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M. CanessaM. CANESSA 0000-0001-5371-8452, G. BavestrelloG. BAVESTRELLO, M. BOM. BO, F. BettiF. BETTI, L. GaggeroL. GAGGERO & R. Cattaneo-ViettiR. CATTANEO-VIETTI

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The influence of the rock mineralogy on population density of *Chthamalus* (Crustacea: Cirripedia) in the Ligurian Sea (NW Mediterranean Sea)

M. CANESSA ^{1*}, G. BAVESTRELLO^{1,2}, M. BO^{1,2}, F. BETTI¹, L. GAGGERO¹, & R. CATTANEO-VIETTI^{1,2}

¹Dipartimento di Scienze della Terra, dell'Ambiente e della Vita, Università di Genova, Genova, Italy, and ²CONISMA, Consorzio Interuniversitario di Scienze del Mare, Roma, Italy

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Abstract

Settlement, recruitment and survival of sessile marine species are driven by many biotic and abiotic factors. Among them, substrate mineral composition is generally a neglected topic, despite it proved to be a relevant contributing variable in driving the structure of benthic communities. Thanks to their ecology, *Chthamalus* species are a good proxy to test the role of substrate in affecting settlement and final population density on exposed rocky shores. Differences in the number of individuals were analysed in eight localities along the Eastern Ligurian Riviera (north-western Mediterranean Sea), from Portovenere to Manara Cape. In this sector of the Ligurian littoral, the coast is constituted by different rocks characterised by variable concentrations of calcite, silicates and quartz. This situation constitutes an ideal setting to evaluate the influence of mineral composition of the rocks in structuring the epilithic macrobiota communities in energetic splash zones and under similar physical pressures. Rocks rich in calcites turned out to be more suitable for *Chthamalus* species than substrates containing high amounts of silicates, and of quartz in particular. Additionally, also the grain size of the main mineral component of the rocks, determining in turn the surface roughness seemed to influence barnacle densities, with a significant preference for finer-grained substrates.

Keywords: Chthamalus, mineralogy, calcite, quartz, Mediterranean Sea

Introduction

Changes and stability in spatial distribution, settlement, recruitment and density of marine sessile species are driven by a plethora of abiotic variables, which, in turn, interact with the biological ones (Dayton 1971; Keough & Downes 1982; Underwood et al. 1983, 1984; Connell 1985; Menge & Sutherland 1987; Barry & Dayton 1991; Pawlik 1992; Raffaelli & Hawkins 1996; Smith & Witman 1999; Benedetti-Cecchi et al. 2000; Sousa 2001; Menge & Branch 2001; Asnaghi et al. 2015). All these variables operate synergistically with different intensities, on different space and time scales. Among the main abiotic factors, that can favour or inhibit species settlement, the mineralogy of the substrate has been only sporadically considered. On the other hand, it has been observed that free larvae of sessile organisms show an unsuspected ability to recognize and select different rocky substrates, with important repercussions on the community structure (Cerrano et al. 1999; Bavestrello et al. 2000, 2018; Cattaneo-Vietti et al. 2002; Guidetti et al. 2004; Calcinai et al. 2008).

In order to evaluate the influence of substrate mineralogy on larval settlement, the upper rocky shore is among the most suitable habitats, thanks to the fact that the influence of the microbial film is often low or absent (Bertness et al. 2001; Maggi et al. 2017), so that the interaction between larvae and rocks is more direct.

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^{*}Correspondence: M. Canessa, Dipartimento di Scienze della Terra, dell'Ambiente e della Vita, Università di Genova, Corso Europa, 26, Genova 16132, Italy. Tel: +39 3425601343. Fax: +39 0103538220. Email: marti.canessa@gmail.com

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Barnacles are considered key species of these upper rocky shore communities; therefore, they represent a good model thanks to their high recruitment, mid-long larval dispersive phase (11-30 days) and a lifespan of 2-3 years (Southward & Crisp 1956). Studies about their biology and ecology (Moore & Kitching 1939; Southward 1967, 1976, 1991; Levinton 1982; Underwood et al. 1983, 1984; Caffey 1985; Moore & Seed 1985; Benedetti-Cecchi et al. 2000; Bertness et al. 2001; Underwood & Keough 2001), dispersal (Crisp & Southward 1958; Grosberg 1982), settlement (Larmon & Gabbott 1975; Crisp et al. 1981; Hawkins & Hartnoll 1982, 1983; Gaines et al. 1985; Gaines & Roughgarden 1985), recruitment and gregariousness (Lewis 1964; Underwood & Fairweather 1989; Sutherland 1990; Lively et al. 1993; Southward et al. 1995; O'Riordan et al. 2004 and references therein; Jenkins et al. 2000; Jenkins 2005), as well as competition and predation processes (Dungan 1985; Lively 1986a, 1986b; Lively & Raimondi 1987; Fairweather 1988; Raimondi 1988a, 1988b; Wahl 2009) have been widely explored topics in marine coastal ecology.

Some substrate features, such as exposure, slope, surface heterogeneities and roughness have been invoked as causal factors influencing barnacle aggregation at small spatial scales (Knight-Jones 1953; Crisp & Barnes 1954; Crisp 1974, 1976; Denley & Underwood 1979; Paine & Levin 1981; Wethey 1986; Raimondi 1990; Lively et al. 1993; Bourget et al. 1994; Hills & Thomason 1996, 1998; Lemire & Bourget 1996; Lapointe & Bourget 1999; Davis 2009). For example, in energetic splash zones, barnacles survive better in crevices, avoiding adjacent horizontal surfaces, where the mechanical stresses and the risk of desiccation are greater (Foster 1971; Bergeron & Bourget 1986; Chabot & Bourget 1988; Menge & Branch 2001). Additionally, the presence of a biofilm (in terms of thickness, composition and age) is known to be an important variable in influencing larval settlement, although with contradictory data (Barnes 1956; Holmström et al. 1992; Walters & Wethey 1996; Wieczorek et al. 1996; Thompson et al. 1998; Wieczorek & Todd 1998; Olivier et al. 2000; Faimali et al. 2004; Hadfield 2011). Other variables affecting barnacle settling are related strictly to lithology of the substratum and include the mineral composition of the rock and its thermal capacity, colour and surface energy (Lewis 1977; Yule & Walker 1984; Wethey 1986; Le Tourneux & Bourget 1988; Holmes et al. 1997; Berntsson et al. 2000, 2004; Herbert & Hawkins 2006).

The barnacles *Chthamalus stellatus* (Poli, 1791) and *Chthamalus montagui* Southward, 1976 are the commonest sessile invertebrates living in the supra- and

midlittoral rocky shores of the NW Mediterranean Sea, forming characteristic belts which can reach densities of up to 30,000 individuals m^{-2} (Pannacciulli & Relini 2000) (Figure 1(a-c)).

In the Ligurian Sea, the vertical distributions of these two species overlap; nevertheless, *C. stellatus* is generally more abundant in the upper level. A third species, *Euraphia depressa* (Poli, 1791), also occurs, generally living higher up in crevices and shades, but it is rarely present in the main barnacle zone on exposed shores (Pannacciulli & Relini 2000).

Chthamalus spp. appear good models to assess the role of substrata mineral composition in determining settlement and recruitment of sessile invertebrates. Moreover, Bavestrello et al. (2018) have observed that the density of *C. stellatus* was very different on two neighbouring ophiolitic outcrops dip into the sea under similar environmental conditions but showing different silica concentrations.

The aim of this study was to test the effect of rock mineral composition on the density of the adult *Chthamalus* at two levels of the splash zone, in some neighbouring localities of the Eastern Ligurian Sea, characterised by different mineral compositions of the rock substrata (Figure 2). Considering the strong differences in calcite, silicates and quartz concentrations present in the rocks of this littoral sector, the selected localities may be considered an ideal study area to evaluate the putative contribution of substrata mineral composition in influencing barnacle population and, from a more general point of view, the structure of the splash zone communities.

Material and methods

Geological context

The characteristics of the *Chthamalus* belt in terms of population density were studied by photographic samplings during summer 2017 in eight selected localities, along 35 km of coastline (eastern Ligurian Riviera) from Portovenere, near the Gulf of La Spezia, to Manara Cape (Sestri Levante) (Table I; Figure 2).

These localities were selected according to the mineral composition of the substrate, inferred from the regional geological map (Carta Geologica d'Italia 2005).

Three localities (Portovenere Castle (Pc), Portovenere Byron Cave (Pbc) and Portovenere East (PE)) are characterized by limestones; the site Portovenere West (PW) shows a red jasper formation; Vernazza (Ve) presents a quartzitic substratum;



Figure 1. (a-c) Different close-ups of a dense *Chthamalus* belt along the upper splash zone of a rocky shore of the eastern Ligurian Riviera. (d) Specimens of *Chthamalus* sp. cut transversally to evidence lack of the carbonatic basal plate. Scale bars: a = 50 cm; b = 5 mm; c = 10 cm; d = 5 mm.

ophiolites outcrop occur at Bonassola (Bo) and Framura (Fr) (metagabbros and basalt, respectively); finally, a carbonatic marl outcrop is present at Manara Cape (Ma).

Petrographic analysis

The lithotypes of the different localities were sampled and investigated as thin sections under polarized light microscopy, and by Scanning Electron Microscopy coupled with Energy Dispersive X-ray Spectrometry (SEM-EDS).

The percentages of the major components $(SiO_2 and CaO)$ within the analysed rock substrates were quantified by Lithium Metaborate/Tetraborate Fusion followed by Inductively Coupled Plasma Mass Spectrometry (ICP/MS) at the ActLabs Laboratories (Ontario, Canada). Three blanks and five controls (three before the sample group and two after) were analysed per group of samples. Duplicates were fused and analysed every 15 samples. Instruments were recalibrated every 40 samples.

Thin sections were observed under a transmitted polarised light optical microscopy to measure crystal

diameters and mineral phase percentages by volume inside rock samples.

Sampling design and statistical analysis

To evaluate the barnacle density, at each locality, 10 photographs of 20×20 cm of the standard surface were taken along a horizontal transect at two levels (+1 m, upper splash zone and +0.2 m, lower splash zone) with the rocky coast showing comparable slope and wave-exposure.

In this way, a total of 160 photos were collected and analysed using the Software package ImageJ64®. The number of *Chthamalus* shells was recorded and related to 1 m² (Table I).

Considering that, along the Ligurian coast, *C. stellatus* and *C. montagui* are widely mixed (Pannacciulli & Relini 2000) the two species were considered together in the analysed images.

Two-way Analysis of Variance (ANOVA) was carried out to test for differences in average barnacle density related to 20×20 cm surface between localities (data distributed homogenously with n = 160, Shapiro-Wilk W p = 1.542e-13). Tested factors ("Locality" and "Height" of the splash zone) were fixed and orthogonal.



Figure 2. (a) Sampling area along the Ligurian coast. (b) Lithological map, redrawn after the Regional Geological Map, 1:50.000 of the eastern Ligurian Riviera with the eight sampled localities. Ma: Manara Cape; Fr: Framura; Bo: Bonassola; Ve: Vernazza; PE: Portovenere E; PW: Portovenere W; Pbc: Portovenere Byron Cave; Pc: Portovenere Castle.

| | | Lithotype | Coord: (WGS) | inates 84) | Average density (ind m^{-2}) ± SE | | |
|-----|------------------------|----------------------------|-----------------|---------------|--------------------------------------|-------------------|--|
| | Localities | | Lat | Long | Upper splash zone | Lower splash zone | |
| Pc | Portovenere Castle | Limestone | 44° 2′53.47"N | 9°49′55.57"E | $20,275 \pm 1980$ | 6,605 ± 1,022 | |
| Pbc | Portovenere Byron Cave | Limestone | 44° 2′56.48"N | 9°49′57.70"E | 28,317 ± 5740 | 10,295 ± 1,942 | |
| PE | Portovenere East | Limestone | 44° 3′24.36"N | 9°49′25.30"E | 34,670 ± 1920 | 4,445 ± 632 | |
| PW | Portovenere West | Jasper | 44° 3′48.85"N | 9°48′27.88"E | 3,780 ± 582 | $1,955 \pm 461$ | |
| Ve | Vernazza | Quartzites | 44° 8′8.90"N | 9°40′57.07"E | 6,150 ± 1166 | $4,572 \pm 740$ | |
| Bo | Bonassola | Ophiolites (Metagabbro) | 44°10′48.34"N | 9°35′3.72"E | 2,320 ± 381 | 4,390 ± 1,280 | |
| Fr | Framura | Ophiolites (Basalt) | 44°11′59.64"N | 9°33′20.50"E | 16,560 ± 2378 | 8,612 ± 2,504 | |
| Ma | Manara Cape | Marl | 44°15′22.78"N | 9°24′41.94"E | 19,332 ± 3454 | $1,017 \pm 2,938$ | |

Table I. Lithology and barnacle density in the upper and lower splash zone in the explored localities along the Eastern Ligurian coastline.



Figure 3. Relationships between average barnacle densities and CaO wt% (a) and SiO₂ wt% (b) percentage concentrations, in the upper (solid spots) and in the lower (open circles) splash zones.

Tukey's test was used to ascertain the significance in pairwise comparisons for each locality-height paired variable. Correlations between average density and CaO and SiO₂ percent concentrations and diameter of crystals of the main component in rocky samples were investigated by regression plots (Figures 3 and 5).

Results

Along the western Mediterranean coastline, from Portovenere (La Spezia) to Manara Cape (Sestri Levante) in the eastern Ligurian Riviera, *Chthamalus* barnacles constitute belts on rocky shores approximately between sea level and 3 m above (Figure 1 (a-c)), reaching high-density values. No evidences of strong predation by whelks or blennies or bulldozing by limpets were observed in the sites considered.

During our study, the density in the upper splash zone ranged from 2,320 \pm 381 individuals m⁻² at Bonassola to 34,670 \pm 1,920 individuals m⁻² at Portovenere East. The lowest values were recorded in the three central-considered localities (Portovenere West, Vernazza and Bonassola) (Table I).

In the lower splash zone, densities were always smaller in all localities, excluding Bonassola: the maximum density $(10,295 \pm 1,942 \text{ individuals m}^{-2})$ was observed at Portovenere Byron Cave and

the minimum one at Manara Cape $(1,017 \pm 293)$ individuals m⁻²).

According to ANOVA analysis and pairwise tests, there were significant differences between localities and levels of the splash zone for the *Chthamalus* densities (Table II).

The interaction between the two factors was also significant in most cases for the high splash zone (Table II): three localities (Portovenere West, Vernazza and Bonassola, characterised by jasper, quartzite and metagabbros, respectively), showing the lowest densities, were separated from all others (limestone and basalt substrates) (Figure 4).

In the upper splash zone, barnacle densities were significantly higher in relation to the CaO percent concentration ($R^2 = 0.87$, Figure 3(a)), while they decreased significantly at high SiO₂ concentrations ($R^2 = 0.78$, Figure 3(b)). No significant relationship was found for the lower splash zone.

From a lithological point of view (Tables I and III; Figure 4), the limestones of Portovenere Castle, Portovenere Byron Cave and Portovenere East hosted the highest average barnacle densities, ranging from 20,000 to 34,650 individuals m^{-2} . Here, the mineral phase was totally represented by calcite. The density values remained high (19,332 ± 3,454 individuals m^{-2}) also on the marl of Manara Cape, which showed high percent of calcite (80% of rock

Table II. Two-Way ANOVA analysis and pairwise tests for barnacle density, in upper (H) and lower (L) splash zones. Bold characters indicate significative values. Only significative values are reported for the LocalityXHeight interaction. Acronomies referred to the toponomies reported in Table I.

| | | SSS | | df | Ν | IS | F | p (same) |
|-----------|------------------|------------------|----------|-----------|----------|----------|-----------|----------|
| Locality: | | 1.02E+07 | | 7 | 1.46 | E+06 | 17.71 | 8.10E-17 |
| Height: | | 6.47E+06 | | 1 | 6.47 | 6.47E+06 | | 2.86E-15 |
| Interact | tion: | 6.20E+06 | | 7 | 885 | 885876 | | 7.64E-11 |
| Within: | | 1.19E+07 | | 144 | 82516.2 | | | |
| Total: | | 3.48E+07 | | 159 | | | | |
| Tukey's | pairwise testFac | ctor: "Locality" | | | | | | |
| | Pbc | Pc | PW | PE | Ve | Во | Fr | Ma |
| Pbc | | 0.1707 | 1 | 6.98E-10 | 2.11E-07 | 2.21E-09 | 0.06867 | 0.474 |
| Pc | 0.1707 | | 0.133 | 0.0001926 | 0.01162 | 0.000462 | 0.9999 | 0.9992 |
| PW | 1 | 0.133 | | 3.83E-10 | 0.9563 | 1 | 0.0008721 | 1.66E-05 |
| PE | 6.98E-10 | 0.0002 | 3.83E-10 | | 1.21E-07 | 1.22E-09 | 0.05088 | 0.4022 |
| Ve | 2.11E-07 | 0.0116 | 1.21E-07 | 0.9563 | | 0.9871 | 0.03707 | 0.001585 |
| Bo | 2.21E-09 | 0.0005 | 1.22E-09 | 1 | 0.9871 | | 0.001971 | 4.31E-05 |
| Fr | 0.06867 | 0.9999 | 0.05088 | 0.0008721 | 0.03707 | 0.001971 | | 0.9813 |
| Ma | 0.474 | 0.9992 | 0.4022 | 1.66E-05 | 0.001585 | 4.31E-05 | 0.9813 | |
| Interact | ion | | р | | | | | |
| Pbc-H | | Pbc-L | 1.15E-05 | | | | | |
| Pbc-H | | PW-H | 3.33E-10 | | | | | |
| Pbc-H | | Ve-H | 1.80E-08 | | | | | |
| Pbc-H | | Bo-H | 2.63E-11 | | | | | |
| Pbc-H | | Fr-H | 0.02938 | | | | | |
| Pc-H | | Pc-L | 0.00371 | | | | | |
| Pc-H | | PW-H | 0.0001 | | | | | |
| Pc-H | | PE-H | 0.00156 | | | | | |
| Pc-H | | Ve-H | 0.00216 | | | | | |
| Pc-H | | Bo-H | 1.27E-05 | | | | | |
| PW-H | | PE-H | 4.20E-14 | | | | | |
| PW-H | | Fr-H | 0.01015 | | | | | |
| PW-H | | Ma-H | 0.00036 | | | | | |
| PE-H | | PE-L | 4.96E-14 | | | | | |
| PE-H | | Ve-H | 3.20E-13 | | | | | |
| PE-H | | Bo-H | 3.02E-14 | | | | | |
| PE-H | | Fr-H | 1.01E-05 | | | | | |
| PE-H | | Ma-H | 0.00047 | | | | | |
| Ve-H | | Ma-H | 0.0065 | | | | | |
| Bo-H | | Fr-H | 0.00188 | | | | | |
| Во-Н | | Ma-H | 4.91E-05 | | | | | |

volume). Different results arose when studying the population densities on substrates particularly rich in silicates and quartz. The jasper of Portovenere West and the quartzite of Vernazza, both with a dominant quartz fraction ((95% and 80% of their volume, respectively, with negligible presence of calcite (5%)), showed the lowest values of barnacle density.

Regarding the ophiolitic rocks, on the Bonassola metagabbro, characterised by plagioclase and clinopyroxene (60% and 40% vol, respectively), *Chthamalus* density was very low, while on the Framura basalt, containing a high fraction of amorphous altered glass (70%) and plagioclase (25%), the density was higher, despite the complete lack of calcite (Table III).

Although the CaO concentration, in particular calcite, appeared as an important driver in determining the barnacle density (Figures 3 and 4), also the crystal size of the most abundant mineral phase of the rocks showed a strong inverse correlation ($R^2 = 0.9$): the highest density values were found on the Portovenere limestone, which has the smallest calcite grain size. This was particularly evident when excluding from the regression the localities characterised by rocks with a very high quartz concentration (Portovenere West and Vernazza), where densities were very low, despite a very small grain size (Figure 5).



Figure 4. Average density \pm SE of the barnacles in the upper (continuous line) and in the lower (dotted line) splash zones. Stacked bars represent the mineral phase composition of each studied rock. Calcite, yellow bars; quartz, blue bars; silicates, green bars; amorphous glass, grey bar. Localities are disposed according to a decreasing concentration of calcite in the rocks.



Figure 5. Relationship between barnacle densities in upper (solid spots) and lower (open circles) splash zones and crystal size of the main mineral occurring in each rock. Please note that in the two rocks with a very high quartz concentration (Portovenere W and Vernazza), barnacle density is very low (in the graph, these two points are represented by squares). Data from Framura are not considered due to the high presence of amorphous altered glass, which has no measurable crystal size.

Discussion

Although a plethora of ecological and biological variables is known to affect barnacle's settling and survival and, consequently, their population structure, our data seem to indicate that the density of the common Mediterranean barnacles, *Chthamalus* spp., in the Eastern Ligurian Sea, is also driven by lithological and mineralogical

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| | | Phase composition [volume%] | Crystal size (mm) | | | | | | |
|----------------------|-------------------------------|-----------------------------------|-------------------|-----------------|-------------------|----------------------|-------------------|-----------------|--|
| | SiO ₂ CaO [wt%] | | | | Silicates | | | | |
| Locality (Lithotype) | | | Calcite (Cc) | Quartz (Qtz) | Muscovite (Ms) | Plagioclase (Plg) | Pyroxene (Cpx) | Olivine (Ol) | |
| Portovenere Castle | 0.01 SiO ₂ | 99 Cc | 0.04-0.08 | | | | | | |
| (Limestone) | 37.04 CaO | | | | | | | | |
| Portovenere Byron | 15.08 SiO ₂ | 70 Cf | 0.01 | | | | | | |
| Cave (Limestone) | 36.45 CaO | 30 Cc | 0.5 | | | | | | |
| Portovenere East | 6.41 SiO ₂ | 100 Cc | 0.01-0.03 | | | | | | |
| (Limestone) | 48.93 CaO | | | | | | | | |
| Portovenere West | 78.26 SiO ₂ | 95 Qtz | | 0.001 | | | | | |
| (Jasper) | 10.82 CaO | 5 Cc | 0.6 | | | | | | |
| Vernazza (Quartzite) | 59.57 SiO ₂ | 80 Qtz | | 0.02-0.06 | | | | | |
| | 7.68 CaO | 15 Ms | | | 0.1 | | | | |
| | | 5 Cc | 0.2 | | | | | | |
| Bonassola | 51.26 SiO ₂ | 60 Plg | | | | 0.04-0.5 | | | |
| (Metagabbro) | 7.48 CaO | 40 Cpx | | | | | 3 | | |
| Framura (Basalt) | 57.15 SiO ₂ | 70 Altered glass | | | | | | | |
| | 3.45 CaO | 25 Plg | | | | 0.2-0.5 | | | |
| | | 5 Ol | | | | | | 0.3 | |
| Manara Cape (Marl) | 55.59 SiO ₂ | 80 Cc | 0.01-0.3 | | | | | | |
| | 22.66 CaO | 13 Qtz | | 0.01-0.25 | | | | | |
| | | 5 Plg | | | | 0.3 | | | |
| | | 2 Ms | | | 0.1 - 0.2 | | | | |

Table III. Mineralogical description of the sampled lithotypes, with weight percentages of SiO_2 and CaO content, their percentage content in volume and dimensions of crystals.

characteristics of the rocky substrates. These features, in fact, explain the quantitative differences between the investigated localities, characterised by an average mutual distance not exceeding 5 km, with similar shore slope and wave exposure.

The density values appeared independent of the seawater littoral quality: in fact, the ecological index EQR-CARLIT, based on macrophyte assemblages, and used to assess the status of coastal waters, evidenced a progressive increase in the ES (Ecological Status), moving away from the Gulf of La Spezia (the largest urbanised zone of the area) towards Sestri Levante (Asnaghi et al. 2009) (Figure 2).

Previous studies had already evidenced the role of rock features in determining the Chthamalus belt density and distribution. Some friable rocks, such as chalk and sandstones, may be more unsuitable compared to harder granites. In fact, in the English Channel, the geographical distribution of C. montagui appears to be driven by the presence of chalk along the coastline; on this substratum, although the recruitment is high, the barnacle survival rate is relatively low. In this way, chalks represent a potential barrier to the eastward range extension of this barnacle (Herbert & Hawkins 2006). Also, the pattern of distribution of C. anisopoma in California is related to a greater post-settlement mortality on

basalts than on granites, probably due to different thermal capacities of each rock (Raimondi 1988a).

In investigated localities of the Ligurian coast, barnacle densities were maximal in the upper splash zones characterised by substrates particularly rich in calcite, with poor levels of silicates and the absence of quartz. This mineral seemed to inhibit the development of the populations, as already documented for other species and habitats in the Mediterranean Sea (Bavestrello et al. 2000, 2003, 2018; Guidetti et al. 2004; Cattaneo-Vietti et al. 2004). The presence of quartz has been considered one of the most important factors in driving larval settling and ultimate species composition on hard substrata. Benthic assemblages set on quartz-rich rocks, in fact, were less diverse and showed a simpler physiognomy, indicating the difficulty of reaching a "mature" condition in presence of quartz, which acts as an inhibiting factor (Bavestrello et al. 2000). Cerrano et al. (1999) suggested that crystalline quartz has an evident negative effect on animals that colonise sands, probably due both to the oxidant properties of the crystal surface, generating silicon-based radicals, and to the formation of .OH radicals in the surrounding aqueous environment (Marasas & Harington 1960; Langer & Nolan 1986; Shi et al. 1988; Vallyathan et al. 1988).

A positive role of calcite, favouring greater Chthamalus settling, is evident. It was demonstrated that the calcium required for the shell growth in Semibalanus balanoides (L. 1767) is supplied by seawater. In fact, during the emersion time, the shell calcification process soon stops (Crisp & Bourget 1985). The Ligurian Sea has a very low tidal amplitude (20-30 cm) and, in this condition, the Chthamalus populations living in the upper splash zone, at least in summertime, are seldom moistened. Consequently, it can be hypothesised that, in these conditions, the calcium supply derives from alternative sources such as the underlying rock. In these barnacles, in fact, the continuous process of shell formation (Bourget 1987) (Figure 1(d)) may be supported through the substrate solubilisation favoured by the lack of a basal carbonatic plate. Also, the limpets ingest large amounts of calcium carbonate that seemingly derive directly from the rock to support the shell growth (Andrews & Williams 2000).

Moreover, the crystal size, in turn determining the surface roughness of the rocks, also provides a good key of interpretation: rocks with small crystal diameter seem to be more suitable for settling. The very low densities recorded on the metagabbro of Bonassola, which shows coarse silicate (clinopyroxene) crystals, support this hypothesis (Table III).

The rock roughness has already been considered as a relevant factor involved in barnacle settling. Amphibalanus improvisus (Darwin, 1854), for example, prefers relatively smooth surfaces (Berntsson et al. 2000, 2004) and this could be due to the antennular adhesive disc, which needs a specific level of roughness to attach firmly (Nott & Foster 1969; Yule & Walker 1984; Berntsson et al. 2000). On the other hand, other species are completely unaffected by roughness: the settlement of cyprids of S. balanoides was tested for 15 different rock types, resulting to be independent of any potential effect of surface roughness or colour cues (Holmes et al. 1997), while for A. amphitrite (= Balanus amphitrite) a preference for red and blue acrylic sheets was demonstrated (Satheesh & Wesley 2010).

Similar results were obtained for the Australian species *Tesseropora rosea* (Krauss, 1848), whose settlement was found to be largely independent of differences in the rocky substrate (Caffey 1982). In these cases, however, the ability to settle on unsuitable substrates could be related to the capacity of the barnacles to quickly produce a calcareous base to isolate themselves from the substrate (Okano et al. 1996; Burden et al. 2012), which is lacking in the studied *Chthamalus*.

Along the Ligurian coast, the barnacle densities in the lower splash zones appeared generally less crowded although the frequent wave washout can lead to a major calcium supply from seawater and minimise the quartz effect. This condition could be related with a major competition for substrate, considering also the presence of a structured biofilm, which could mediate the interaction between barnacle cyprids and rock surface.

In conclusion, our results suggest that the mineralogical features of the substrate may play an important role in structuring supralittoral benthic communities. Calcite-rich rocks emerge as more suitable substrates for *Chthamalus* settlement than compounds rich in silica and quartz. Moreover, the lack of a carbonatic basal plate in this genus could allow a calcium uptake even in a habitat rarely affected by waves, such as the upper splash zone. Therefore, our results suggest a crucial role of the coastal mineralogy in influencing the density of *Chthamalus* in Mediterranean rocky habitats when the biofilm coverage is lacking.

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Disclosure statement

No potential conflict of interest was reported by the authors.

ORCID

M. Canessa D http://orcid.org/0000-0001-5371-8452

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