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Recruitment and growth of the gooseneck barnacle *Pollicipes pollicipes* (Gmelin, 1791) in the Cantabrian Coast (Northern Spain, Gulf of Biscay)

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ABSTRACT

Recruitment and growth of the gooseneck barnacle *Pollicipes pollicipes* (Gmelin, 1791) are essential life history parameters needed for the monitoring and assessment of the fishery performance and establishment of sustainable management practices. Here, intra-annual variability in recruitment and growth of the gooseneck barnacle *P. pollicipes* was first investigated in the Cantabria region (N Spain, Gulf of Biscay). The recruitment index IR1 as the number cyprids with rostro carina length (RC)<1 mm was estimated at two different intertidal levels and along the stalk of adult barnacles. The relationship of recruitment with sea surface temperature (SST) associated to breeding and with significant wave height was explored. For growth, RC length of juveniles, pre-adults and adults was measured in aggregated individuals. Recruitment was weak, showing a peak in autumn at the low tidal zone. Its relationship with SST was unclear, possibly due to the low intensity of the recruitment pattern, and no correlation was found with wave height. The great majority of recruits attached to the lower part of the adult stalk. The mean growth rate was significantly higher for juveniles (0.72 mm month^{-1}) compared to adults (0.36 mm month^{-1}), with peak growth occurring in spring. Based on these findings, regional shellfishery management guidelines are proposed, and future research directions are outlined, considering the limitations of this study in terms of spatial replicability

1. Introduction

The gooseneck barnacle *P. pollicipes* is a sessile pedunculate cirriped that lives on very exposed rocky shores ranging from the shallow subtidal to mid intertidal zones of highly energetic coastal areas (Barnes, 1996; Borja et al., 2006; Cruz et al., 2010). This species is distributed mainly from the northwest coast of France (Brittany, 48°N) to the northwest coast of Africa (Senegal, 15°N) and the Mediterranean (Algeria) occurring in dense clusters or aggregates due to gregarious settlement of larvae on adult peduncles (Barnes, 1996).

On the coastlines of Morocco, Portugal, and Northern Spain, the gooseneck barnacle is extensively harvested due to its significant value as a resource. Consequently, there is a clear necessity to implement management strategies grounded in scientific knowledge to prevent the risk of overexploitation (Molares and Freire, 2003; Bald et al., 2006; Jacinto et al., 2010). In this context, understanding recruitment and growth emerges as crucial elements in the life history of this species for evaluating fisheries performance and implementing sustainable management approaches.

Recruitment plays a fundamental role in shaping marine communities (Woodin et al., 1995). For *P. pollicipes*, recruitment success depends on a sequence of interdependent stages: brooding, larval dispersal, and settlement (Cruz and Hawkins, 1998; Pavón, 2003). The breeding season, which is closely tied to sea water temperature, typically begins in March and extends through October, peaking between May and August (De La Hoz and Garcia, 1993; Molares and Martín, 1994; Cardoso and Yule, 1995; Cruz, 1993; Cruz and Araújo, 1999). Approximately 3 or 4 months after hatching, the larvae settle (Pavón, 2003; Cruz, 2000). Recent research by Román et al. (2022) demonstrates that thermal variability strongly mediates mesoscale patterns in barnacle reproduction, highlighting the broader role of environmental conditions in influencing reproductive and recruitment dynamics across regions.

The recruitment of the genus *Pollicipes* displays high variability in both space and time, predominantly occurring in barnacle aggregates

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along the stalks of adult conspecifics. This behavior aims to mitigate both physical and biological stress (Barnes, 1996; Cruz et al., 2010; Pavón, 2003; De La Hoz and Garcia, 1993; Cruz, 2000; Bernard, 1988; Kugele and Yule, 1993, 2000; Cruz et al., 2022). Additionally, recruits can be found on alternative surfaces such as barnacles, algae, or mussels (Bernard, 1988; Hoffman, 1984, 1988). Although research on the temporal and spatial variability of recruitment is limited, a few studies, such (Fernandes et al., 2021) in SW Portugal and (Molares, 1993; Sestelo et al., 2007; Pavón, 2003; De La Hoz and Garcia, 1993) in N Spain, have explored this subject. Recently, a large-scale comparison of reproduction and recruitment of *Pollicipes pollicipes* across Europe was conducted (Aguión et al., 2022) including the Iberian Peninsula (SW Portugal, Asturias and Galicia (N Spain)) and Brittany (France). These investigations employed various indices based on the number and sizes of recruits attached to adults (De La Hoz and Garcia, 1993; Pavón, 2003; Cruz et al., 2010; Fernandes et al., 2021; Aguión et al., 2022) or percentage of recruits with adults (Molares, 1993; Macho, 2006), revealing distinct patterns. In SW Portugal, recruitment intensity peaks in summer and autumn, particularly from August to October. Conversely, in the NW Spain coast, recruitment is more prominent from August to December, with peak months occurring from September to December. Notably, recruitment is more intense on the lower half of the adult stalk and at low tidal levels. To the best of our knowledge, there is no available data on the recruitment of this species in the inner Spanish regions of the Gulf of Biscay.

Factors influencing recruitment variability include water flows and processes, such as thermocline presence, upwellings, offshore currents, eddies, and swell (Barnes, 1996; Pineda, 1991; Pavón, 2003; Connell, 1985; Shkedy and Roughgarden, 1997; Roughgarden et al., 1988; Connolly and Roughgarden, 1998; Quinteiro et al., 2007). These phenomena are closely linked to surface temperature (SST) and wind conditions (Pineda, 1994; Pavón, 2003; Cruz and Hawkins, 1998; Cardoso and Yule, 1995; Barnes, 1992; Bertness et al., 1996; Carroll, 1996). In SW Portugal, recruitment appears to coincide with maximum SST and weakened upwelling (Fernandes et al., 2021). Conversely, using a simplified biophysical model, Rivera et al. (2013) predicted heightened recruitment on the Cantabrian coast during years of increased upwelling activity. Additionally, reduced upwelling is associated with limited larval dispersal and self-recruitment events (Parrondo et al., 2022). Mortality and post-mortality factors during settlement/recruitment, along with the duration of the larval phase, contribute to the intra- and inter-annual variability in recruitment (Pavón, 2003; Molares and Martín, 1994; Kugele and Yule, 1996).

Research on the growth of *P. pollicipes* has primarily been conducted in SW Portugal, where size increments of monitored individuals have been measured (Cruz, 1993, 2000; Cruz et al., 2022; Jacinto et al., 2010, 2015). In Spain, growth estimates have only been obtained indirectly by analyzing size structure over time (Sestelo et al., 2007; Sestelo and Roca-Pardiñas, 2011), resulting in a higher growth rate for juveniles than for adults. In contrast, species like *P. polymerus* have undergone more extensive growth investigations. Barnes (1996), Barnes and Reese (1960), Bernard (1988), Hoffman (1988), Lewis and Chia (1981), Page (1986) and Hoffman (1989) which suggest that *P. polymerus* juveniles may exhibit greater feeding efficiency than adults, as they beat their cirri into the water flow, as opposed to holding them out like adults. Physical factors such as temperature (Crisp and Bourget, 1985), wave exposure (Sanford and Menge, 2001) and light or food supply, linked to immersion time, influence growth rates. Juveniles of *P. pollicipes* within aggregates maintain a relatively constant growth rate across seasons, while for adults, growth is faster in winter and spring compared to summer (Cruz, 1993). Additionally, growth rates have been explored on cleared surfaces, revealing a substantially faster pace compared to growth within aggregates (Cruz et al., 2010).

This study examined temporal (intra-annual) and spatial (tidal level) variations in the recruitment and growth of *P. pollicipes* at Ubiarco on the Cantabria coast (northern Spain). The relationship of recruitment with wave height and sea surface temperature (SST) was also explored. It aimed to provide an initial assessment of *P. pollicipes* recruitment and growth on this rocky shore, contributing to knowledge on the effectiveness of existing fisheries management measures. Additionally, the study sought to complement previous findings on recruitment in northern Spain and growth in SW Portugal.

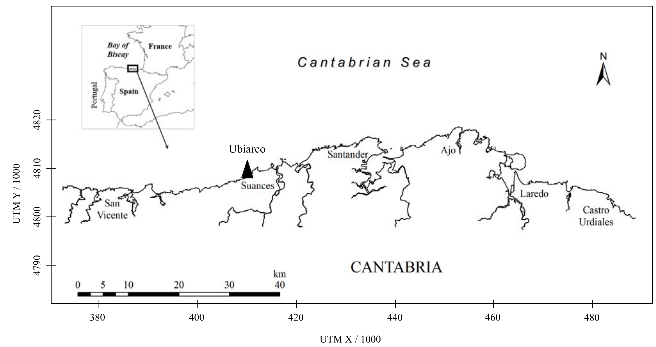

Fig. 1. Study site located in the coast of Ubiarco (N Spain, Cantabria).

2. Material and methods

2.1. Study site and sampling

Sampling for recruitment estimation and the in-situ growth experiment was conducted in the intertidal area of a highly exposed rocky shore on the NE coast of Spain (Ubiarco, Cantabria, 43°25′N: 4°06′W) (Fig. 1) during spring low tides throughout January to December 2011. The rocky shore at this location features steep slopes and is primarily influenced by NW waves. The site was chosen for its reasonably good accessibility and previously observed high levels of barnacle coverage in surveys conducted by Bidegain et al. (2015).

2.2. Estimation of recruitment

To estimate recruitment, we studied two tidal levels: the high tidal level (H), representing the upper intertidal distribution zone of *P. pollicipes*, and the low tidal level (L), corresponding to the lowest intertidal distribution zone. Monthly, whenever feasible given wave and tide conditions, individuals of *P. pollicipes* were collected from randomly selected aggregates, involving three replicates of approximately 100 adult individuals each. These samples were labeled, stored in plastic bags, transported to the laboratory, and frozen until processing.

The recruitment rate was estimated using the IR1 recruitment index (Pavón, 2003; Cruz et al., 2010), which is based on the rostro-carina (RC) length of early recruits (RC $<$ 1 mm) attached to adult hosts (RC $>$ 12.5 mm). The barnacle length chosen for this assessment was RC (Fig. 2), known as the optimal variable for describing the growth of *P.pollicipes* (Cruz, 1993), and widely utilized in previous studies (Cruz et al., 2022).

The examination of the recruitment rate along the stalk and capitulum of adult barnacles was also conducted. The allocation of early recruits attached to conspecifics involved categorizing the adult host into three zones: Zone 1, corresponding to the capitulum; Zone 2, representing the half of the stalk closer to the capitulum, and Zone 3, indicating the half of the stalk closer to the base of the barnacle (Fig. 2).

2.3. Spatial and temporal variability of recruitment rate

The Local Weighted Least Squares Regression smoothing technique (LOESS) (Cleveland and Devlin, 1988) was applied to examine the fluctuations in the recruitment index IR1 throughout the year and across low (L) and high (H) tidal levels. Due to its non-parametric nature, LOESS can adeptly portray this relationship with increased resilience and adaptability compared to parametric models. This flexibility enables LOESS to discern information, encompassing ecological and biological intricacies, within the data that could be disregarded by more constrained parametric models.

2.4. Temporal variability of sea surface temperature (SST)

This study analyzed monthly variations in sea surface temperature (SST) at the study site, comparing the sampling year with the climatological mean. The primary objective was to investigate the relationship between SST and the onset and intensity of the recruitment season. Particular attention was given to the sea water temperature associated to the main breeding season of *P. pollicipes* (14.5 °C–19.5 °C (Pavón, 2003), 14.8 °C–21.0 °C (Aguión et al., 2022)) and the period during which SST remained above this threshold.

Two sets of SST data were employed for this analysis to cover the time span and area relevant to this study and previous research in recruitment, taking into account data availability. The first dataset enabled the estimation of monthly mean SST values. Monthly remotely-sensed Advanced Very High Resolution Radiometer (AVHRR) data from the Jet Propulsion Laboratory Physical Oceanography Distributed Active Archive Center (JPL PODAAC) were utilized for this purpose. These data, part of the NASA/NOAA AVHRR Oceans Pathfinder project, underwent processing at JPL. The SST data were derived from the AVHRR radiometers (NOAA -7, -9, and -11) using an enhanced non-linear algorithm (Walton, 1988). The dataset covered the period from 1982 to 2018 and consisted of night-time passes on global equal-angle grids with a resolution of 4 km. Night-time passes were chosen to minimize the influence of solar warming during the day. Only "best SST" data, indicating the highest quality pixel values free of cloud or cloud shadow interference, were included. The second dataset was sourced from gap-free daily images from the Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) at the UK National Centre for Ocean Forecasting. OSTIA utilized multi-satellite data from AVHRR, AATSR, MODIS, and SWIR, provided by the Group for High Resolution Sea Surface Temperature (GHRSST), along with in-situ observations. The spatial resolution of OSTIA was approximately 1/20° (5 km), and the analysis employed a variant of optimal interpolation (OI) as described by Martin et al. (2007).

2.5. Relationship between recruitment and significant wave height

Relationship between swell and recruitment was analyzed in order to determine whether this physical factor have a role on the variability of recruitment patterns. The hypothesis was that wave height could influence recruitment patterns, either positively or negatively, due to its impact on larval settlement and dispersal. Higher wave heights could enhance recruitment by increasing water turbulence, which may facilitate the transport of larvae to suitable habitats. Conversely, excessively high wave heights could have a negative effect by increasing the mortality rate of settlers or dislodging newly settled juveniles. Thus, the aim was to investigate the direction and strength of this relationship through correlation analyses.

To investigate this, hourly significant wave height (Hs) data from October 2010 to December 2011 were obtained from a buoy located near Ubiarco (La Virgen del Mar, 43°29′N: 3°52′W). The mean Hs was calculated for two time periods: (i) the month preceding each sampling date, and (ii) the three months preceding each sampling date. The relationship between Hs and the recruitment of cyprids and small juveniles was examined. Spearman's correlation analysis was conducted between the recruitment index IR1 at both tidal levels and the mean Hs for both time periods.

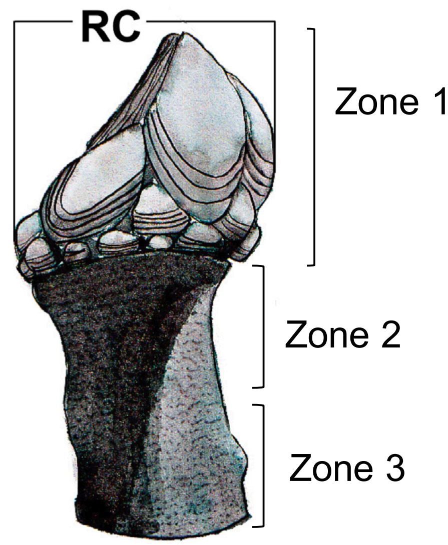

Fig. 2. Rostro-Carina (RC) and Rostro-Tergo (RT) size measures, and zones of recruitment (1, 2 and 3) along the stalk and capitulum of adults.

2.6. Estimation of growth

For growth estimation, the rostro-carinal (RC) size was measured monthly, whenever feasible, in 90 individuals from two aggregates at the lower tidal level. To ensure individual identification across visits, a schematic representation of the most easily identifiable individuals was created. This allowed the same barnacles to be tracked and measured consistently over the study period. Each studied individual was assigned to its maturation phase based on the rostro-carinal (RC) length at the time of measurement (Cruz and Hawkins, 1998): juveniles (RC < 10 mm, sperm production is achieved at this length) pre-adults (10 mm < RC < 12.5 mm), and adults (RC > 12.5 mm, minimum size for maturity). This assignment was updated for each sampling date as the barnacles grew.

The total growth was measured as the increase in RC length (mm) over the eleven-month sampling period from January to November. The monthly growth rate (mm RC month^{-1}) for different intervals between sampling dates was calculated as the average monthly increase in RC length (mm) for each period. These intervals spanned the full sampling period (January–November) and shorter intervals, such as January–March–May–June–August–November. The intervals varied because wave and tidal conditions occasionally restricted access to the sampling site on scheduled dates.

Statistical analyses were performed using the R statistical software (R Core Team, 2023).

3. Results

Recruitment exhibited a consistently low and stable pattern from January to September (Fig. 3). During these months, the recruitment rate was slightly elevated, albeit not significantly, at the high tidal level. However, from September onward, recruitment experienced a notable upswing, culminating in a pronounced peak in November, with a significant increase particularly observed at the low tidal level.

Recruitment was significantly higher on the half stalk closer to the base of the peduncle of the barnacles (Zone 3) compared to that on the half stalk closer to the capitulum (Zone 2) and on the capitulum (Zone 1) (Fig. 4). On zones 1 and 2 the settlement was patently sparse. Recruitment on zones 1 and 2 was significantly higher at low tidal level, while on zone 3, it was significantly higher at high tidal level (Fig. 4).

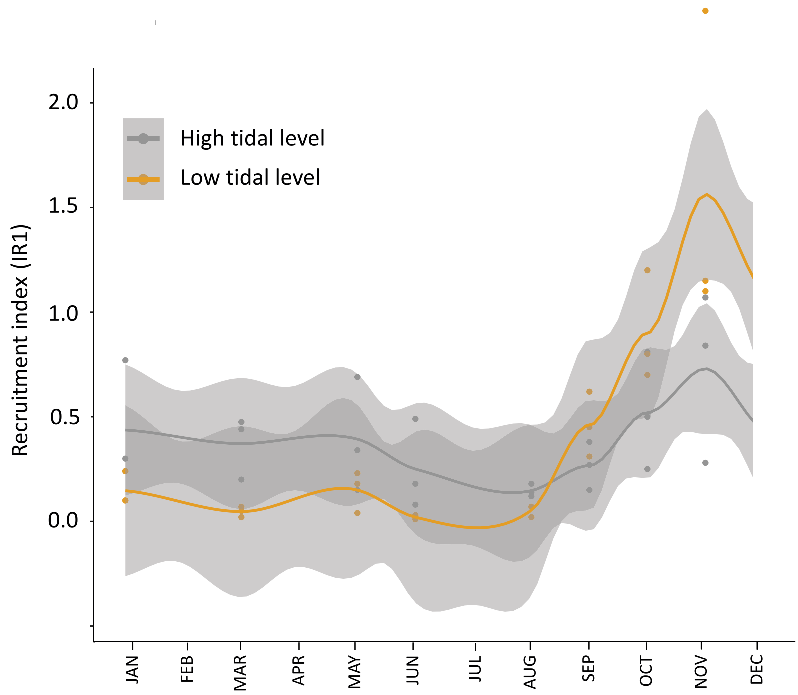

Fig. 3. Loess regression models for the recruitment index IR1 (Cruz et al., 2010) of *P. pollicipes* at high and low tidal levels at Ubiarco (N Spain) in 2011. The regression curves are represented by solid lines with smoothing based on 95% confidence intervals (shaded areas).

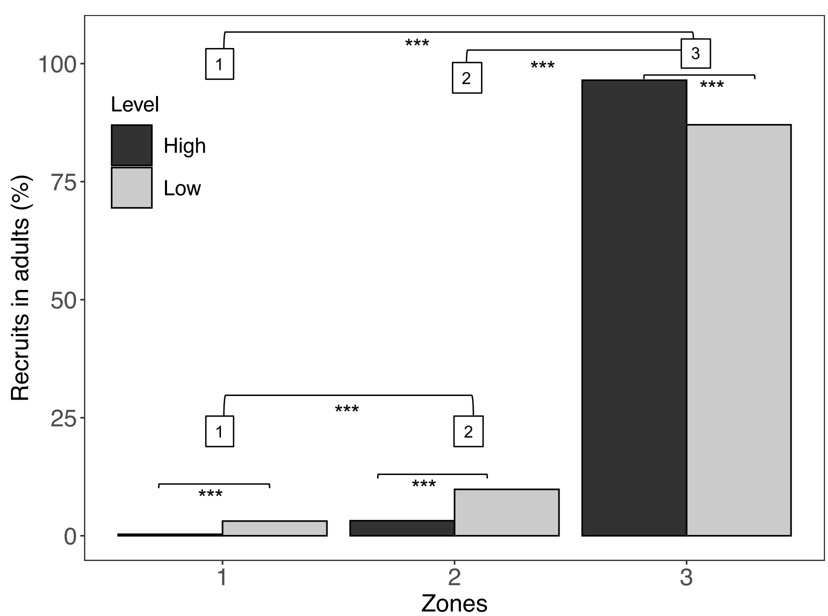

Fig. 4. Percentage of recruits (RC < 1 mm) on each zone of adult conspecifics (Zone 1, capitulum; Zone 2, half of the stalk closer to the capitulum; Zone 3, half of the stalk closer to the base of the barnacle) at high (n = 627) and low (n = 417) tidal levels at Ubiarco from monthly samplings during 2011. Significant differences ($p < 0.0001$, proportions Z-test) among tidal levels (High and Low) for each zone, and between zones 1, 2, and 3 are represented by ***.

3.1. Temporal variability of sea surface temperature (SST)

The mean SST at Ubiarco during the sampling year (2011) showed a very close alignment with the climatological mean SST indicating that there were no significant deviations or anomalies in temperature patterns (Fig. 5). The mean SST in 2011 remained between the temperature range associated with the main breeding season in *P. pollicipes* (red dashed line, Fig. 5) from early April to November, while for the climatological mean SST the breeding conditions were met from late April/early May to November.

3.2. Relationship between recruitment and significant wave height (Hs)

The recruitment index IR1 showed no statistically significant correlation (at the 95% confidence level) with the mean significant wave

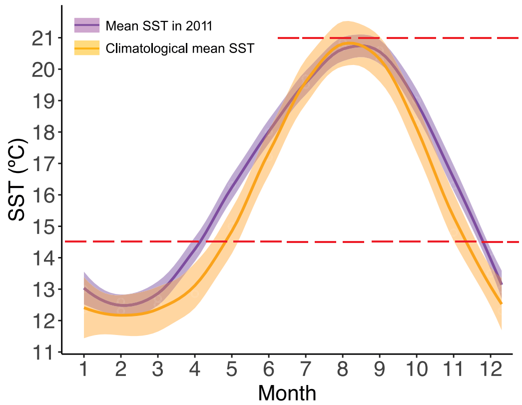

Fig. 5. Time series of monthly SST values (solid lines) at Ubiarco in 2011 and climatological mean SST values from 1982–2018. Shaded areas represent 95% coinfident intervals. Red dashed line represents the SST range for breeding conditions (14.5 °C–19.5 °C (Pavón, 2003), 14.8 °C–21.0 °C (Aguión et al., 2022)). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

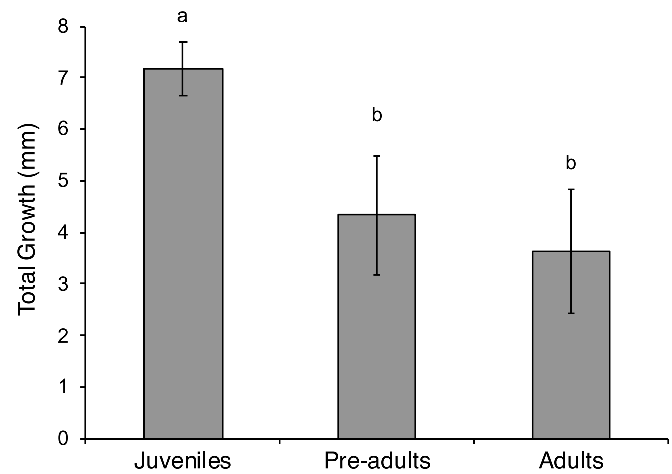

Fig. 6. Total growth (mean (bar) ± SD (error bar)) in terms of increase in RC size (mm) from January to November for *P. pollicipes* individuals categorized as juveniles (RC < 10 mm) (n = 28), pre-adults (10 mm < RC < 12.5 mm) (n = 32), and adults (RC > 12.5 mm) (n = 30). Different letters above the bars indicate statistically significant difference at p < 0.05 (ANOVA and Tuckey HSD).

height for either the month prior or the three months preceding the recruitment estimation sampling date (Table 1). This lack of correlation was consistent across both tidal levels.

3.3. Growth patterns

Fig. 6 illustrates the total growth of *P. pollicipes* in terms of RC length (mm) throughout the entire year of 2011. Individuals initially classified as juveniles exhibited the most substantial total growth (7.17 ± 0.5 mm, mean ± SD), significantly surpassing pre-adults (4.33 ± 1.1 mm) and adults (3.62 ± 1.2 mm). Concerning monthly growth throughout the studied year, the average monthly growth was 0.72 ± 0.16 mm/month for juveniles, 0.43 ± 0.36 mm/month for pre-adults, and 0.36 ± 0.38 mm/month for adults.

Juveniles exhibited a significantly faster growth rate than pre-adults and adults from January to August. Notably, there was a distinct growth peak for both juveniles (1.32 ± 0.14 mm/month) and pre-adults (0.72 ± 0.19 mm/month) from March to May. Apart from this period, pre-adults and adults displayed similar, slow and consistent monthly growth rates (Fig. 7)

4. Discussion

This study provides the first assessment of *P. pollicipes* recruitment and growth on the rocky shore of Ubiarco (Cantabria, N Spain, Gulf of Biscay). While valuable insights were gained, shedding light on the effectiveness of existing fisheries management measures in the region, recruitment and growth patterns of *P. pollicipes* may vary across spatial scales, including localized site-specific differences. The findings of this study complement previous research on recruitment in N Spain (Aguión et al., 2022; Pavón, 2003) and growth in SW Portugal (Cruz, 1993, 2000; Cruz et al., 2022; Jacinto et al., 2010, 2015).

Recruitment

The recruitment intensity of *P. pollicipes* on conspecifics was weak with a relative notable intensification in autumn (November) at both tidal levels, reaching a maximum IR1 index of around 2 recruits per adult (Fig. 3). This IR1 peak value defines a very limited recruitment in 2011 considering that Cruz et al. (2010) suggested IR1 values greater than 3 define the main recruitment season of *P.pollicipes*. Examining variations between tidal levels, recruitment intensity was comparable or slightly elevated at the high tidal level during non-peak recruitment months. However, in the peak recruitment period (autumn, November),

Table 1
Correlation coefficients of Spearman rank analyses (r_s) between recruitment index IR1 (at high and low tidal levels) and mean significant wave height (H_s) for the (i) month prior and (ii) three months preceding the recruitment estimation sampling date.

Recruitment (IR1)	H_s	r_s	p-value
Low tidal level	Preceding month	0.37	0.47
Low tidal level	3 months preceding	0.14	0.79
High tidal level	Preceding month	0.03	0.96
High tidal level	3 months preceding	0.11	0.82

recruitment significantly increased at the low tidal level, aligning with observations made by Cruz et al. (2010) and Pavón (2003). These tidal-level variations in recruitment may be associated with differences in settlement rates due to longer immersion times (Lauzier, 1999b,a) or to the fact that recruitment on conspecifics is an adult density dependent process that is amplified in situations where barnacles are scarce (Jacinto, 2016). The recruitment index IR1 represents the number of cyprids attached to conspecific adults of *P. pollicipes*. Thus, looking closely at the "adult host", this number was much higher on the lower half of the stalk, while on the upper part of the stalk and the capitulum, the presence or recruits was very limited (Fig. 4). Similar results found by Cruz et al. (2010) and Sestelo et al. (2007) may be explained by cyprids in the lower half of the stalk obtaining more refuge against predators and desiccation, reduced chemical signals concentrations in the capitulum, the process of delaminating of the layers in the capitulum and the adults' feeding "shadow effect" occurring in the upper part of the peduncule (Barnes and Reese, 1960; Chaffee and Lewis, 1988; Lewis and Chia, 1981; Cruz, 2000). This hypothesis however was not supported by Hoffman (1984, 1989) for *P. polymerus* and Pavón (2003) for *P. pollicipes* where the half stalk closer to the capitulum was the most colonized area of conspecifics. Differences into the population density between studied zones could be the explication of the lack of consistency between studies; higher density of adults within aggregates means that the basal area of the stalks is less accessible for settlement (Cruz et al., 2010). Overall, the recruitment distribution patterns may be also the result of differential mortality induced by both biological and physical factors operating at that scale.

Regarding the temporal variation of recruitment, our findings align partially with observations in adjacent coastal regions (Pavón, 2003; Macho, 2006; Aguión et al., 2022; Cruz et al., 2022). While the primary recruitment season at Ubiarco exhibited similarities to those observed

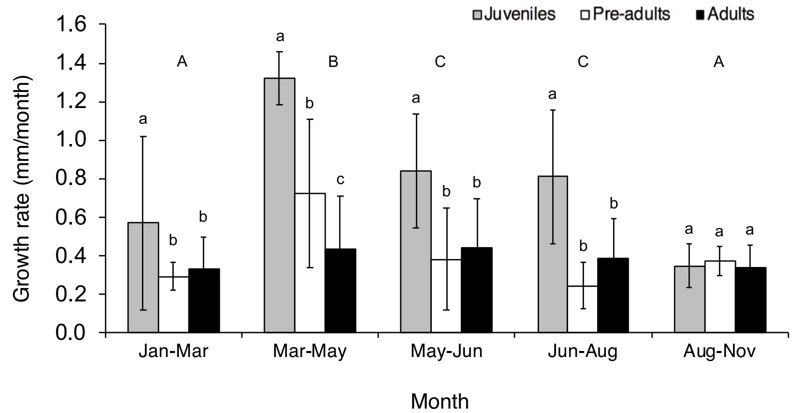

Fig. 7. Monthly growth rates (mean (bar) ± SD (error bar)) in terms of increase in RC size (mm) for *P. pollicipes* individuals categorized as juveniles (RC < 10 mm)(n = 28), pre-adults (10 mm < RC < 12.5 mm) (n = 32), and adults (RC > 12.5 mm) (n = 30) throughout different sampling periods from January to November. Different letters above the bars denote statistically significant differences in growth at $p < 0.05$ (ANOVA and Tukey HSD). Lowercase letters indicate differences between maturation phases and Uppercase letters indicate differences between sampling periods.

in neighboring coasts, particularly in years characterized by poor recruitment, the intensity of recruitment showed considerable variability across different studies and years (Cruz et al., 2010; Pavón, 2003; Fernandes et al., 2021; Aguión et al., 2022). In the neighboring region of Asturias (Pavón, 2003) reported a weak recruitment in 2000 with a relative maximum in November/December and an appreciably higher recruitment in 2001 with an earlier marked peak of 22 recruits per adult earlier in August/September. Aguión et al. (2022) also observed a similar pattern in Asturias, where a weak recruitment year in 2017 coincide with a recruitment peak recorded in autumn, and a more intense recruitment in 2018 was joined with an earlier and more prolonged recruitment season. O'Riordan et al. (2004) recorded a low recruitment intensity in northern populations of Europe as a consequence of colder waters shortening the breeding season (Pavón, 2003; Aguión et al., 2022)

In SW Portugal, however, Cruz et al. (2010) found that recruitment began earlier (July) reaching a peak IR1 of 60 recruits per adult in September at Cape Sardão and 20 recruits per adult in August at Cape Sines. Additionally, Fernandes et al. (2021) observed longer recruitment seasons (9 months) in 2016–2017 compared to those recorded in 2007–2010 (less than 5 months), suggesting a trend toward extended recruitment seasons and higher recruitment intensity in recent years. Recruitment values in SW POrtugal were much higher recruitment values than those observed at our study site, as well as those reported by Pavón (2003) in the neighboring region of Asturias. Cruz et al. (2022) reviewed the recruitment patterns of this species observing that recruitment phenology was variable among regions; overall, as in our study, shorter an less intense main recruitment seasons were detected in Brittany, Galicia and Asturias compared to SW Portugal (Aguión et al., 2022). The fact that the SST of SW Portugal is warmer and summer is longer than that in N Spain could be a factor explaining higher recruitment intensities as the sea temperature is related to breeding (Cruz et al., 2022; Page, 1983).

The range of SST necessary for breeding at Ubiarco was assumed to be from 14.5 °C to 21.0 °C, assuming a similar pattern than that observed in Asturias by Pavón (2003) from 14.5 °C to 19.5 °C and by Aguión et al. (2022) from 14.8 °C to 21.0 °C. The minimum of this temperature range for breeding was reached in April, although regarding the climatological mean SST this temperature usually is reached in May. The temperature remained above the breeding threshold until November. Aguión et al. (2022) also found that in Asturias (2018), breeding started in April but was intense from May to October (around 50% of barnacles with eggs). In SW Portugal in 2018, the minimum temperature for breeding (range 15.5 °C–16.8 °C), Aguión et al. (2022) seems to have reached earlier leading to intense breeding from April to August. Over 25% of barnacles still carried eggs until October (Aguión et al., 2022).

Recruitment season seems to begin three/four months after the sea surface temperature (SST) reached the minimum threshold for breeding: in SW Portugal, recruitment started in August, while in Asturias it occurred in July (Aguión et al., 2022). These results are consistent with those obtained by Pavón (2003) in her analysis about the duration of the larval phase of *P.pollicipes*. At our study site, recruitment remained very weak in July, three months after the SST threshold was reached, started increasing in August, and peaked in November (1.5 recruits per adult). The reason for this pattern observed elsewhere is unclear in our study, potentially due to the unusually weak recruitment compared to Asturias (25 recruits per adult) SW Portugal (75 recruits per adult). The number and intensity of broods could be also explaining these differences (Cruz et al., 2022). Aguión et al. (2022) detected 3 to 5 broods per year in SW Portugal, while in N Spain around two broods per year were described by Pavón (2003) in 2001 and Sestelo and Roca-Pardiñas (2011) in 2007, and around four broods per year by Aguión et al. (2022) in 2018. According to Román et al. (2022) SW Galicia had a much higher number of broods (around 9 broods) compared to NE Galicia (around 3 broods). Moreover, the fact that 2011 was not an anomalously cold year in terms of SST suggests the absence of a persistent coastal front. Cold fronts are associated with higher primary productivity, potentially serving as indicators of increased food availability and supporting continuous reproductive investment throughout the year (Cruz et al., 2022). However, the relationship between SST and breeding/recruitment is complex. A recent study by Román et al. (2022) found that SST plays a significant role as an environmental driver, accounting for half of the variability in the proportion of breeding individuals in southern locations, while SST-breeding individuals goodness-of-fit declined sharply in northern regions.

Given the complexity of environmental factors influencing recruitment, the study aimed to investigate whether wave height plays a role in this specific region or under varying conditions, contributing to a deeper understanding of recruitment variability. Previous research in this area is limited, but findings have shown that increased energy levels lead to greater coverage and abundance of *P. pollicipes* (Basque Country, N Spain) (Borja et al., 2006), while no correlation between wave height and recruitment was observed in Asturias. In our study, the lack of correlation between mean significant wave heights in the months leading up to recruitment sampling aligns with the findings of Pavón (2003). This suggests that wave height in this region is not a key factor influencing recruitment success for this species. Other physical processes, such as internal tidal motions, nearshore surface bores, water column stratification, and local winds that generate trapped waves, may play a more significant role in the onshore transport of larvae (Pineda, 2000).

Growth

Juveniles of *P. pollicipes* at Ubiarco exhibited significantly faster growth (0.72 mm RC month^{-1}) compared to pre-adults (0.43 mm RC month^{-1}) and adults (0.36 mm RC month^{-1}). This distinctive growth rate of juveniles is more evident from spring to summer (March to August), coinciding with rising temperatures from 13 °C to 20.5 °C (Fig. 5). Juveniles reached a significant growth peak of 1.32 mm RC month^{-1} in early spring, while adults showed a relatively stable growth rate, with a non-significant relative maximum of 0.44 mm RC month^{-1} in late spring and summer.

In Portugal, similar patterns in growth differences between juveniles and adults, as well as seasonal variations, were observed by Cruz (1993) (juveniles: 0.17–0.66 mm RC month^{-1}; adults: 0.08–0.48 mm RC month^{-1}) and by Cruz (2000), Cruz et al. (2010), Jacinto et al. (2015), Fernandes et al. (2021) and Cruz et al. (2022) (juveniles: 0.18–5.20 mm month^{-1}; adults: 0.11–0.47 mm RC month^{-1}). These findings support the hypothesis proposed by Lewis and Chia (1981), which suggested that *P. polymerus* juveniles have greater feeding efficiency than adults due to their tendency to beat their cirri into the water flow, as opposed to holding them out passively like adults. Growth estimate studies based on maturation classes are unavailable in northern Spain for comparison. The only growth estimates reported by Sestelo et al. (2007) for large individuals in N Spain (Galicia) (0.34 mm RC month^{-1}) is consistent with this study, although it must be noted that Sestelo et al. (2007) estimated growth using size-structure data.

On average, juvenile barnacles in SW Portugal grew at a rate of 1.3 mm RC month^{-1} (Cruz et al., 2010), which is significantly faster than the growth observed in the present study (0.72 mm RC month^{-1}). Most growth estimates in SW Portugal also reported faster growth rates compared to those observed at Ubiarco (Cruz et al., 2022). This difference was expected due to the higher temperatures in SW Portugal compared to Ubiarco during the study period. Crisp and Bourget (1985) demonstrated that barnacle growth increases with rising temperatures. The relatively warmer conditions and extended summers in SW Portugal (Cruz et al., 2022) contributed to faster juvenile growth, as also observed by Sanford and Menge (2001) in acorn barnacles. For adults, however, the impact of summer temperatures on growth is less pronounced.

Sanford and Menge (2001) suggested that acorn barnacles grow faster on highly wave-exposed coasts and at lower tidal levels, where they generally experience stronger flows with a high delivery of suspended particles available for feeding (Sanford et al., 1994; Bustamante et al., 1995; Leonard et al., 1998), and longer submergence times providing more feeding opportunities (Barnes, 1996; Barnes and Reese, 1960). These conditions also reduce periods of aerial exposure and thermal stress (Sanford and Menge, 2001). Thus, the higher growth rates observed in SW Portugal compared to our study may also be attributed to a more favorable combination of physical and biological factors. Although both studies were conducted at the mid/low intertidal level on exposed coasts, significant regional/local differences in submergence times and wave heights, which could affect growth rates, are plausible.

P. pollicipes reaches maturity at an RC size of 12.5 mm (Cruz and Araújo, 1999). Based on our growth rate estimates for juveniles and pre-adults at Ubiarco, *P. pollicipes* would likely reach maturity approximately 1.5 years after settlement. This suggests that mature individuals observed in summer 2001 may have settled in the autumn/winter of 2000. Additionally, the current minimum catch size in Cantabria (RC size of 18 mm) (BOC, 2023) might be reached approximately 2.5 years after settlement. It is noteworthy that this catch size is smaller than the estimates provided by Bidegain et al. (2015) in Cantabria (RC size of 23 mm) and Sestelo and Roca-Pardiñas (2011) in Galicia (RC size of 21.5 mm).

This study provides the first insights into the growth of *P. pollicipes* in northern Spain and enhances understanding of regional recruitment patterns. The findings here may help guide management recommendations within existing regulations. In Cantabria, seasonal closures outlined by regional regulations (BOC, 2023) address overexploitation concerns (Bidegain et al., 2015) by implementing a May-to-October closure with a rotational zonal approach, except in permanently protected areas. However, this seasonal rotation may not sufficiently support sustainable management, as it does not fully account for the main recruitment season (autumn) or the growth period required to reach harvestable size. Aligning seasonal closures with peak recruitment or extending them to 2–2.5 year fishery moratoriums could further support population recovery and enhance zonal fishery yields. In the same direction, Geiger et al. (2024) recently suggested two-year harvest bans to improve fishery sustainability. Enhanced enforcement of minimum legal size regulations and monitoring of shellfish catches are essential to prevent overexploitation, along with stronger measures against illegal fishing (Geiger et al., 2022).

To monitor and assess stocks of *P. pollicipes* populations, annual surveys evaluating recruitment, population size structure, and biomass could help gauge fishing pressure and stock levels across zones. This information would support evaluating the effectiveness of management plans and guide necessary adjustments that are currently not feasible without such a monitoring program.

The limitations of this study include the lack of spatial replication, as data were collected from a single location. Although valuable insights were obtained, recruitment and growth patterns of *P. pollicipes* may vary across different spatial scales, including smaller, site-specific variations within the same region. Previous studies suggest that environmental conditions, such as wave exposure, temperature fluctuations, and food availability, can vary even over short distances, potentially influencing local recruitment dynamics (Bidegain et al., 2015; Cruz et al., 2010; Fernandes et al., 2021; Sanford and Menge, 2001). Therefore, to gain a more comprehensive understanding of *P. pollicipes* population dynamics, future research would benefit from spatial replication across multiple sites within the region. This approach would allow for an assessment of whether our findings hold across locations, thereby strengthening the management recommendations based on broader spatial patterns. Furthermore, additional research efforts to understand temporal variability both interannual and intra-annual are essential. For instance, biweekly sampling during the recruitment season could more precisely determine the exact timing and intensity of peak recruitment. Studies focused on larval stages, mortality-survival rates, and environmental factors such as wind, bathymetry, chlorophyll, and population density are also recommended.

CRediT authorship contribution statement

Gorka Bidegain: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **María Belén Gutiérrez-Cobo:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Xabier Guinda:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization. **Ana Silió:** Writing – review & editing, Formal analysis, Data curation. **Araceli Puente:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization. **José Antonio Juanes:** Supervision, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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