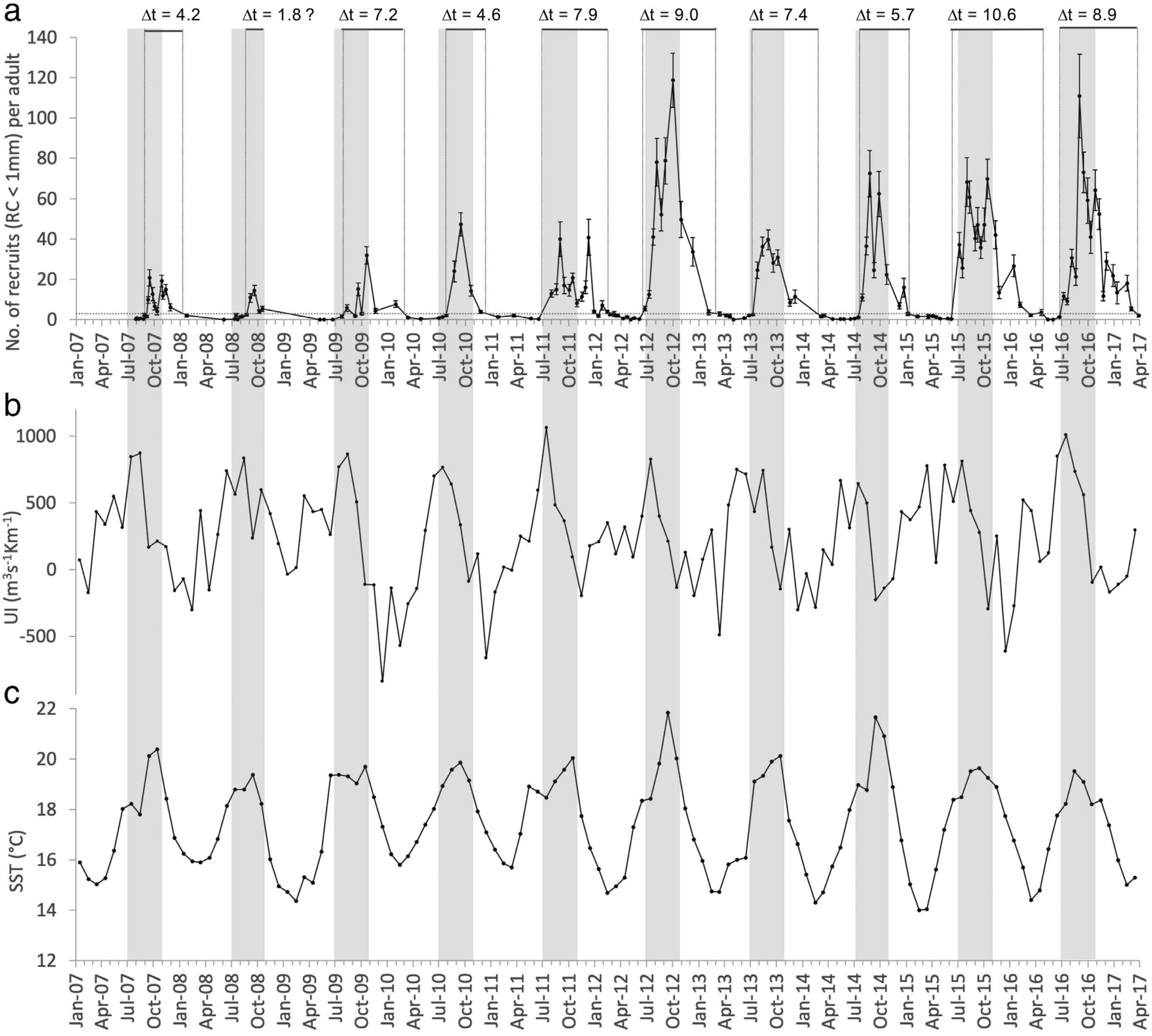

**Fig 2.** (**a**) Monthly recruitment of *Pollicipes pollicipes* (mean ± SE; $n = 20$–$50$), (**b**) monthly mean upwelling index (UI), and (**c**) monthly mean sea surface temperature (SST), from January 2007 to March 2017. Area inside dotted traces in (**a**) represents main recruitment season; $\Delta t$ is the length of main recruitment season in months; "?" means that the end of the main recruitment season was not defined in 2008 due to rough seas that prevented sampling between October 2008 and May 2009. Gray vertical bars across graphics represent the July–October period in each year, corresponding to the time period where correlations between recruitment and physical variables were analyzed.

to October; *n* ranged 39–42). For each physical variable, mean values over 30 d (to assess cumulative environmental variability over a monthly scale) were backward calculated from each monthly recruitment date. Spearman correlation coefficient was used rather than Pearson correlation due to nonnormality evidenced by some variables. Since the UI used in this study was obtained from sea level pressure data and corresponding wind components, and not from temperature anomaly as it is often calculated (e.g., Pfaff et al. 2011), and due to the relationship among the physical variables UI, SST, and Chl *a* previously found in upwelling systems (e.g., Oliveira et al. 2009), Spearman correlations between each pair of these three variables were also calculated.

To investigate interannual variability in recruitment and its relationship with physical variables, annual means for the July–October period were calculated for all the physical variables based on all daily mean values for each year ($n = 123$), and Spearman correlation analyses were performed between annual recruitment and all physical variables ($n = 10$). In addition, due to a significant correlation of monthly recruitment with UI and with SST found in the previous long-term analysis (see "Results" section), the maximum and minimum annual values for UI and SST were calculated from all daily mean values for each year ($n = 123$), and Spearman correlations with annual recruitment were also performed.

## Results

Observations of monthly recruitment of *P. pollicipes* over a 10-yr period, from July 2007 to March 2017, revealed variability in timing, length, and intensity of recruitment in different years (Fig. 2a). The beginning of the main recruitment season (monthly recruitment > 3) was frequently in June (2011, 2012, 2015, and 2016) or July (2009, 2010, 2013, and 2014), but in certain years started later, as in September in 2007 and August in 2008. The end of the main recruitment season was more variable and occurred in December (2010), or January (2007, 2014), February (2009, 2011, 2013), March (2012, 2016), and April (2015) of the following year. The length of the main recruitment season varied between 4.2 months in 2007 and 10.6 months in 2015, with an average duration of 7.3 months. In general, from 2007 to 2016, there was a tendency for the length of the recruitment season to increase, starting earlier and ending later in recent years.

Maximum values of monthly recruitment during the main recruitment season varied between 14 ± 2.5 recruits adult$^{-1}$ in 2008 and 119 ± 13.4 recruits adult$^{-1}$ in 2012.

Long-term correlation analyses (July–October period, from 2007 to 2016) between monthly recruitment and monthly means of physical variables revealed a significant positive correlation with SST and a significant negative correlation with the UI (Table 1). During the period from July to October, typically, the monthly UI is higher in the beginning of the period and decreases toward the end, and it is generally associated with an increase of SST in mid and late summer (Fig. 2b,c). During this period, monthly mean SST varied between 17.8°C in August 2007 and 21.8°C in September 2012.

Correlations among UI, SST, and Chl *a* were all significant ($n = 42$) for the same time period: UI vs. SST ($r_s = -0.441$; $p = 0.041$); UI vs. Chl *a* ($r_s = 0.316$; $p = 0.004$); and SST vs. Chl *a* ($r_s = -0.335$; $p = 0.030$).

Despite a higher annual recruitment observed when there were lower values of UI and higher values of SST (Fig. 3a,c,e), interannual correlation analyses (July–October period) between annual recruitment and the annual means of physical variables were not significant (with UI, $r_s = -0.588$, $p = 0.074$; with SST, $r_s = 0.559$, $p = 0.093$; Table 1). Conversely, a positive significant correlation between annual recruitment and maximum annual values of SST and a negative significant correlation between annual recruitment and maximum annual values of UI were found (Table 1). Higher recruitment years occurred when the maximum values of SST were observed and the maximum values of UI were lower (Fig. 3a,b,d).

Annual recruitment (July–October period) varied between 5 ± 2.6 recruits adult$^{-1}$ in 2008 and 64 ± 13.0 recruits adult$^{-1}$ in 2012 (Fig. 3a). From 2012 to 2016, annual recruitment was above the 10-yr average of recruitment, while it was below the average from 2007 to 2011, showing a tendency for a higher intensity of recruitment in recent years (Fig. 3a).

## Discussion

Our long-term observations supported the hypothesis that upwelling influences the recruitment of *P. pollicipes*. The main recruitment season began in the end of July, August, or beginning of September in the first 4 yr of monitoring, and in June or July in later years. The end of the recruitment season was more variable, ranging from December in 2010, to March in 2012 and 2016, and April in 2015. It was not possible to determine the period in 2008 due to lack of sampling during autumn and winter. Consequently, the main recruitment season increased from less than 5 months in 2007 and 2010 to

**Table 1.** Spearman correlation coefficients ($r_s$) and significance ($p$) between the physical variables and monthly and annual recruitment of *Pollicipes pollicipes* ($n = 42$ and $n = 10$, respectively), for the period of July to October, from 2007 to 2016. The values in bold indicate significant correlations.

| | **Monthly recruitment** | | **Annual recruitment** | |
|---|---|---|---|---|
| **Environmental variables** | $r_s$ | $p$ | $r_s$ | $p$ |
| Upwelling index | **−0.366** | **0.017** | −0.588 | 0.074 |
| Wave height | −0.046 | 0.774 | 0.248 | 0.489 |
| Wave period | 0.185 | 0.242 | 0.261 | 0.467 |
| Sea surface temperature | **0.449** | **0.003** | 0.559 | 0.093 |
| Chlorophyll *a* | −0.104 | 0.512 | −0.503 | 0.138 |
| Maximum upwelling index | — | — | **−0.733** | **0.016** |
| Minimum upwelling index | — | — | −0.236 | 0.511 |
| Maximum sea surface temperature | — | — | **0.681** | **0.030** |
| Minimum sea surface temperature | — | — | 0.377 | 0.283 |

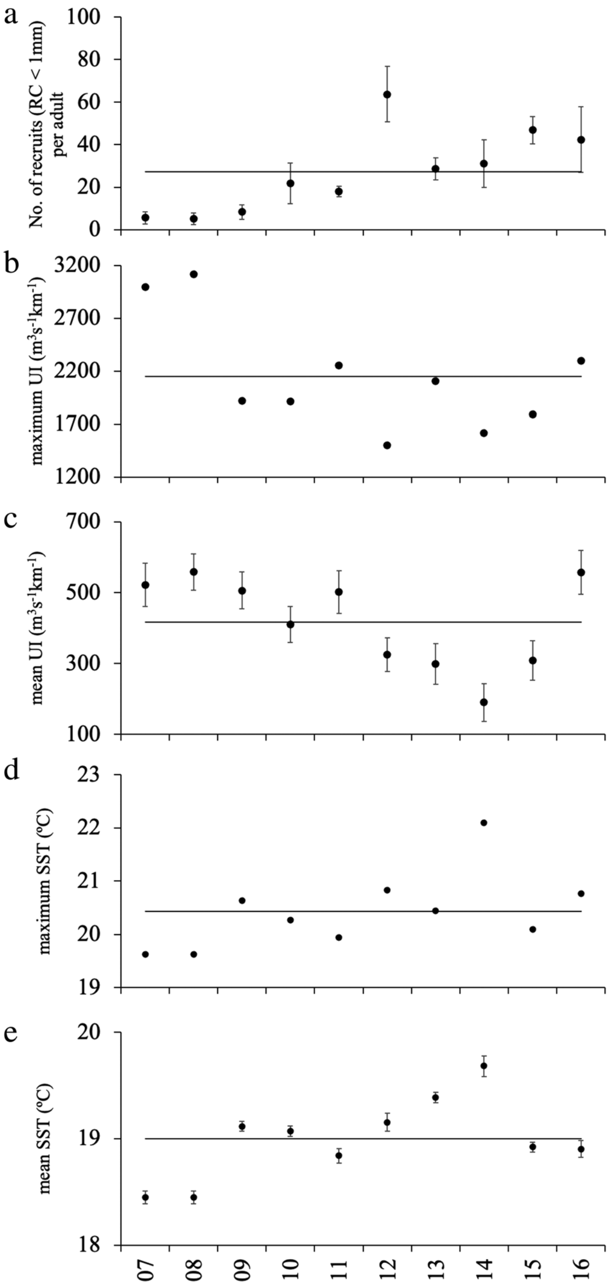

**Fig 3.** Annual variability from 2007 to 2016 for the July–October period of (**a**) annual recruitment of *Pollicipes pollicipes*; (**b**) maximum upwelling index; (**c**) upwelling index (UI); (**d**) maximum sea surface temperature; (**e**) sea surface temperature (SST), in the Cape of Sines. Black horizontal line in the *y*-axis represents the global mean across years for each variable. Symbols and bars represent mean ± SE except for (**b**) and (**d**).

approximately 9–10 months more recently (2012, 2015, and 2016). The trend is supported by the results of a study of recruitment of *P. pollicipes* for the same location in 1990–1992, which determined that the main recruitment season started in July or September and ended in October or December (Cruz et al. 2010). Similar studies in Spain in 1999–2001 also found that the main recruitment season extended from July or August to November or December (Pavón 2003; Macho 2006). Considering these former studies and the present series of 10 yr of observations, it is possible to suggest that there has been a trend toward a longer recruitment season in recent years. It is unknown if this trend corresponds to an increase in the length of the reproductive season, as studies on the temporal variability of reproduction in SW Portugal date from the 1990s (Cruz and Hawkins 1998), in which the most important breeding season of *P. pollicipes* was defined as lasting from April to September.

Care must be taken when estimating the end of the main recruitment season and, consequently, its duration. The recruitment index used in the present study, in Pavón (2003) and in Cruz et al. (2010) (i.e., number of cyprids plus juveniles [RC < 1 mm] per adult) was considered a good proxy of monthly recruitment, by comparing it with recruitment indices measured on artificial substrate, in which it was possible to measure recruitment based on a period of time (recruits of known maximum age) (Mateus 2017). It was assumed that juveniles with < 1 mm RC settled less than 1 month prior to sampling, which might not be always accurate, especially in autumn, when growth of juveniles might be low (Darras 2017) and potentially negatively affected by the large number of bigger and older juveniles (RC > 1 mm) on conspecifics. Density-dependent effects on growth rates of juvenile stalked barnacles have been found in relation to adult *P. polymerus* (Helms 2004) and have been suggested among juveniles of *P. pollicipes* on artificial substrate (Mateus 2017). The absence of cyprids after November in the present study (results not shown) is also an indication of a possible bias in the extension of the recruitment season. In the beginning of the recruitment season, this potential bias does not exist, as large barnacles have no recruits (Cruz et al. 2010), and cyprids and juveniles (RC < 1 mm) correspond undoubtedly to new recruits.

The variation in the magnitude of monthly recruitment over the 10-yr period and of annual recruitment for each year (during the July–October period) was described and correlated with several oceanographic variables. The higher values of annual recruitment were observed during the last 5 yr of the study, which may be related to the association between recruitment and relaxation of upwelling and seawater warming. Recruitment from 2012 to 2016 was about four times higher (ca. 43 recruits adult$^{-1}$) than in the first 5 yr of the 10-yr period (ca. 12 recruits adult$^{-1}$), which was comparable to the average recruitment observed in 1991 for the same location and period and using the same methodology (ca. 10 recruits adult$^{-1}$) (Cruz et al. 2010). Briefly, there seems to be a tendency towards higher intensity of recruitment in recent years.

The most important results linking recruitment to oceanographic variability involved the UI and SST. Specifically, the negative relation between monthly recruitment and UI, the positive relation between monthly recruitment and SST, the negative relation between annual recruitment and the maximum annual value for UI, and the positive relation between annual recruitment and the maximum annual value of SST. In general, recruitment of *P. pollicipes* was higher during upwelling relaxation and downwelling and when SST was higher. Higher recruitment was found in years when the maximum value of UI was lower, and the maximum value of SST was higher. Although causality cannot be directly inferred by a significant correlation, these results clearly indicate an association between recruitment of *P. pollicipes* and upwelling mechanisms as initially predicted.

The positive relation with SST found in our study is the opposite of the pattern described by Pineda (1991) while studying daily settlement of *P. polymerus* at a rocky shore in San Diego, California, USA. In that study, a negative significant correlation was obtained between daily settlement and surface water temperature (in situ measurements), and internal tidal bores were suggested as the mechanism driving drops in water temperature and larval transport onshore. This divergence might be related to the different temporal scale of monitoring (daily settlement in Pineda 1991; monthly recruitment in the present study), as different processes may act at different temporal scales. In the Benguela Current Upwelling System, Pfaff et al. (2015) suggested that sequential mechanisms appear to be utilized by larvae to get to the shore, namely, that the delivery of barnacle larvae to the inner shelf occurred during relaxation and downwelling events and that settlement coincided with spring tides, suggesting a role for internal tides in their onshore transport.

In acorn barnacle recruitment studies, when a relationship with upwelling was inferred, the main theory was that larvae were carried away from shore during upwelling and transported shoreward during downwelling or upwelling relaxation (e.g., Roughgarden et al. 1988; Farrell et al. 1991; Connolly and Roughgarden 1999). Transport of larvae in the California Current Upwelling System was also predicted to occur associated with a poleward flow of warmer water during upwelling relaxation or with larval dispersal from accumulation zones in the lee of capes during relaxation events (Wing et al. 1995; Mace and Morgan 2006; Dudas et al. 2009). Alternatively, as suggested by Pfaff et al. (2015) and Pineda et al. (2018), internal tidal waves and bores might be the driving force, as relaxation and downwelling is associated with water-column stratification, a prerequisite for the propagation of these internal motions. In addition, water column stratification has been related with larval distribution closer to the shore, for another temperate barnacle (Hagerty et al. 2018).

The main characteristics of the Canary-Iberia Current Upwelling System are comparable to the other major upwelling systems (California, Peruvian-Chilean, Benguela) with similar forcing and morphological features (Relvas et al. 2007). Off SW Iberia, where the Cape of Sines region is located, there is evidence of the development of a warm countercurrent over the inner shelf, progressing poleward from the Gulf of Cadiz and potentially reaching the Cape of Sines, that is associated with periods of weakening or relaxation of upwelling favorable winds (Relvas and Barton 2005; Relvas et al. 2007). In situ measurements of nearshore currents in the lee of Cape of Sines indicated a predominantly southward flow being interrupted by short-period (1–4 d) current reversal episodes, which occur during periods of relaxation of the northerlies or weak southerly winds (Oliveira et al. 2008). North of the Cape of Sines, the coast is sandy (ca. 60 km of sandy shoreline until the nearest rocky shore), while south of the Cape of Sines, the coast is mostly rocky and *P. pollicipes* is abundant in very exposed shores. Consequently, this coastal poleward current might transport cyprids along-shore, coming from the south or from a larval retention area located at the lee of the Cape of Sines or both. In fact, this region can be considered an upwelling shadow in the downstream of the Cape of Sines, formed by larvae trapped between the upwelling front and the shore, and that never leave the inner shelf (Trindade et al. 2016). Therefore, along-shore currents and accumulation of larvae in the lee of the Cape of Sines might explain the negative relationship between recruitment of this species and the UI and the positive relationship between recruitment and SST. However, recruitment is determined by many factors operating and interacting during the larval phase, settlement and the postsettlement phase, so using recruitment observations to infer mechanisms of larval delivery to the shore is complex due to postsettlement mortality, density-dependent effects on settlement (Shanks 2009*a*), and statistical problems related to sampling frequency and aliasing (Shanks 2009*b*). Observations on the larval distribution and on settlement rates of *P. pollicipes* are needed to investigate hypotheses derived from the upwelling relaxation theory, and on putative sequential, interacting, or alternative mechanisms (e.g., internal tidal bores), but this is challenging since this species recruits in extremely high hydrodynamic conditions.

Although SST is likely to have an indirect effect on the recruitment of *P. pollicipes* being a proxy of upwelling relaxation (SST and UI are significantly correlated), an influence of SST on recruitment independently of upwelling is also possible. A positive relation between SST and recruitment of an acorn barnacle was found in a region without the influence of upwelling (northwest Atlantic coast in Canada), and this 12-yr study suggested that SST could increase pelagic larval survival (Scrosati and Ellrich 2016). An additional influence of SST on *P. pollicipes* recruitment might be predicted by the fact that warmer temperatures might have an effect on reducing the planktonic larval duration (Franco et al. 2017). Consequently, larval dispersal might be shortened in warmer waters, which would potentially enhance the proximity between hatching and settlement sites and increase larval survival and settlement rate.

The trend for a longer recruitment season and a higher recruitment intensity in recent years together with the influence of upwelling in the recruitment patterns, observed in the present study, should be better investigated in light of climate change predictions, although the potential strengthening or weakening of upwelling in the Canary-Iberia Current upwelling system is still in debate (e.g., Sousa et al. 2017; Sousa et al. 2020). Regarding *P. pollicipes* exploitation, recovery of harvested populations might be facilitated with a longer recruitment season and a higher recruitment intensity. Furthermore, if larval supply and recruitment are not limiting this species in this region, more attention should be given to the effect of post-recruitment processes contributing to the dynamics and persistence of these populations.

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## Conflict of Interest

None declared.

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