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Living coralligenous as geo-historical structure built by coralline algae

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The most important reef of the Mediterranean is the Coralligène (Coralligenous = C), including several types of calcareous algal-invertebrate build-ups growing in normal open marine conditions. We analyzed and compared two C samples from the Ligurian Sea developed in different environmental settings: 1) off Portofino on a rocky cliff, at a depth of about 40 m and 2) in front of Bogliasco, on a sub-horizontal substrate at a depth of 10 m. The maximum AMS radiocarbon dating provided an older age for Bogliasco (about 5 ka BP) than for Portofino (about 3.6 ka BP), and the mean accumulation rate of the Portofino build-up (about 80 $\mu\text{m y}^{-1}$) was found to be higher than the one in Bogliasco (about 65 $\mu\text{m y}^{-1}$). The different sides of each build-up showed a remarkable heterogeneity in the dominant cover by living organisms, and the comparison between the two build-ups highlighted an evident diversity in their taxonomic composition and structure, although crustose coralline algae (CCA) are the dominant framework builder and major autogenic ecosystem engineers at both localities, in the present as in the past millennia. Other major components of the structure are bryozoans and serpulids, and an important role is played by sediment filling. In Bogliasco, extreme climate events and major peaks of fine matrix and terrigenous grains are observed, lithologically related to the drainage basin of the Poggio creek and associated with charophyte occurrence and reduced CCA abundance. The occurrence of the rare *Sporolithon ptychoides* was observed both in Portofino at about 750 BCE and in Bogliasco. These *Sporolithon* phases are likely related to warm and humid spells punctuating the Holocene climate fluctuations in the Ligurian Sea. Because coralline algae are confirmed to be the most important habitat engineer of the Mediterranean reefs, they deserve more attention in the framework of any monitoring initiative aimed at C management and conservation.

KEYWORDS

coralligenous, algal reef, coralline algae, *Sporolithon*, Ligurian Sea, extreme climate events, Holocene

1 Introduction

Coralline algae are autogenic habitat engineers responsible for the formation of intertidal algal rims, subtidal rhodoliths, and algal reefs known in the Mediterranean as Coralligène (Coralligenous = C). Coralligenous is known in the Mediterranean as a hard biogenic substrate mainly produced by the superposition of several generations of calcareous red algae, living in dim light conditions. In the framework of marine benthic bionomics, C is identified as the ecological climax stage for the Mediterranean circalittoral zone (Pérès, 1982), although further studies recognized also C in dim-light infralittoral settings (Ballesteros, 2006; Bracchi et al., 2016).

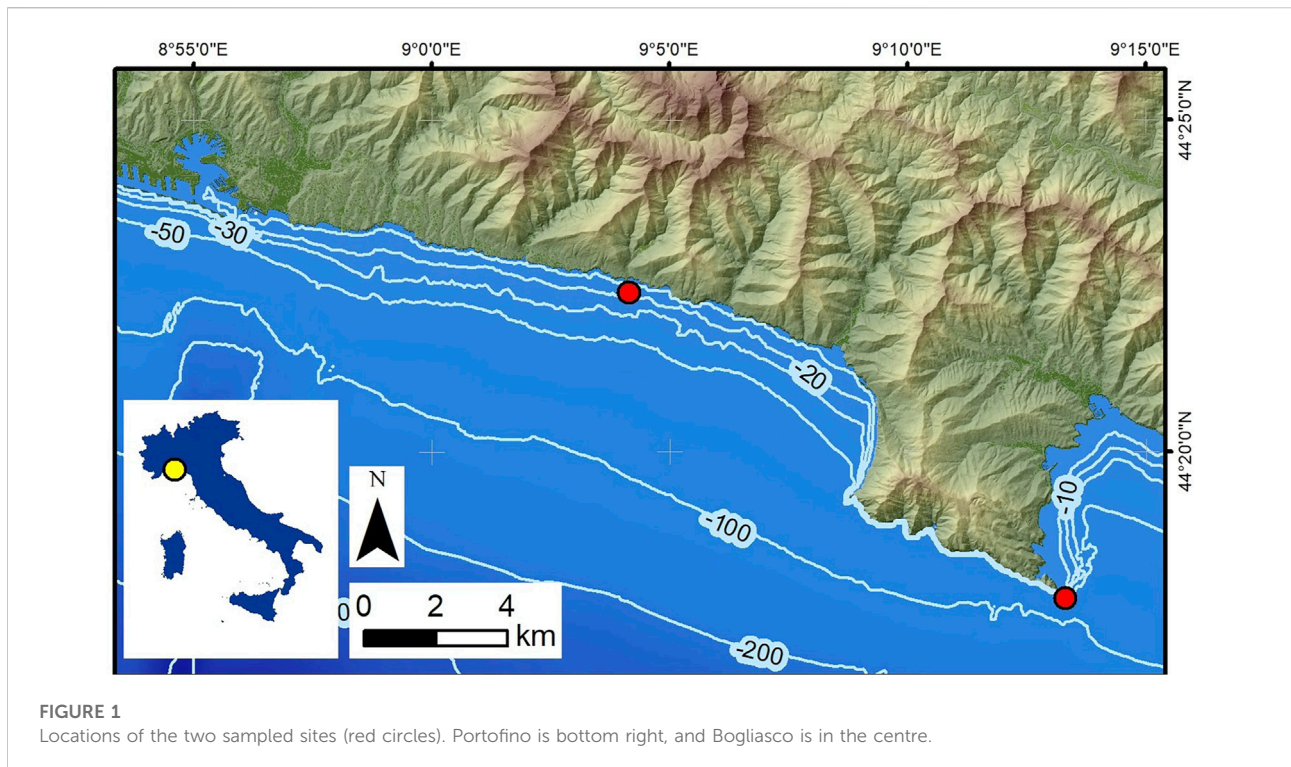
The C bio-constructions grew at a water depth of 20–140 m (Laborel 1961, 1987) by *in situ* superposition of carbonate skeletal material, produced during the last Holocene sea level rise (Sartoretto et al., 1996). Coralligenous is a heterogeneous habitat (Sartoretto, 2017) and a prominent biogeological system of the Mediterranean seascape (Ballesteros, 2006; Casas-Guell et al., 2016; Bracchi et al., 2017; Pierdomenico et al., 2021), a unique hot spot of marine biodiversity (Laubier, 1966; Ballesteros, 2006; Di Iorio et al., 2021; Piazzini et al., 2021), a major carbonate factory and storage (Canals and Ballesteros, 1997; Cebrian et al., 2000; Marchese et al., 2020), and a target of EU environmental protection, due to the ecosystem services that it provides and its sensitivity to direct and indirect human impacts, including the ongoing climate change (among others: Balata et al., 2005; Martin and Gattuso, 2009; Piazzini et al., 2011; Gatti et al., 2015; Montefalcone et al., 2017; Costanzo et al., 2021).

C includes several types of open marine algal-invertebrate reefs, a few centimeters to several meters in thickness, which can be described in terms of benthic zonation, build-up morphology, type of basal substrate, style of development, and components (Pérès 1982; Laborel 1987; Bracchi et al., 2017; Bracchi et al., 2019). Several species of calcareous red algae Corallinophycidae (crustose coralline algae, CCA) and some calcareous Peyssonneliales are characteristic habitat-engineers (Laubier 1966; Pérès 1982; Ballesteros, 2006; Rosso and Sanfilippo 2009; Ponti et al., 2011; Boudouresque et al., 2016; De Jode et al., 2019) and the volumetrically most important fossil framework builders in C (Basso et al., 2007; Titschack et al., 2008; Bracchi et al., 2014, 2016, 2022). Other important builders are bryozoans, polychaetes, and cnidarians (Ballesteros 2006; Bellan-Santini et al., 2007; Corriero et al., 2019), and bryozoans producing large, long-lived, habitat-forming colonies may be primary builders (Cocito, 2004; Di Geronimo et al., 2002; Novosel et al., 2004; Rosso and Sanfilippo 2009). The coralligenous habitat has been defined as an eco-ethological crossroads and an assemblage of several communities rather than a unique community (Sartoretto, 2017), and several different associations and facies have been described under the term “coralligenous” (Ballesteros, 2006; Casas-Güell et al., 2016; Sartoretto, 2017; Corriero et al., 2019). The most obvious

and coarse distinction is between C developing on rocky walls and C developing from subhorizontal substrates (sedimentary or rocky) (Pérès 1982; Bracchi et al., 2017; Sartoretto, 2017; Piazzini et al., 2009; Piazzini et al., 2022). The interplay of biotic and abiotic factors (mainly light exposure, availability of trophic resources, substrate exposure, sedimentation rate, freshwater influence, and biotic interactions) controls the several facies of C, unevenly distributed along geographical and depth gradients (among others: Gili and Ros 1985; Sartoretto, 1994; Garrabou et al., 2002; Di Geronimo et al., 2001; Virgilio et al., 2006; Casellato and Stefanon, 2008; Ponti et al., 2011; Falace et al., 2015; Çinar et al., 2020).

Our knowledge about C accumulation rate and age, although very fragmentary (Sartoretto et al., 1996; Bertolino et al., 2017a; Sartoretto, 2017), suggests that present-day conspicuous algal build-ups required thousands of years to form, depending on favorable combinations of biologically mediated carbonate precipitation by algal engineers, persistence of compatible oceanographic conditions, and sedimentation rate, in turn controlled by the overarching geological setting. Radiocarbon dating has revealed that the accumulation rate of the C build-ups is very low (0.006–0.83 mm y⁻¹). It has been suggested that after 6,000 years BP, the accretion rate of deep C, below a depth of 60 m, could have been very low to nil, possibly because of the increasingly unfavorable environmental conditions during Holocene sea level rise (Sartoretto et al., 1996) or the human pressures which strongly affected the species living on the surface of the biogenic build-ups (Montefalcone et al., 2017; Zunino et al., 2019; Gómez-Gras et al., 2021). For example, the increase in turbidity, burial, and sediment deposition represents threats to coralligenous assemblages, leading to a shift in the community structure and influencing its spatial and temporal variability (Bourcier, 1986; Balata et al., 2005).

Increasing atmospheric CO₂ concentration is leading to global warming, marine pH decrease, and lower carbonate saturation state (Sarmiento et al., 1998; IPCC 2022). High-Mg calcite CCA and aragonite skeletal remains of invertebrates are the most soluble carbonates to respond to ocean acidification (Hall-Spencer et al., 2008; Kuffner et al., 2008; Rodolfo-Metalpa et al., 2010; Basso, 2012), and in the meantime, both chemical and biogenic erosion of marine carbonates will be enhanced by marine acidification (Wisshak et al., 2014). Predictions of future habitat evolution require knowledge of former climates and can be modeled on the basis of long time-series and information recorded in the recent geological past (Alverson and Kull 2003; Luterbacher et al., 2012). The coralline-engineered habitats identified as C are structured by a range of physical forces and geobiological processes over geological times and are complex paleoenvironmental archives (Nalin et al., 2006; Titschack et al., 2008; Bracchi et al., 2014, 2016). The aim of this study is to assess the contribution of calcareous autogenic engineers to the present-day Ligurian C growing on rocky wall vs.



sub-horizontal substrate, to define its age and mean accumulation rate, and to explore the response of C structural composition and major calcareous bio-engineers to climate and oceanographic Holocene changes potentially recorded in the build-ups.

2 Materials and methods

Coralligenous build-ups were sampled by SCUBA diving from two localities along the Ligurian coast (NW Italy) (Figure 1; Bertolino et al., 2014). One was collected using a hammer and chisel from the base of a submerged vertical cliff in Portofino (P), at a water depth (wd) of 40 m in front of Punta del Faro (Figures 1, 2A; Cánovas Molina et al., 2016, Figure 4). The other one was recovered 150 m off Bogliasco (B) at a water depth (wd) of 10 m (Figures 1, 2B), where it lay on a sub-horizontal seafloor among the *Posidonia* meadow (Bertolino et al., 2017b, Figure 1).

2.1 Build-up surface cover

The external surface of each build-up was studied in terms of cover and coverage of 12 major categories, based on their visual distinctivity and potential role in bioconstruction: FilF_A, filamentous algae and algal turf <2 cm high (Connell et al.,

2014); ErF_A, erect fleshy macroalgae, including *Halimeda*, *Flabellia*, and *Padina* sp.; Pey, other weakly calcified or fleshy laminar algae, mainly *Peyssonnelia* spp.; CCA_CCPEy, non-geniculate Corallinophycidae and completely calcified *Peyssonnelia* spp; FORAM, encrusting foraminifera; SPNG, sponges; Encr_ ANTH, encrusting corals; Er_ ANTH, erect corals; MOL, mollusks; ANN, tube-dwelling annelids; Encr_ BRY, encrusting bryozoans; and Er_ BRY, erect bryozoans. The acronym CCA to indicate crustose coralline algae is widely used in the scientific literature, although the term crustose is not correct within the accepted nomenclature for coralline growth forms (Woelkerling et al., 1993). For the sake of simplicity, we use the term CCA to indicate the non-geniculate Corallinophycidae, with no implication about their growth-form.

We indicate as *cover* the percentage of surface occupied by live organisms vs. dead skeletal remains (based on preservation of soft tissues and delicate structures, original sheen, and color). Because the build-up is biogenic, the live + dead covers give 100%. We indicate as *coverage* the sum of the percentage of surface covered by each category. Because of possible superposition of different organisms, the sum of *coverages* may exceed 100%. We approximated each build-up to a hexahedron and named the six sides from A to F. Each side was sampled with 15 × 15 cm frames, in order to map the surface and to calculate the percentage cover and the total coverage for each category. Manual mapping of each component has been performed using ImageJ Image Analysis

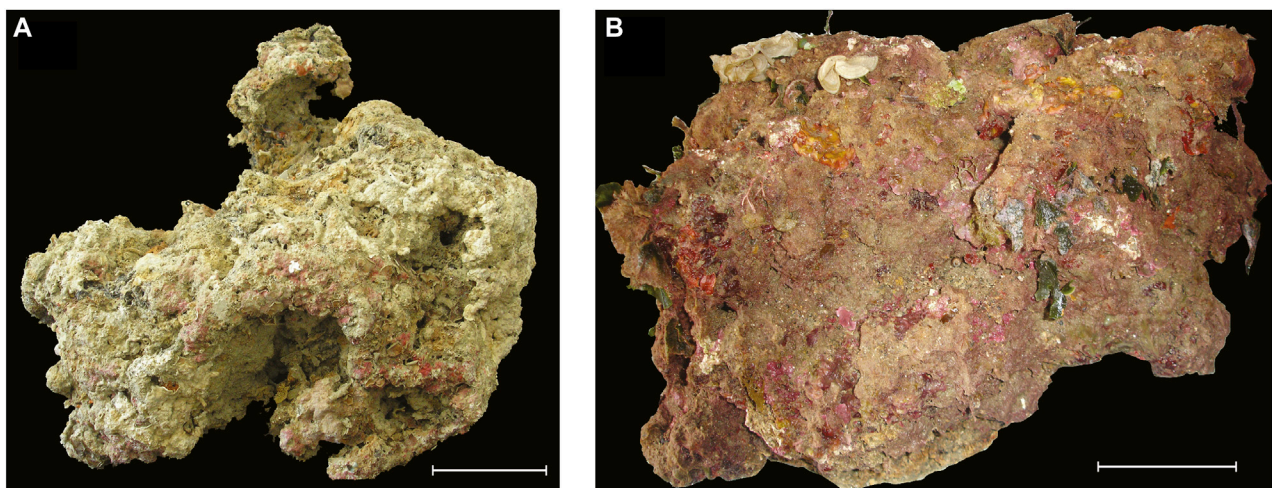


FIGURE 2
Two build-ups before slicing/coring. **(A)** Portofino side A. **(B)** Bogliasco side E. Scale is 10 cm.

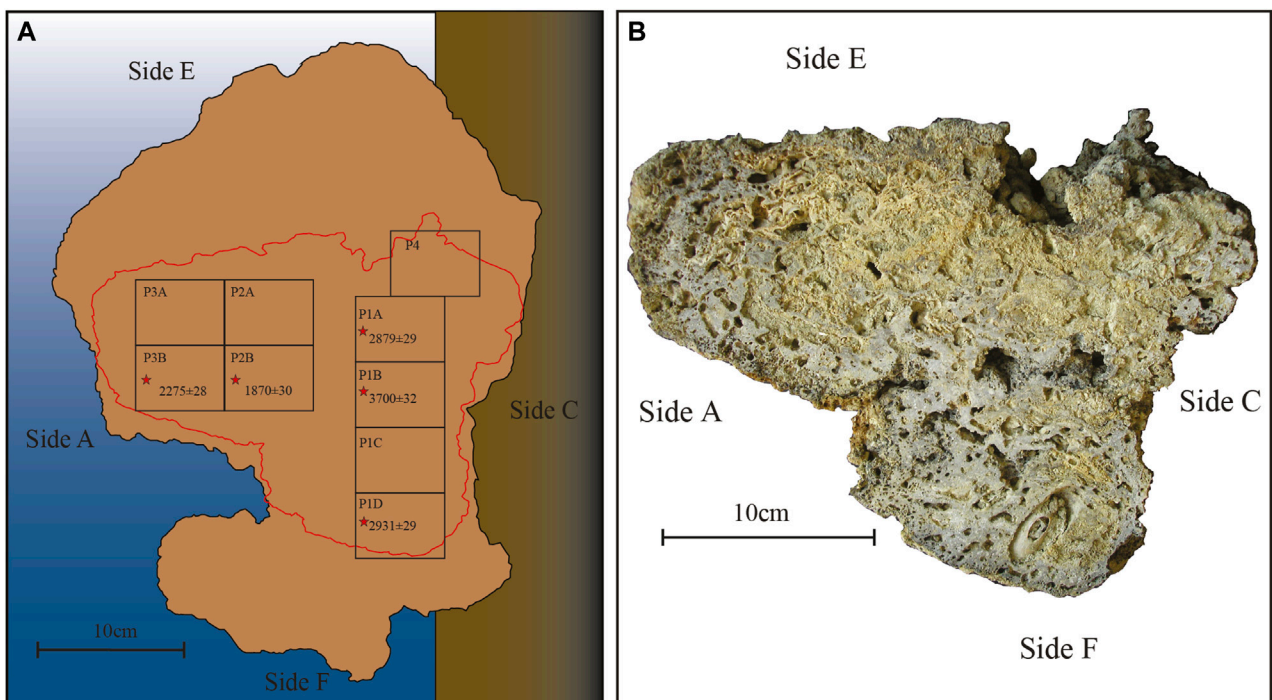
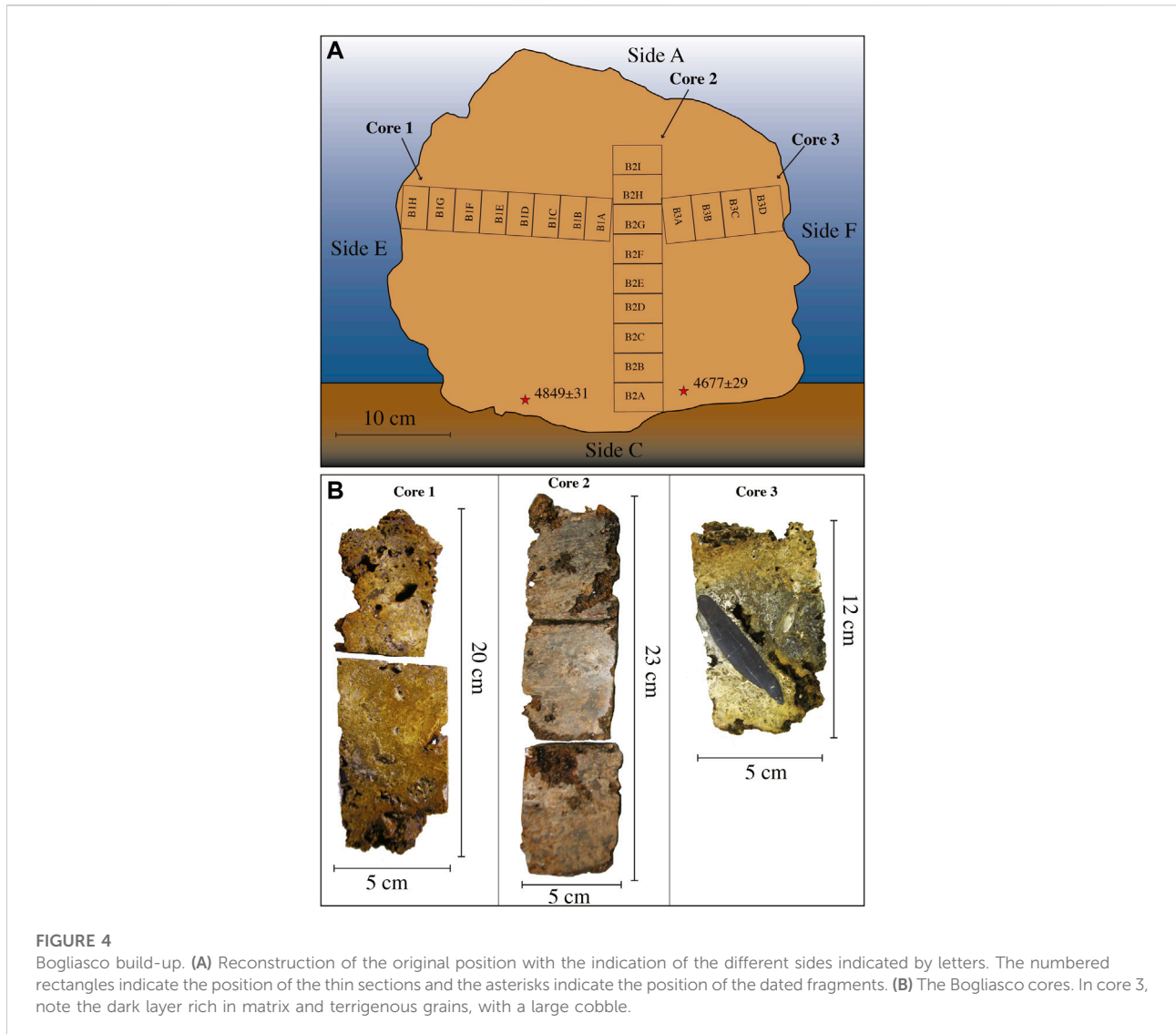


FIGURE 3
Portofino build-up. **(A)** Reconstruction of the original position with the indication of the different sides indicated by letters. The red line indicates the position of the slice from which the panoramic thin sections (= numbered rectangles) have been obtained. The asterisks indicate the dated thin sections along with their tRC age (BP) (Table 4). **(B)** The slice before cutting for thin sections, oriented on the base of the build-up sides. Note the large embedded *Lithophaga* shell close to side F.



Software (Rasband, 1997). Voucher specimens were detached from the build-up surface for identification at the lowest possible taxonomic level, under an optical microscope and/or a scanning electron microscope (SEM) (soft-bodied and calcareous algae, mollusks, bryozoans, corals, and annelids). Live crustose coralline algae were identified under an SEM following the morphoanatomical keys provided by Irvine and Chamberlain, (1994), Bressan and Babbini (2003) and more recent updates (among others: Basso and Rodondi, 2006; Athanasiadis and Ballantine, 2014; Pezolesi et al., 2019). *Lithophyllum stictiforme* is a common species of C encompassing a group of molecularly defined cryptic species (Pezolesi et al., 2019). For this reason, in absence of molecular data and with the aim to keep a uniform taxonomic framework both for the living and the dead/fossil corallines, this species is indicated here as *Lithophyllum* group *stictiforme*. Algal taxonomy

follows AlgaeBase (Guiry and Guiry, 2022), and invertebrate taxonomy follows WoRMS (WoRMS Editorial Board, 2019).

2.2 Multivariate statistics

The percentage values of the categories identified in the external cover of the two build-ups were considered separately for each of the 12 surfaces of the build-ups (6 for Portofino and 6 for Bogliasco) and statistically treated using the software Past (Hammer et al., 2001). A Q-mode clustering of the surfaces based on percentage data was performed by Euclidean distance with no preliminary transformation. The same similarity data were used for the ordination of the surfaces by 2D Multidimensional Scaling and Correspondence Analysis.

TABLE 1 Percentage values of total superficial cover (live vs. dead) and categories' coverage on the surface of the Portofino build-up.

Code	Portofino	Side A	Side B	Side C	Side D	Side E	Side F
	Total surface cm²	1,092	962.5	1,452.5	827	1,014	905
	Living cover %	92	69	32	42	89	43
	Dead cover %	8	31	68	58	11	57
FilF_A	Algal turf	22	19	2	0	13	13
Pey	Fleshy Peyssonneliales	16	8	2	0	13	0
CCA_CCPEy	CCA & calc. Peyssonneliales	49	45	17	3	50	2
FORAM	Encrusting Foraminifera	0	0.1	0.1	0	0	0.1
SPNG	Sponges	4	0	1	3	1	3
Encr_ANTH	Encrusting Anthozoa	0	0	1	7	0	6
Er_ANTH	Erect Anthozoa	3	0.1	0.5	4	1	2
MOL	Mollusca	0	0.1	0.1	1	1	1
ANN	Annelida	12	2	6	7	4	10
Encr_BRY	Encrusting Bryozoa	9	8	7	21	8	17
Er_BRY	Erect Bryozoa	2	0	1	1	1	1
	Total coverage %	117	82	38	47	92	55

Coverage can exceed 100% due to superposition.

TABLE 2 Percentage values of total superficial cover (live vs. dead) and categories' coverage on the surface of the Bogliasco build-up.

Code	Bogliasco	Side A	Side B	Side C	Side D	Side E	Side F
	Total surface cm²	1770	1,307	2,845	973	1,431	1,457
	Living cover %	99	71	23	60	84	57
	Dead cover %	1	29	77	40	16	43
FilF_A	Algal turf	69	36	0	22	49	22
ErF_A	Erect fleshy algae	10	5	0.3	5	6	12
Pey	Peyssonneliales	9	6	0	2	4	4
CCA_CCPEy	CCA & calc. Peyssonneliales	22	21	4	12	19	13
FORAM	Encrusting Foraminifera	0.1	0.2	0.3	0.6	0.5	0.3
SPNG	Sponges	1	0.2	1	0	7	0
MOL	Mollusca	0.1	0.3	0.5	0.1	2	0.5
ANN	Annelida	0.1	4	11	9	6	8
Encr_BRY	Encrusting Bryozoa	0.1	3	8	14	4	5
Er_BRY	Erect Bryozoa	0	2	0.3	0	0.3	0.5
	Total coverage %	111.4	83.7	25.4	65.7	94.8	66.3

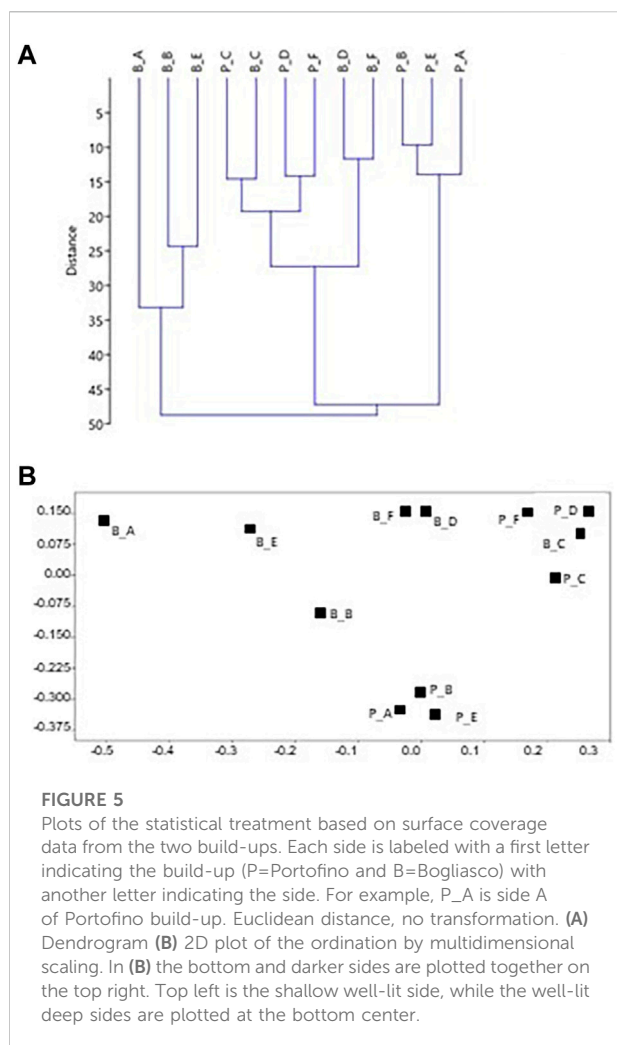
Coverage can exceed 100% due to superposition.

2.3 Carbonate framework builders

In order to study the internal structure of build-ups, the Portofino sample has been sliced along the apparent growth direction, normal to side A. Nine panoramic thin sections (60 × 45 mm) were prepared from the slice (Figure 3).

The sample of Bogliasco has been cored (Figure 4). Three cores with a diameter of 50 mm and different lengths have been obtained. Core 1 (cm 20) was sampled from side E toward side F,

and core 3 (cm 12) joined core 1 from side F. Cores 1 and 3 were more or less perpendicular to core 2. Core 2 had a recovery of 23 cm, from side C toward side A, stopping at 9 cm below the surface of side A. Thus, a total sample thickness of 32 cm (23 cm cored + 9 cm not cored) was measured from side C to side A. Cores have been hardened by embedding in resin, in order to avoid fragmentation, and sliced in half. Twenty-one standard petrographic thin sections (48 × 28 mm) have been obtained from the Bogliasco cores (Figure 4).



Observation and identification of the build-up components in petrographic thin sections were performed under transmitted-light optical microscopes (an Olympus BH-2 and a Leica Leitz-Laborlux-S) in the facilities of the Milano-Bicocca University. The biological literature has been integrated with paleontological contributions for the identification of fossil algae (Braga and Bassi, 2007; Basso et al., 2009; Hrabovský et al., 2016).

Point counting was performed on a total of 30 thin sections to quantify the contribution of the major coralligenous builders (Flügel, 2010). We analyzed a grid of 100 points for each of the 21 standard petrographic thin sections obtained from the Bogliasco cores and 200 points each for the 9 panoramic thin sections from the Portofino slice. Identified categories in the thin section were as follows: porosity, CCA, geniculate coralline algae, Peyssonneliales, unidentified encrusting algae; Charophyceae; bryozoans; annelids; mollusks; foraminifera; muddy matrix; terrigenous grains. Points corresponding to voids within the buildup framework, such as spaces between different skeletal particles, have been considered and counted as indicative of

structural porosity of the build-up, whilst microcavities inside individual skeletal elements, like the interior of conceptacles or annelid tubes, were not considered. We counted as terrigenous grains those extrabasinal elements corresponding to sand grains or larger ($>63\ \mu\text{m}$), while the finer fraction ($<63\ \mu\text{m}$) was attributed to the matrix category, with no distinction about its composition.

2.4 Radiocarbon dating

Radiocarbon dating was performed by the Milano-Bicocca University Centre for Dating and Archaeometry (CUDAM) on selected fragments of CCA from both build-ups, after ascertaining the absence of diagenetic overprints and recrystallization. Five samples for radiocarbon dating were collected from the Portofino slice, numbered RC300, 301, 302, 303, and 304 moving from side F to side E (Figure 3), and 2 samples from the Bogliasco build-up, just internally to the C surface, named RC305 and 306 (Figure 4). The net accumulation rate was assumed as constant and calculated upon the vertical distance between the dated samples (calibrated ages) and the top living surface. We use the term accumulation rate to indicate the net accretion of the build-up that results from the interplay of the original growth rate of the builders, the accumulation of sediment, and the erosion. For the Bogliasco build-up, assuming a more or less constant accumulation rate along the vertical direction, we associated an approximate age to each thin section of the vertical core 2.

3 Results

3.1 Build-up surface cover

3.1.1 Portofino

The build-up sample was a $45 \times 37 \times 41$ cm block, irregularly shaped, with a protuberance toward side F (Figure 2A).

Side C was partially attached to the sub-vertical substrate and had only 32% of living cover. Sides D and F showed a low percentage of living cover, 42% and 43% respectively (Figure 3), whereas sides A, B, and E had the most abundant cover of living organisms, up to 92% (Figure 3; Table 1).

Coverage showed the highest percentages on sides A, B, and E (up to 117%, Table 1).

The most abundant organisms were calcareous algae (up to 50%), with the exception of sides D and F where encrusting bryozoan colonies dominated. Filamentous algae were also abundant (up to 22%), while erect fleshy algae were not observed. Bryozoans and, among them, encrusting colonies were abundant. Tube-dwelling annelids reached considerable percentage cover on sides A and F (13 and 10%, respectively) (Supplementary Table S2).

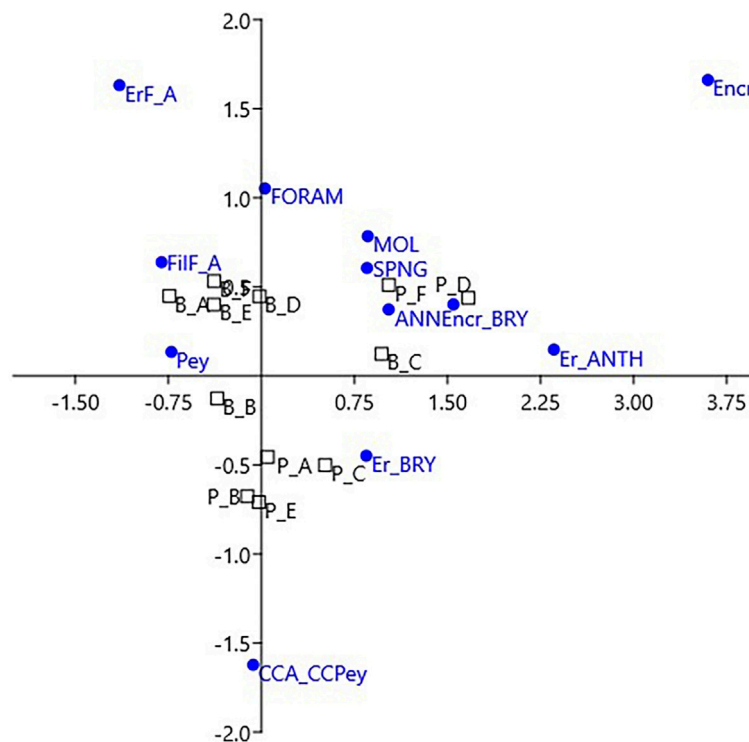


FIGURE 6

Correspondence analysis for the coverage data of the two build-ups. Labels of sides as in Figure 5. Labels of categories as in Tables 1, 2.

3.1.2 Bogliasco

The build-up sample was a $50 \times 40 \times 40$ cm block, showing a porous surface with cm- to mm-sized irregular cavities (Figure 2B). The block clearly showed a more densely populated portion with a high living cover, corresponding to the sides originally exposed to light (sides A, B, and E, Figure 4), contrasting with the very low living cover of side C, which was partially in contact with the seafloor, and almost devoid of algae. Sides A, B, and E were dominated by filamentous (up to 69%) and subordinate calcareous algae (up to 22%, Table 2). Erect fleshy algae are reported for all sides but were most abundant on sides A (10%) and F (12%). Bryozoans were abundant on side D (14%), whereas annelids are dominant on side C (11%) (Table 2). Anthozoa were not observed (Supplementary Table S2).

3.2 Multivariate statistics

The percentages of the identified categories for each side of the two build-ups (Tables 1, 2) were plotted in the dendrogram (Figure 5A). At the Euclidean distance of 35%, three clusters of similar sides are identified (1–3), based on their cover components. Cluster 1 exclusively contains the well-lit sides of

Bogliasco, while cluster 3 is composed of the Portofino sides with the highest cover of calcareous algae. The same clusters were recognized in the 2D MDS (Euclidean distance, no transformation, Figure 5B). Cluster 2 contains the remaining sides, highlighting a similarity (only 15% distance) between the “dark” sides C of both build-ups.

The correspondence analysis (CA) of the same data showed the plot of the build-up sides in a space with 3 opposite vertices (Figure 6). The upper left corresponds to erect fleshy algae, calcareous algae are plotted below, and encrusting corals on the upper right, respectively. All of the fleshy algae (turf and filamentous, erect, and laminar *Peyssonnelia*) fell in the upper left quadrant, while the upper right quadrant is animal-dominated. In the lower half of the CA plot, calcareous algae drive the position of the Portofino sides belonging to cluster 3 (Figures 5B, 6).

3.3 The build-up framework builders

3.3.1 Radiocarbon dating and accumulation rates

Radiocarbon dating of the Portofino build-up provided a calibrated age ranging between 1720 and 1620 BCE (3700 ± 32 years BP, RC301) in the proximity of side F and between

TABLE 3 Point counting results for the 9 thin sections of the Portofino build-up.

Components	P1C	P1B	P1D	P1A	P3B	P2B	P2A	P3A	P4
Porosity	15.3	13.9	16.8	21.3	19.8	20.6	12.1	13.7	16.1
CCA	46.8	41.5	35.6	53.2	27.9	56.2	51.7	46.6	42.4
<i>S. ptychoides</i>	0.0	0.0	11.4	0.0	0.0	0.0	0.0	0.0	0.0
<i>T. pustulatum</i>	8.1	3.1	2.7	8.5	5.4	5.5	3.5	11.0	12.7
<i>S. fruticosus</i>	10.8	16.9	0.0	4.3	1.8	16.4	15.5	0.0	0.0
<i>L. stictiforme</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.7
<i>L. sonderi</i>	0.0	1.5	0.0	0.0	0.0	1.4	0.0	0.0	0.0
<i>P. cf. lenormandii</i>	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0	0.0
<i>M. cf. philippii</i>	3.6	7.7	0.0	0.0	0.0	5.5	0.0	2.7	0.0
CCA ind.	24.3	12.3	21.5	40.4	20.7	24.7	32.8	32.9	17.0
Genic. corallines	0	0	0	0	0	0	0	0	0
Peyssonneliales	5.4	1.5	2.0	4.3	0	4.1	5.2	4.1	2.5
Bryozoans	0	6.2	1.3	8.5	0.9	0	0	1.4	0.9
Annelids	0.9	1.5	0.7	6.4	3.6	4.1	3.5	2.7	3.4
Foraminifers	0.9	0	0	0	0.9	0	0	0	0
Mollusks	0	3.1	2.0	0	3.6	0	1.7	8.2	0.9
Matrix	30.6	32.3	41.6	6.4	43.2	15.1	25.9	23.3	33.9
Terrigenous	0	0	0	0	0	0	0	0	0

The abundance of the identified components is shown as a percentage.

485 and 585 CE (1870 ± 30 years BP, RC303) in the proximity of side E (Supplementary Table S1). The oldest material was recovered from the side of the build-up that was in close proximity of the substrate from which the build-up developed, whereas the youngest portion was located near the photophilous side of the coralligenous block. The mean calculated accumulation rate is $80 \mu\text{m y}^{-1}$.

Two separate CCA fragments at the base of the Bogliasco sample (side C, bottom) were dated at 3290–3130 BCE (4849 ± 31 years BP, RC305) and 2985–2895 BCE (4677 ± 29 years BP, RC306). The mean calculated accumulation rate corresponds to $65 \mu\text{m y}^{-1}$.

3.3.2 Portofino

Dating the internal structure of the Portofino build-up revealed a complex pattern of growth direction. For this reason, thin sections have been reorganized on the basis of the results of radiocarbon dating, from the oldest one (P1B) to the most recent (P4), the latter obtained next to side E (Figure 3). The inner structure was macroscopically porous but hard and lithified, with cm-thick compact areas. Crustose coralline algae were the dominant component in most sections, ranging from 28% (P3B) to 56% (P2B) (Table 3, Figures 7, 8). In sections P1D and P3B, the most abundant component was matrix (Figure 8), formed by microgranular mud, mainly composed of biogenic fragments. Matrix typically filled the intraskeletal porosity or the interskeletal porosity between adjacent algal crusts.

Among the other biogenic components, bryozoans were abundant in sections P1B (6.15%) and P1A (8.51%), annelids

had a significant cover in section P1A (6.38%), and mollusks were relatively abundant in section P3A (8.22%) (Table 3, Figure 8). Peyssonneliales and encrusting foraminifera, although present, were never abundant. Porosity was more or less constant, ranging from 13.70% to 21.28% (Table 3, Figure 8).

The most abundant species of coralline algae were *Spongites fruticosus* Kützing (up to 16.92% in P1B), *Titanoderma pustulatum* (J.V.Lamouroux) Nägeli (up to 12.71% in P4), and *Mesophyllum cf. philippii* (Foslie) Adey (7.68% in P1B) (Table 3). *Lithophyllum* group *stictiforme* (12.71%) was identified only in thin section P4, whereas *Phymatolithon cf. lenormandii* (Areschoug) W.H.Adey (2.74%) was identified only in thin section P2B. Thin section P1D also contained *Sporolithon ptychoides* Heydrich (11.41%) (Table 3).

3.3.3 Bogliasco

Core 2 was sampled from side C (bottom) to side A (top), almost crossing the whole build-up along its mainly vertical growth direction (Figure 4). The 9 thin sections, named from B2A (bottom) upward to B2I, showed a poor preservation of the calcareous skeletal components, hindering the identification of calcareous algae, which nevertheless remained the dominant biogenic component with up to 57% in thin section B2E (Table 4, Figure 9). Among the identified species, the most common were *T. pustulatum* and *L. gr. stictiforme*. *S. fruticosus* was identified in thin section B2G, whereas the uncommon *S. ptychoides* was detected in B2H, associated with *T. pustulatum* and a significant contribution by bryozoans, annelids, and foraminifera. Uncommon

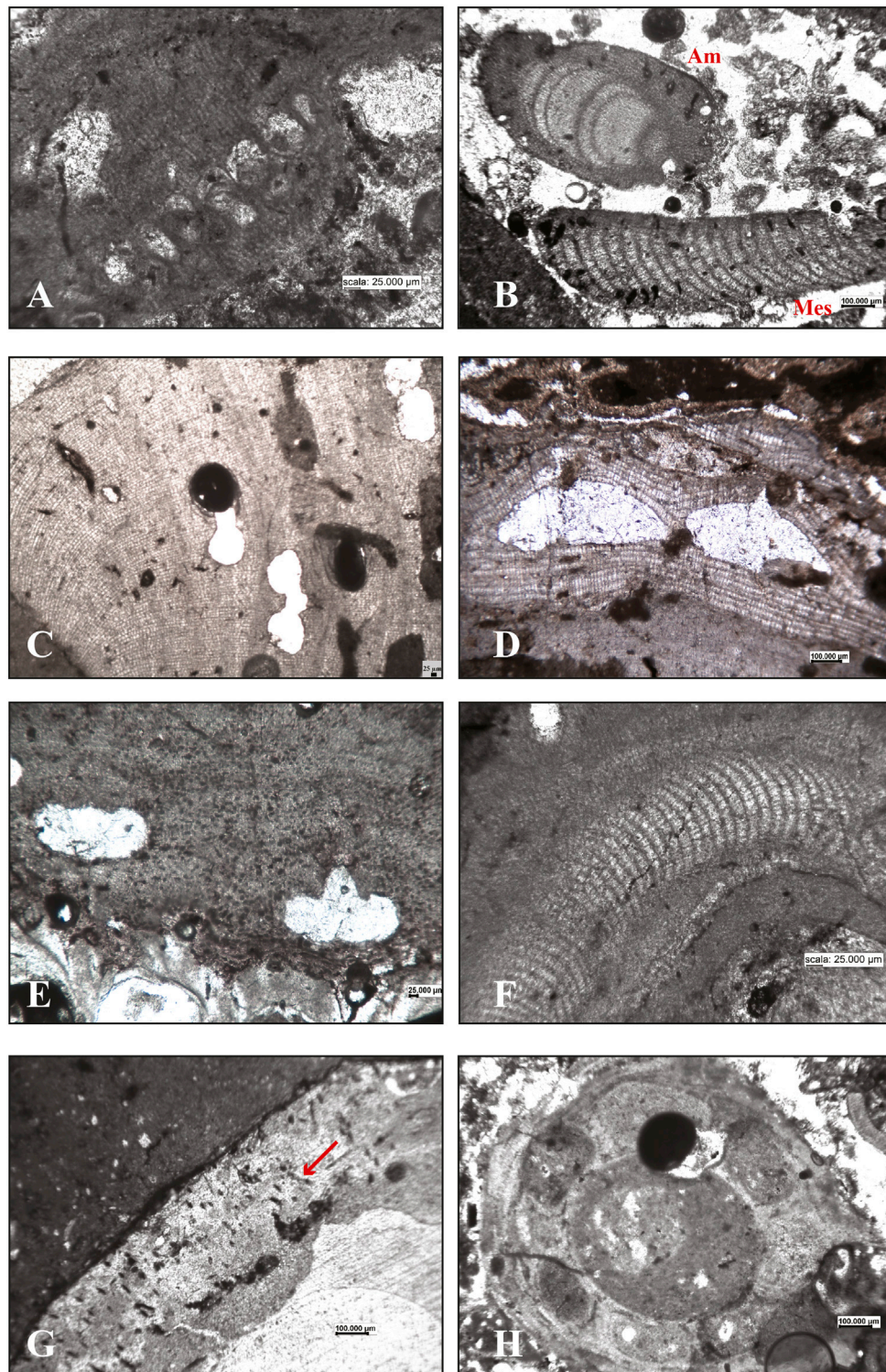
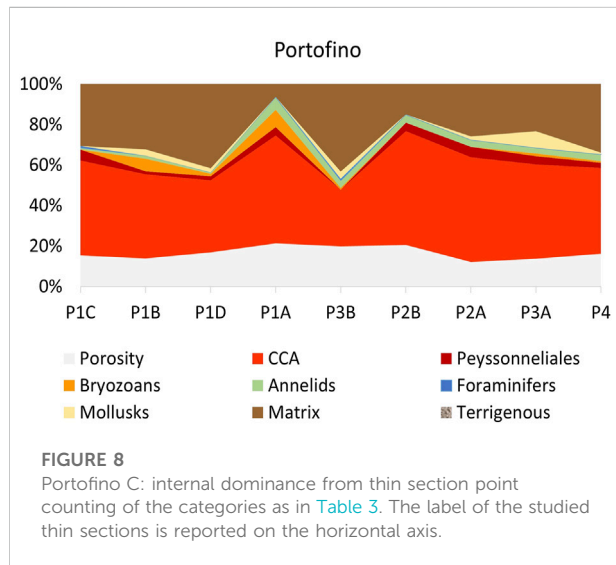


FIGURE 7

Calcareous algae in the internal structure of the studied build-ups. Corallinophycidae: (A) oblique section of solitary sporangia of *Sporolithon ptychooides*; (B) longitudinal section of *Amphiroa intergeniculum* (Am) and a fragment of a *Mesophyllum* sp. hypothallus (Mes); (C) longitudinal section of *Lithophyllum* gr. *stictiforme*; (D) longitudinal section of *Titanoderma pustulatum* showing the distinctive palisade cells and two uniporate conceptacles; (E) *Spongites fruticulosus* growing on a bryozoan colony; (F) the hypothallus of a *Mesophyllum* sp. Peyssonneliales: (G) *Peyssonnelia* sp. hypobasal aragonite calcification showing traces of rhizoids (arrow). Charophyta: (H) unidentified charophyte remains.



intergenicula of articulated coralline algae occurred randomly (B2E and B2G) (Table 4).

Bryozoans were co-dominant with CCA in thin sections B2F (35.7%) and common elsewhere, with the exception of the CCA-dominated section B2E, where bryozoans were missing. Annelids were abundant in thin section B2G (18.7%), whereas foraminifera were abundant on thin sections B2F (14.3%) and B2H (14.7%) and mollusks on thin sections B2D (39.39%) and B2F (14.3%).

Matrix and terrigenous were variable through the core, absent from section B2F and up to 42.5% in B2B. Section B2G records about 34% of the sedimentary infill associated with the maximum abundance of annelids and the occurrence of charophytes. Porosity varied cyclically along the core (Table 4, Figure 9).

TABLE 4 Point counting results for Bogliasco core 2.

Components	B2A	B2B	B2C	B2D	B2E	B2F	B2G	B2H	B2I
Porosity	14.6	0	5.5	6.1	7.1	0	0	14.7	7.4
CCA total	33.3	30	5.7	6.1	57	35.7	21	26.5	29.7
<i>S. ptychoides</i>	0	0	0	0	0	0	0	16.3	0
<i>T. pustulatum</i>	16.1	10	5.7	0	0	5.7	12	10.2	10.4
<i>L. gr. stictiforme</i>	17.2	20	0	0	2	0	0	0	0
<i>S. fruticulosus</i>	0	0	0	0	0	0	1	0	0
CCA ind.	0	0	11	6.1	55	30	8	0	19.3
Genic. cor.	0	0	0	0	0.1	0	0.9	0	0
Charophyceae	0	0	0	0	0	0	9.4	0	0
Bryozoa	8.3	12.5	11.1	3.0	0.0	35.7	12.5	8.8	18.5
Annelida	0.0	7.5	0.0	0.0	0.0	0.0	18.7	5.9	0.0
Foraminifera	4.2	2.5	5.6	9.1	2.4	14.3	3.1	14.7	11.1
Mollusca	2.1	5.0	11.1	39.4	2.4	14.3	0.0	2.9	11.1
Matrix	18.8	42.5	33.3	24.2	26.2	0.0	25.0	14.7	14.8
Terrigenous	18.7	0.0	16.7	12.1	4.8	0.0	9.4	11.8	7.4

The abundance of the identified components is shown as a percentage.

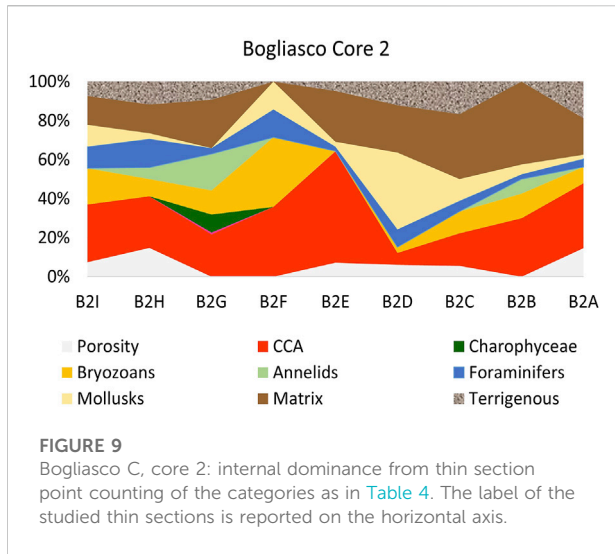
Cores 1 and 3, perpendicular to core 2, have been considered as representative of the presumed lateral development of the build-up (Figure 4). The inner structure was found to be lithified and locally highly compact, although pluricentimetric irregular cavities were observed.

In the thin sections obtained from Core 1, from B1A (internal) to B1H (toward side E) (Figure 4), the most abundant biogenic component was CCA (up to 61.11% in B1A) (Table 5). Among them *L. gr. stictiforme*, which was always present, and *T. pustulatum* were the most abundant species (Table 5). The species *S. fruticulosus* was uncommon, identified only in thin section B1G (Table 5).

Bryozoans were ubiquitous and particularly abundant in thin sections B1D (20%) and B1F, where they overcome CCA abundance (Table 5). Annelids were also common and abundant in thin section B1E, where they equaled CCA (18.2%) and where foraminifers also reached an important percentage. Mollusks were remarkably common in thin section B1C (14.3%), associated with the occurrence of charophytes and abundant sedimentary infill (matrix + terrigenous = 42.8%), while both bryozoans and annelids were missing (Table 5).

Matrix, as microgranular mud mostly of biogenic origin, was very abundant in thin sections B1D (50%), B1C (37.1%), and B1F (35.3%) (Table 5). Terrigenous grains were dominant in thin sections B1G (41.2%) where, adding to matrix, the sum of these two categories reached the maximum value, exceeding 55% (Table 5).

The thin sections of Core 3 (B3A internal, to B3H, close to side F, Figure 4) showed CCA as the most abundant biogenic component, although percentages did not exceed 31.8% (B3A) (Table 5). Bryozoans, annelids, and mollusks remarkably overtook where CCA were absent (B3D). The identified CCA species were *L. gr. stictiforme* and *T. pustulatum*.



Matrix was ubiquitous and abundant, and together with terrigenous grains, these two abiogenic components became dominant in thin sections B3A and B3B (Table 5), coarsely corresponding to a gray layer where terrigenous grains up to 6 cm long occurred (Figure 4). The largest fragments showed an elongated shape with well-rounded margins and were composed of calcareous shale.

4 Discussion

4.1 External components

The quantitative analysis of surface cover and coverage of both coralligenous build-ups easily allows us to identify the photophilic

and sciaphilic sides, highlighting an important variability in C surface associations, depending on substrate orientation. The Portofino C, overhanging on a rocky wall at a depth of about 40 m, shows the most abundant living cover and coverage on its best-lit sides A and E, with calcareous algae as the dominant category. Filamentous algae, although present, are never dominant, as expected on the basis of the water depth of the sample close to the lower limit of the infralittoral zone in the Mediterranean. An important reduction of the live cover is observed on the other sides, with Bryozoa and tube-dwelling Annelida becoming dominant on the westward side D and on the lower and darkest side F. Both octocorals and Scleractinia are also more common on the dim-lit sides, although with low total dominance.

The Bogliasco C is presently growing within the infralittoral *Posidonia* meadow, with its upper, best-lit side dominated by filamentous and fleshy algae, with subordinate Peyssonneliales and CCA. Bryozoans are also important contributors, especially on sides D and F, together with annelids, confirming their preference for the shadowed and protected substrates (Rosso and Sanfilippo, 2009; Sanfilippo et al., 2011), including the lower surface of calcareous laminar algae.

The comparison between the overhanging and deeper Portofino C and the shallower Bogliasco build-up highlights the abundant fleshy algal cover and the absence of corals as the most distinctive traits of Bogliasco C, likely due to its shallow position. The distinctive green algae *Halimeda tuna* and *Flabellia petiolata* are scattered over the Bogliasco C surface, as commonly reported in other shallow coralligenous algal assemblages (Ballesteros, 2006; Piazzini et al., 2022), while they were not observed in the Portofino sample. Calcareous algae in Bogliasco exhibit about half of the cover in Portofino, confirming their basically sciaphilic nature and the negative effect of space competition with the faster-growing fleshy algae.

TABLE 5 Point counting results for Bogliasco cores 1 and 3.

Components	B1H	B1G	B1F	B1E	B1D	B1C	B1B	B1A	B3A	B3B	B3C	B3D
Porosity	15.8	0.0	11.8	18.2	0.0	8.6	22.7	5.6	13.6	7.4	17.9	0
CCA total	52.0	35.3	8.8	18.2	15.0	36.4	18.2	61.1	31.8	25.9	20	0
<i>T. pustulatum</i>	31.0	18.3	6.5	0	0	21.0	0	6	22.8	10.4	0	0
<i>L. gr. stictiforme</i>	19.0	8.5	2.3	18.2	15.0	15.4	18.2	55.1	9	15.5	20.0	0
<i>S. fruticulosus</i>	0	8.5	0	0	0	0	0	0	0	0	0	0
<i>M. cf. philippii</i>	2	0	0	0	0	0	0	0	0	0	0	0
Genic. cor.	0	0	0	0	0	0	0	0	0	0	0	0
Peyssonneliales	0.6	0	0	0	0	0	0	0	0	0	1.4	0
Charophyceae	0	0	0	0	0	2.9	0	0	0	0	0	0
Bryozoa	5.3	5.9	14.7	0.0	20.0	0	13.6	11.1	9.1	3.7	17.9	38.9
Annelida	0	2.9	2.9	18.2	5.0	0	0.0	5.6	0	3.7	3.6	22.2
Foraminifera	5.3	0	2.9	9.1	5.0	0	0.0	5.6	4.6	11.1	7.1	5.6
Mollusca	0	0	8.8	0	5.0	14.3	4.5	0	0	0	7.1	16.7
Matrix	10.5	14.7	35.3	18.2	50.0	37.1	27.3	5.6	22.7	22.2	25.0	16.7
Terrigenous	10.5	41.2	14.7	18.2	0	5.7	13.6	5.6	18.2	25.9	0	0

Thin sections are ordered from side E (B1H) to side F (B3D), as in Figure 4. The abundance of the identified components is shown as a percentage.

The surface of C pillars in Sicily (Di Geronimo et al., 2001) presents a similar pattern of algal dominance, confirming the early reports of shallow-water corallines becoming hidden under a canopy of *H. tuna* and *F. petiolata* (Laborel, 1987).

Coralligenous was indicated as the climax biocenosis of the circalittoral zone (Pérès, 1982; Ballesteros, 2006; Cánovas Molina et al., 2016), although C habitats are considered as heterogeneous systems, showing high spatial, morphological, and biological variability (Ferdeghini et al., 2000; Casas-Güell et al., 2015; Cánovas Molina et al., 2016; Sartoretto, 2017; Piazzini et al., 2022). Light exerts a major control on the depth extent of the infralittoral and circalittoral zones and certainly also on the depth distribution of the various coralligenous facies (Pérès, 1982; Ballesteros, 2006; Cánovas Molina et al., 2016). C is reported to develop between 0.05% and 3% of the surface irradiance (Ballesteros, 2006). Irradiance values >3% correspond to the shallowest coralligenous, once defined as “precoralligenous” (Pérès, 1982) because they typically hosted a higher diversity of fleshy algae, among which were *Flabellia petiolata* and *Halimeda tuna*.

Coralligenous is known in the circalittoral zone mainly 1) on rocky cliffs, 2) on sedimentary seafloors, and 3) as an enclave of circalittoral, in the shadow of the canopy of leaves at the base of the infralittoral *Posidonia* meadows (Sartoretto 2017). Portofino C clearly corresponds to the first type, while Bogliasco C is not completely included in category 2) nor 3) above, being developed among *Posidonia* plants and reaching a considerable height in the middle of the meadow that, by definition, characterizes the infralittoral zone. A similar infralittoral coralligenous, apparently a paradox of benthic bionomics, was reconstructed in the Quaternary marine terrace of Le Castella (MIS 3, Bracchi et al., 2016; Nalin et al., 2020).

4.2 Framework builders and Holocene oceanographic fluctuations

Crustose coralline algae showed a roughly antithetical pattern with matrix, alternating as the dominant components of the C internal structure. Although present and locally abundant, the other biogenic components played a secondary role as framework builders (Figures 8, 9).

4.2.1 Portofino

The interior structure of the Portofino build-up was very compact, with a rather constant percent porosity, never exceeding 21.28%. Among CCA, the most common species belong to the genus *Mesophyllum*. Contrarily to previous reports indicating *M. alternans* (junior synonym of *M. philippii* (Athanasiadis and Ballantine, 2014) as a shallow component (Sartoretto et al., 1996; Ballesteros, 2006), this coralline species was remarkably abundant in the relatively deep Portofino C (40 m).

T. pustulatum was ubiquitous. This species is widespread in the Mediterranean (Babbini and Bressan, 1997) and has already been indicated as an important framework builder in C (Sartoretto et al., 1996). This suggestion was confirmed in the Pleistocene C examples outcropping in the Cutro terraces (Nalin et al., 2006; Basso et al., 2007).

S. fruticulosus is also widespread in the Mediterranean Sea (Babbini and Bressan, 1997; Basso and Rodondi, 2006), where it occurs as rhodoliths on soft bottoms (Basso and Rodondi, 2006; Barberá et al., 2012; Joher et al., 2015), and was rarely reported as a component of the coralligenous build-ups, down to a water depth of 75 m (Basso and Rodondi, 2006; Catra et al., 2007). *S. fruticulosus* occurred cyclically in the Portofino build-up, around 3700 BP (P1B), 2879 BP (P1A), and 1870 BP (P2B), always together with low matrix abundance. Therefore, it can be associated with periods with low sedimentation rate and consequently interpreted as a species with a low tolerance for disturbance by sediment deposition, and likely associated turbidity.

In the Portofino inner structure, up to 40.43% CCA did not show or preserve sufficient diagnostic features for taxonomic identification. Nevertheless, merging the two components (identified + non-identified coralline algae) highlights CCA as the most important framework builder in late Holocene coralligenous build-up, as already reported for the Ligurian Sea (Sartoretto et al., 1996; Cerrano et al., 2001; Bertolino et al., 2017a; Bertolino et al., 2017b). All the other calcareous organisms showed negligible contributions and rather invariant quantitative distribution in the inner structure. Across the build-up, high CCA abundance was accompanied by a minor matrix, filling the sub-millimeter cavities between crusts. On the contrary, local dominant matrix was observed filling not only the cavities between crusts but also cm-size voids, apparently corresponding to a phase of slow growth of the primary builders. In correspondence of high-matrix content, the most abundant CCA species was *T. pustulatum* for thin sections P1D and P3B and *S. ptychooides* for thin section P1D.

Thin section P1D corresponded to a calibrated age of 790–745 BCE which is known as a phase of increasing temperature in the Alboran Sea (Martrat et al., 2014; Bazzicalupo et al., 2020) and increased humidity and terrestrial runoff in the Southern Alps and in the Gulf of Lyon (Wirth et al., 2013; Jalali et al., 2016), associated with negative North Atlantic Oscillation (NAO) index (Faust et al., 2016) (Figures 8, 10). During this time interval, warm summers and dry winters characterized the south-western Mediterranean (Zielhofer et al., 2019). The genus *Sporolithon* is considered a warm-water taxon (Bressan and Babbini, 2003; Braga and Bassi, 2007; Basso et al., 2009). In particular, the species *S. ptychooides* is common at tropical latitudes (Adey and Macintyre, 1973; Johansen, 1981), overgrowing coral on shallow fringing reefs and reef flats 1–1.5 m deep (Richards et al., 2017), or in relatively deep water and cryptic sites (Adey, 1979, 1986). *S. ptychooides* is

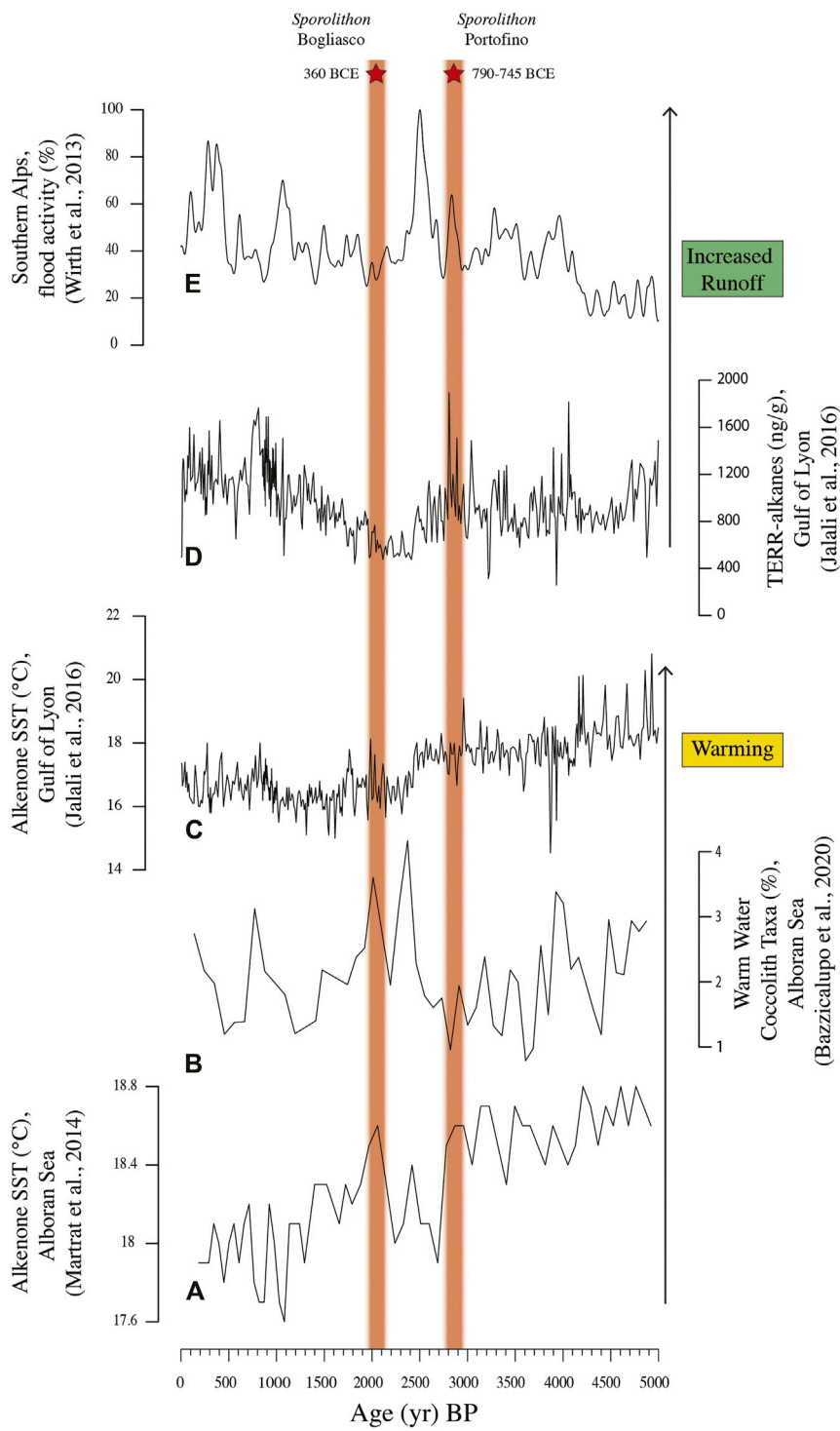


FIGURE 10
Late Holocene climate fluctuations and the stratigraphic position of the *Sporolothion* occurrences recorded in the Portofino and Bogliasco build-ups.

rarely reported in the Mediterranean; it is mainly reported in the central and southern Tyrrhenian Sea and in the Ionian Sea (Alongi et al., 1996; Babbini and Bressan, 1997; Di Geronimo et al., 2002). The occurrence of *S. ptychoides* in the Portofino build-up is therefore a possible index of a milder climate than today. The matrix-dominated thin section P3B corresponded to a calibrated age of 85–175 CE, which falls within the early Roman Climate Optimum. Also, this period is reported in literature as warm and humid, supporting terrestrial run off and sediment deposition at coastal sites (Bini et al., 2020).

The calculated accumulation rate of 0.08 mm y^{-1} for the Portofino C is compatible with previous results from the north-western Mediterranean (Sartoretto et al., 1996).

4.2.2 Bogliasco

The inner structure of the Bogliasco build-up appeared compact, with porosity never exceeding 22.73%. A major contribution of both matrix and terrigenous clasts was reported (up to 42.50% in thin section B2B, Figure 9), as already observed in other shallow coralligenous build-up on horizontal substrate (Cocito et al., 2002). Among CCA, *L. gr. stictiforme* was the commonest species. The basal side C was consistently dated at 3,290–3130 BCE (RC305) and 2,985–2895 BCE (RC306); thus, the inception of the Bogliasco build-up occurred during the warm Copper Age, about 5 ka BP. At this time, the sea-level was at least 3 m below the present one along the Ligurian coast (Lambeck et al., 2004); therefore, the build-up started to grow at a water depth of about 7 m, in a very shallow infralittoral environment. Although the abundant matrix and terrigenous grains recorded at the base of the build-up are not surprising in this shallow coastal setting (Figure 9), it should be considered that a coincident phase of wet winters has been reported for the southwestern Mediterranean (Zielhofer et al., 2019), probably favoring the development of sedentary heterotrophs such as annelids and boring mollusks, through the increased food supply from continental weathering. Interestingly, the terrigenous and matrix components showed a decrease toward the core top, although the trend is broken in correspondence to thin section B2F, when these sedimentary components abruptly disappear. This seems to correspond to the end of the Late Bronze Age, ca. 1000 BCE. B2F shows the equal contribution by CCA and bryozoans, accompanied by mollusks and foraminifera. This association might have developed during an arid period, recorded in the western Mediterranean by dry winters and warm summers (Jalut et al., 2000; Bond et al., 2001; Zielhofer et al., 2019; Figure 10).

Successively, a wetter climate fostered the freshwater input from the continent and sedimentation in shallow settings. This was testified in the Bogliasco build-up by an increase in annelids and the occurrence of charophyte remains in thin section B2G, at about 400 BCE (Figure 9). Freshwater and sedimentation are not favorable to CCA, which reduced in abundance. The Roman Period (about 250 BCE–400 CE) brought a warmer phase,

probably recorded in the overlying thin section B2H, as testified by the occurrence of the warm-water taxon *S. ptychoides* (Figures 7, 9, 10).

Cores 1 and 3 have been collected more or less normal to core 2. Core 1 crossed core 2 approximately at the level of thin section B2F, thus covering approximately the last 3,000 years, which is compatible with the calculated mean accumulation rate for the Bogliasco build-up.

As already observed in core 2, core 1 also recorded the passage from the drier Late Bronze Age, when CCA were abundant (thin section B1A) to the warm and wetter Roman Period, when sedimentation was favored. This is supported by the abundance of matrix and terrigenous grains in thin sections B1B to B1F, accompanied by the occurrence of charophyte remains (B1C). CCA increased toward the surface of side E in thin sections B1G and B1H.

Core 3 was shorter and recorded a striking and extreme event of sedimentation, likely induced by a flood, with the accumulation of coarse terrigenous clasts up to cobble size (thin sections B3A and B3B). The largest clasts had a rounded shape, supporting the hypothesis of a long transport from the provenance site. The calcareous shale recognized in the largest clasts is compatible with the lithologies of the drainage basin of the Poggio creek, where the Monte Antola Formation outcrops. This Formation is a turbiditic limestone with levels of shales, Upper Cretaceous-Medium Eocene in age (Abbate and Sagri, 1967; Scholle, 1971). The calculated ages of these thin sections were related to the Roman Period.

4.2.3 Build-ups comparison

The inner structure of the build-ups revealed that matrix or biogenic/terrigenous sediments have filled the originally vacuolar framework, resulting in an inner compact structure in both Portofino and Bogliasco build-ups. The overhanging Portofino build-up revealed a complex pattern of growth direction, while the Bogliasco build-up had a more regular vertical accretion. Both build-ups revealed that the most important contributors to the structural development of the rigid framework are CCA. The conservation of calcareous algae was generally poor, despite their very young geological age, and they did not often show the diagnostic features that are required for species identification. This observation opens further questions about the relationship between age and taphonomic signatures in calcareous frameworks. In both build-ups, the genus *Titanoderma* plays an important role among CCA, although its highly distinctive vegetative anatomy may result in an overestimation of its abundance, in comparison to other corallines. The most common species in the shallow Bogliasco C was *L. gr. stictiforme*, while the genus *Mesophyllum* was found to be more common in the deeper Portofino C. A very shallow distribution of *L. gr. stictiforme* is in agreement with previous observations for the Apulian C (unpublished); however, the observed depth distribution of

the two genera show an opposite pattern with respect to other published records for the NW Mediterranean (Sartoretto et al., 1996). In the C from Banyuls (France), distributed from 20 to 40 m in depth, *Mesophyllum philippi* (as *Mesophyllum lichenoides*) was reported as the most abundant framework builder, with *Lithophyllum stictiforme* (as *Pseudolithophyllum expansum*) also being abundant (Bosence, 1985). However, the paucity of quantitative data suggests caution, and further investigations are required to clarify the matter.

Di Geronimo et al. (2002) reported the occurrence of *S. ptychoides* inside the Sicilian bio-constructed pillars, although they did not provide any temporal frame for the growth of the bioconstruction. In our samples, *S. ptychoides* is reported for thin section P1D in Portofino, dated at 790–745 BCE, and for thin section B2H in Bogliasco, indirectly attributed to the Roman Period. Based on literature data, both intervals correspond to phases of warm and rather humid climate in the western Mediterranean. However, the two occurrences of *Sporolithon* are separated by a few centuries (Figure 10), and the B2H date was calculated on the basis of a presumed constant accumulation rate. Therefore, we cannot exclude the possibility that only one warm “*Sporolithon* event” occurred in the Ligurian build-ups at about 2.7 ka BP. This age corresponds to a negative NAO Index (Faust et al., 2016), but it should be considered that the Portofino and Bogliasco build-ups grew on the Ligurian continental shelf during the Late Holocene, when the teleconnection between the Western Mediterranean winter rains and the NAO index show an opposite pattern (Jalali et al., 2018; Zielhofer et al., 2019; Figure 10).

The main factors influencing structure, biomass, and metabolism of marine benthic organisms such as CCA are sedimentation-related mechanisms, namely, burial or changes in the quantity/quality of suspended matter and water transparency (Balata et al., 2005), which in turn influence light penetration and may alternatively favor the photoautotrophs or the suspension feeders (Laborel, 1961).

Sedimentation in littoral systems is linked to terrestrial sources and can be affected by natural processes and human activities that have historically altered the coastal erosion/deposition profiles and the transport of suspended particles (Owens, 2020).

Marine sedimentation affects the horizontal rather than the vertical surfaces more easily (Cocito et al., 2002), and shallow-water settings are expected to be more frequently affected by terrigenous input than the deeper settings. In the case of the studied build-ups, differences in the sedimentary regime can be traced between the build-up on the vertical cliff in Portofino and the one from the sub-horizontal substrate in Bogliasco. Most of the Portofino build-up had a contribution higher than 40% by calcareous algae, both on its surfaces and in the inner structure, and minor phases of dominance by annelids and bryozoans, as already reported for build-ups on vertical substrate (Balata et al., 2005).

Portofino build-up contained matrix, as microcrystalline mud with abundant biogenic grains, but no larger terrigenous grains were observed, indicating a minor influence of transport from land.

On the contrary, as expected, the sediment contribution was more abundant in the Bogliasco build-up, both as matrix and as terrigenous fragments, partially inhibiting the surficial coralline algal development, which never exceeds 30.67%. The vicinity of the Bogliasco build-up to the coast also allowed the reconstruction of a past extreme event of flood, recorded inside the bioconstruction as an interval of abundant and large terrigenous clasts lithologically related to the drainage basin of the Poggio creek.

In both build-ups, the identification of levels with abundant calcareous skeletal components alternating with levels of matrix/terrigenous suggests the occurrence of a cyclicity in the formation of the framework.

As already indicated, the reconstruction of C build-up development is not trivial. This is related to the alternation of favorable phases of deposition of carbonate and, in particular, calcareous algae as a major framework builder, and disruption linked to high sedimentation transport that results in shifts of abundance among major components, as already observed for sponge diversity (Bertolino et al., 2017a).

According to many authors (Antonoli et al., 2001; Antonoli et al., 2002; Lambeck et al., 2004; Taricco et al., 2009), the Mediterranean sea level rose from –10 m to –4 m about 6.5 ka BP. The studied area is considered as tectonically stable and the estimated sea-level rise is 0.3 mm y⁻¹ with slight deceleration during the last 1,500 years and stabilization near the present datum from about 500 years BP (Laborel et al., 1994; Pirazzoli, 2005). Therefore, the Portofino build-up did not undergo any significant depth variation, while the Bogliasco one developed at a depth changing from about 7 m, 5 ka BP, to the present water depth of 10 m.

Sartoretto et al. (1996) reported that after 5 ka BP, the accumulation rate of C should be insignificant below 60 m wd. We did not deal with the C growth below 60 m; however, both the studied Ligurian build-ups are younger than 5 ka BP and are slowly but actively growing, as demonstrated by the occurrence of live habitat formers at their surfaces and by their growth rates, which are compatible with published data for other relatively shallow C build-ups (Sartoretto et al., 1996; Bertolino et al., 2017b).

5 Conclusion

Coralligenous build-ups are among the most important biogenic frameworks of the Mediterranean shelf (Ingrosso et al., 2018), characterized by slow but continuous growth on both vertical and horizontal substrates.

The quantitative analyses of the major components at the surface of the two studied samples of C, collected in the Ligurian

Sea, show an important variability depending on orientation and exposure (Figures 5, 6). The abundant fleshy algal cover and the absence of corals are the most distinctive traits of Bogliasco C when compared with Portofino (Figures 5, 6). Calcareous algae in Bogliasco exhibit about half of the cover in Portofino, confirming their basically sciaphilic nature and the negative effect of higher sedimentation and space competition with the faster-growing fleshy algae, resulting in a lower accumulation rate of the Bogliasco build-up. Surface and internal components indicate that coralline algae and completely calcified Peyssonneliales represent the most important framework builders, with the genus *Lithophyllum* apparently more common in the shallow Bogliasco C, while *Mesophyllum* plays a major role in the deeper Portofino C. Bryozoans are the second most significant contributor to the C framework, locally showing an opposite trend of abundance with respect to coralline algae.

The studied build-ups developed during the Late Holocene, recording its numerous climate fluctuations. Matrix and terrigenous fragments are negatively correlated with calcareous algae, due to the detrimental effect of a high sedimentation rate on the growth of these photosynthetic organisms. Therefore, we recognize a cyclicity in the inner structure of both build-ups, with the framework composition shifting from calcareous algae-dominated to matrix-dominated. These shifts correspond to Late Holocene climate fluctuations, and in particular, matrix-dominated intervals are correlated with wetter periods, under which sediment transport from the continent is favored, whereas calcareous algae-dominated intervals correspond to drier spells. Coralligenous build-ups are special recorders, able to catch extreme events of flooding and the occurrence of warm “*Sporolithon* events.”

While the internal structure of the Bogliasco build-up is completely coherent with the definition of Coralligenous, its present-day shallow distribution, growing amid *Posidonia*, documents an important exception to the rule. In fact, this supports the concept that C is not only the climax of the circalittoral zone, also occurring in the *enclave* at the base of *Posidonia* leaves, but it may also develop and gain significant vertical accretion within the infralittoral zone (Ballesteros, 2006; Bracchi et al., 2016). A mosaic of benthic biocoenoses is expected to occur across ecological boundaries, and further investigations are required to clarify the controls of this spatial pattern.

The occurrence of live calcifiers at the surface of the studied build-ups and their accumulation rates of 0.080 mm y⁻¹ for Portofino and 0.065 mm y⁻¹ for Bogliasco demonstrate that the Ligurian C is slowly but actively growing.

Physical forces and geological and biological processes controlling the build-ups act at variable temporal and spatial scales, which explains the disparate disciplinary and technical approaches displayed for their exploration. The consequence, however, is an insufficient interdisciplinary communication leading to a fragmented and incomplete understanding of the phenomenon of bioconstruction, an inadequate short-term

vision, and poor management of these important habitats. Brief, local investigations, and those monitoring methods based exclusively on visual census of the mega-epibenthos presently dwelling on the algal substrate, appear largely insufficient for describing the diverse expressions of the coralline-engineered habitats as historical structures, and should be integrated in the framework of a geobiological approach. Adding the correct temporal and spatial frame has important implications for our understanding of the history and fate of marine temperate/cold biogenic habitats under the ongoing human impacts, ocean warming, and acidification and for improving their management.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material; further inquiries can be directed to the corresponding author.

Author contributions

Conceptualization, DB; methodology, DB, VB, and FM; formal analysis, DB and VB; investigation, DB, VB, FM, and GB; data curation, VB, DB, FM, and PB; writing—original draft preparation, DB and VB; writing—review and editing, DB, VB, PB, and GB; supervision, DB; project administration, DB; funding acquisition, DB. All authors have read and agreed to the published version of the manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial

relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/feart.2022.961632/full#supplementary-material>.

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