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In situ growth rates of cold-water corals fouling oceanographic moorings in the Central Mediterranean Sea

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Cold-water corals (CWCs) are vital deep-sea ecosystem engineers, yet their growth dynamics remain poorly understood. This study quantifies *Desmophyllum dianthus* growth in the Southern Adriatic Sea using two unplanned but ideal long-term natural experiments. The first derives from an oceanographic mooring lost at ~1200 m depth, allowing a rare four-year *in situ* assessment via high-resolution ROV footage collected in 2024. The second involves physical specimens from a mooring at ~500–600 m in Bari Canyon, recovered after one year. Image-based measurements showed an average linear growth rate of 8.06 ± 0.41 mm yr^{-1}, while physical samples recorded a one-year extension of 6.5 ± 0.6 mm. These *in situ* growth rates exceed previous records and suggest rapid early growth consistent with asymptotic dynamics. The findings offer crucial benchmarks for natural CWCs growth and support effective conservation and restoration efforts, aligning with goals set by the EU Nature Restoration Law.

Keywords Cold-water corals, Deep sea, Growth rate, Mooring, Restoration, Mediterranean Sea

The scleractinian cold-water corals (CWCs) *Desmophyllum pertusum*, *Madrepora oculata* and *D. dianthus* build extensive carbonate frameworks along continental margins, submarine ridges, and canyons, enhancing biodiversity and providing essential ecosystem functions[1–6]. These organisms typically colonize natural hard substrates, yet evidence exists that CWCs can also successfully settle and grow on artificial structures in the deep sea. *D. pertusum* has been reported thriving on trans-Atlantic cables, oil platforms, and shipwrecks[7,8], deep-water oil and gas installations in the Gulf of Mexico[8] and self-sustaining subpopulations observed on North Sea platforms since the late 1990s[9]. More recently, *D. pertusum* and *D. dianthus* were found fouling scientific moorings, including plastic-covered floats, deployed at ~ 1000 m depth at the Darwin Mounds (UK), within just a few years[10]. Similarly, lost fishing gear and submerged plastic debris have served as colonization substrates for both species, suggesting a capacity to exploit anthropogenic substrates under suitable environmental conditions[10–13].

Such findings are particularly relevant, given the growing imperative to restore CWCs habitats, which are affected by bottom-contact fishing, marine litter, and climate-induced stressors[14–19]. Passive protection measures proved crucial in preventing further impacts yet may be insufficient to recover degraded situations[20,21]. Consequently, there is a growing interest in developing active restoration strategies for CWCs, especially in the wake of recent policy developments such as the EU Nature Restoration Law (2024/1991). This legislation mandates the rehabilitation of degraded ecosystems and sets ambitious targets for marine restoration, including the recovery of at least 20% of degraded marine areas by 2030[22], thereby providing a concrete framework to support the implementation of restoration initiatives in vulnerable deep-sea habitats.

However, translating restoration goals into action remains challenging, especially in the deep sea, where fundamental ecological data, such as species-specific growth rates and colonization dynamics, are still scarce. Available evidence indicates that CWCs exhibit slow growth under natural conditions. For example, *D. pertusum* in the Gulf of Mexico showed *in situ* linear extension rates of 3.6–8.4 mm yr^{-1}[23], while laboratory experiments

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found growth rates up to 18.2 mm yr^{-1} under controlled conditions[24]. Radiometric dating of *D. dianthus* skeletons revealed vertical extension rates ranging from 0.1 to 3.1 mm yr^{-1}[25–28], although faster growth (2–5 mm yr^{-1}) has been recorded for shallow-water pseudo-colonies in the Chilean fjords where high productivity may enhance accretion[29].

Benthic ROV (Remotely Operated Vehicle) surveys conducted over the last 20 years in the southern Adriatic Sea (Mediterranean Sea) documented a widespread presence of CWCs habitats, with the Bari Canyon area hosting the highest abundances and representing one of the five CWCs provinces in the Mediterranean Sea[11,30–34]. Situated along the Southern Apulian margin, the canyon exhibits extensive coral colonization along its steep, current-swept flanks and scarps, between 200 and 1000 m depth. This site is dominated by *Madrepora oculata*, with occurrences of *D. pertusum*, *Dendrophyllia cornigera*, and *D. dianthus*, and supports dense and structurally complex communities that act as essential fish habitats (EFHs) and biodiversity hotspots[30,35]. Occurrence of CWCs has also been documented at depths between 550 and 786 m off Monopoli[11,36]. On the eastern Adriatic margin, a rich and diverse CWCs assemblage has also been documented in submarine canyons off Montenegro, where *M. oculata* and *D. cornigera* co-occur between 420 and 540 m depth on hard substrates emerging from muddy seafloors[11].

In this study, we take advantage of two complementary natural experiments to investigate *in situ* growth dynamics of *Desmophyllum dianthus* in the Southern Adriatic Sea. The first is the accidental partial loss of a scientific mooring deployed at ~ 1200 m depth offshore the Bari Canyon (mooring EE). The mooring's deepest section remained anchored on the seafloor from 2020 to 2024, offering a unique, time-bounded four-year window for colonization and growth. A subsequent ROV survey aboard R/V *Gaia Blu* revealed extensive colonization along the mooring components. The second dataset consists of physical specimens of *D. dianthus* retrieved from a separate mooring part of the EMSO (European Multidisciplinary Seafloor Observatory) infrastructure deployed at ~ 500–600 m within the Bari Canyon (mooring BB) and recovered after one year.

Together, these datasets allowed us to estimate linear extension rates from both image-based measurements and direct sampling. We discuss the observed growth patterns in the context of environmental conditions and species-specific growth strategies and consider the broader implications for restoration and monitoring of deep-sea coral habitats.

Results

Megafaunal colonization of mooring EE and BB

A total of 182 coral specimens, all identified as *D. dianthus*, were observed along the vertical profile of mooring EE, with individuals distributed across the full range of instrumented depths (1171–1194 m, Fig. 1,2). The highest densities occurred at intermediate depths, particularly on the plastic cage structure (1178 m) which hosted 55 specimens (30.22% of the total) (Fig. 2, 3). The SeaCat instrument at 1183 m supported 39 specimens (21.43%), while the deepest device, the acoustic release at 1188 m, was colonized by 18 individuals (9.89%). Coral presence progressively decreased upward along the mooring, with 31 (17.03%) and 19 (10.44%) specimens associated

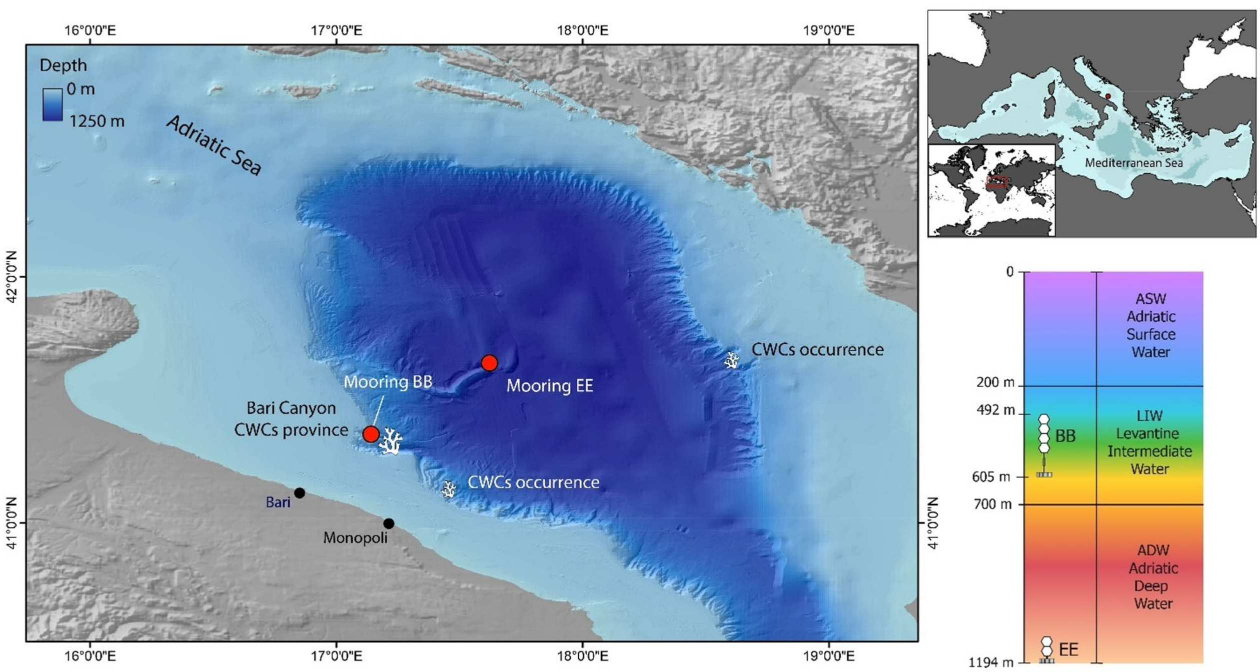

Fig. 1. Geographic location of the mooring systems, known occurrences of cold-water corals (CWCs), and schematic representation of the main water masses characterizing the southern Adriatic Sea with the vertical (not to scale) position of the moorings. Maps generated using ©ESRI ArcGIS Pro 3.3.2. The bathymetric data are derived from the EMODnet Bathymetry portal - http://www.emodnet-bathymetry.eu.

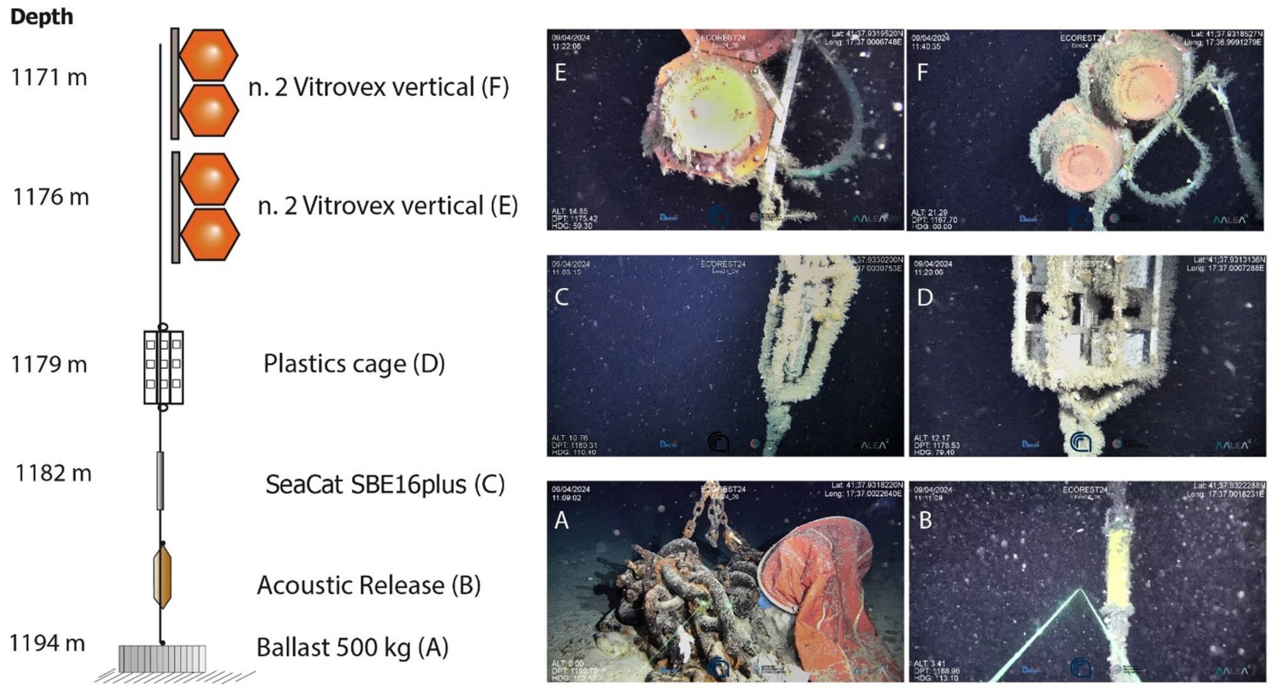

Fig. 2. Diagram illustrating the vertical configuration of the EE mooring system, with ROV frames showing examples of biological fouling by sessile organisms on mooring components (not in scale). Reported depths correspond to the mean depth of each component or component group.

with the first (1176 m) and the second (1171 m) group of buoys, respectively. An additional 20 individuals (10.99%) were located directly on the mooring rope. No corals were found colonizing the ballast at 1194 m.

On mooring BB, 4 specimens of *D. dianthus* were collected (Fig. 4), colonizing buoys between 571–504 m depth (1 individual), buoys of sediment traps at 595–571 m (1 individual), and acoustic releaser between 605–595 m depth (2 individuals).

Organisms size and growth rates estimation

The linear dimensions of *D. dianthus* individuals were measured across all usable video frames, yielding a mean size of 32.24 ± 1.66 mm (mean ± SE) for the population observed on mooring EE. Size distributions were relatively homogeneous across depth, with no statistically significant differences among mooring components. Mean corals size was 29.07 ± 0.50 mm on the acoustic release (1190 m), 32.68 ± 2.40 mm on the cage (1179 m), 33.13 ± 2.90 mm on the first group of buoys (1176 m), and 31.43 ± 1.00 mm on the second group of buoys (1171 m), indicating that environmental conditions conducive to coral growth were present throughout the mooring depth range (Fig. 3). Based on these size measurements and assuming colonization occurred at the time of mooring deployment (4 years), the estimated average growth rate for *D. dianthus* was 8.06 ± 0.41 mm yr^{-1}.

Coral specimens collected from mooring BB showed an average linear length of 6.5 ± 0.6 mm after one year (Fig. 4). The individual colonizing the buoys measured 6 mm, the larger specimen found on the buoys of sediment traps measured 8 mm, while the linear lengths of those found on the acoustic releaser (605–595 m) were 7 mm and 5 mm.

Oceanographic data

Oceanographic records from moorings BB and EE provide a characterization of the physical environment at the study sites (Table 1).

At mooring BB (Bari Canyon, 600 m depth), data collected between 11 April 2024 and 19 May 2025 indicate temperatures ranging from 13.78 to 14.75 °C (mean = 14.48 ± 0.15 °C) and salinity between 38.73 and 38.98 PSU (mean = 38.95 ± 0.04). The mean near-bottom current speed was 0.035 ± 0.0014 m s^{-1}, with a maximum of 0.21 m s^{-1}, showing two prevailing flow directions along the canyon axis (120° N and 290° N). The observed variability matches long-term data (2012–2020), showing temperatures between 12.5 and 14.78 °C and salinity between 38.59 and 38.97[37].

At mooring EE (South Adriatic Pit, 1194 m depth), measurements obtained between 2 April 2016 and 25 March 2019 recorded temperatures between 12.97 and 13.67 °C (mean = 13.38 ± 0.07 °C) and salinity between 38.72 and 38.93 PSU (mean = 38.79 ± 0.08). Mean current velocity was 0.064 ± 0.07 m s^{-1}, with a maximum of 0.49 m s^{-1}, and a dominant eastward direction (100–110° N).

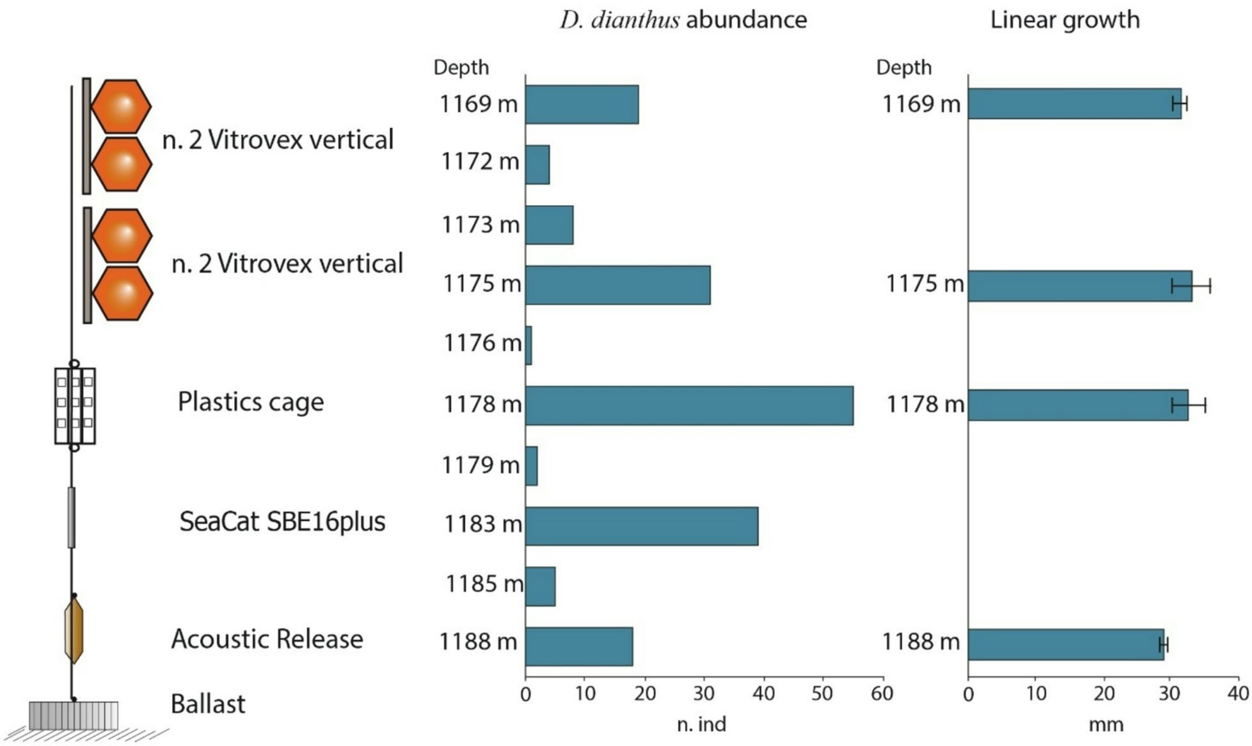

Fig. 3. Diagram of the vertical configuration of the mooring EE with boxplot of the number of *D. dianthus* specimens observed fouling mooring parts, and boxplot of linear growth of *D. dianthus* estimated from images processing. Error bars refer to standard errors. The diagram is not in scale.

Discussion

Cold-water corals (CWCs) are key ecosystem engineers in deep-sea environments, forming complex bioconstructions that enhance biodiversity and provide essential ecological functions[38,39]. Among these, *D. dianthus* is known to colonize both natural and artificial hard substrates[8,9], demonstrating remarkable ecological plasticity. This study provides new *in situ* evidence of its growth dynamics on two oceanographic moorings at 500–1200 m depth in the Southern Adriatic Sea based on ROV explorations and physical samples.

ROV surveys revealed extensive colonization by sessile fauna of the mooring EE, counting a total of 182 *D. dianthus* specimens along its vertical profile (1171–1194 m), with higher densities observed on plastic components such as the cage, suggesting a broad tolerance of *D. dianthus* to varying substrates. Image-based estimates yielded an average linear extension rate of 8.06 ± 0.41 mm yr^{-1} for *D. dianthus*, notably higher than most previous values derived from radiometric dating (0.1–3.1 mm yr^{-1}[25–28]), and comparable to values reported from high-productivity fjords (2–5 mm yr^{-1}[29]). Rate estimated from image analysis was confirmed by physical samples collected from mooring BB, where *D. dianthus* specimens recovered after one year displayed an average linear extension of 6.5 ± 0.6 mm. Our findings indicate growth rates that markedly exceed the majority of values traditionally employed in literature to estimate coral age[13]. This raises the possibility that such estimates, when based on lower growth assumptions, may substantially overestimate actual coral ages, especially in settings with environmental conditions conducive to faster growth. Such sustained growth observed in our study, in fact, may be favored by local environmental conditions. In particular, the Bari Canyon is influenced by episodic dense water cascading events, which are known to enhance benthic productivity by transporting organic-rich particles downslope while simultaneously limiting sediment deposition[40,41]. The mooring's suspended configuration, isolated from direct contact with the seafloor, may have further reduced sediment stress, creating a microhabitat particularly favorable to coral larval settlement and growth. Structural features such as surface complexity, material type, and orientation may also play a role and should be considered in future experimental design. However, the high growth rates observed may reflect the early life stage of the individuals sampled, capturing an initial phase of rapid extension that is characteristic of an asymptotic growth pattern in *D. dianthus*[28]. The slightly lower average linear growth observed in specimens collected from mooring BB after one year (6.5 ± 0.6 mm) could be explained by the time required for larval arrival, settlement, and successful attachment, processes that typically occur over several weeks[42], before measurable skeletal growth begins. Alternatively, part of the discrepancy between image-derived and physical estimates might reflect a minor systematic overestimation in size measurements from ROV imagery, due to optical distortions and perspective effects inherent to underwater imaging[43]. Although such errors were minimized through laser scaling and the use of planar reference frames, they cannot be completely excluded and could have slightly inflated the apparent extension rates in mooring EE. However, this potential bias is likely counterbalanced by an opposite source of uncertainty, since the annual rate derived for mooring EE assumes immediate post-deployment recruitment, a scenario that is improbable.

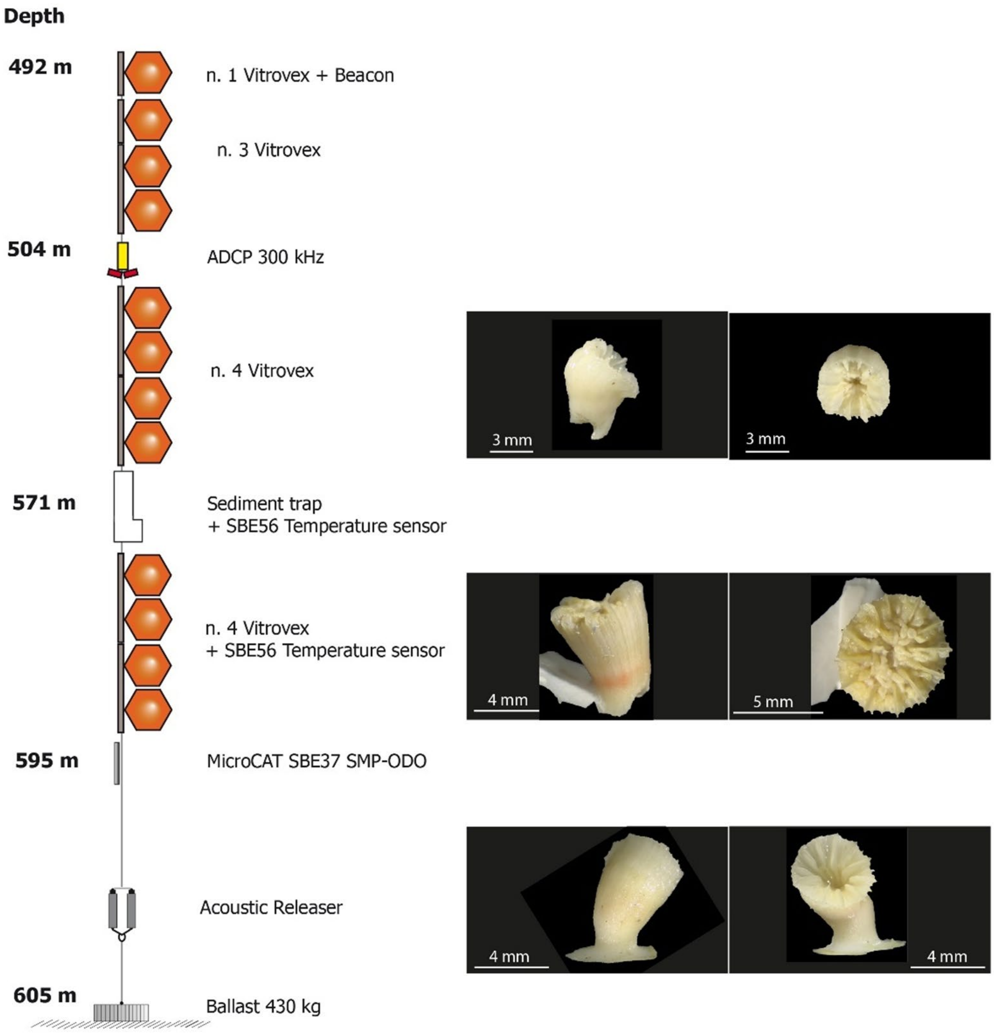

Fig. 4. Diagram illustrating the vertical configuration of the BB mooring system with individuals of *D. dianthus* found colonizing mooring components (not in scale). Reported depths correspond to the mean depth of each component or component group.

Mooring	Period (dd/mm/yy)	Range T (°C)	Average T (°C)	Range S (PSU)	Average S (PSU)	Average C (m s^{-1})	Max C (m s^{-1})	Prevailing current direction (°*N*)
BB	11/04/24 –19/05/25	13.78–14.75	14.48 ± 0.15	38.73–38.98	38.95 ± 0.04	0.035 ± 0.0014	0.21	120°–290°N
EE	02/04/16–25/03/19	12.97–13.67	13.38 ± 0.07	38.72–38.93	38.79 ± 0.08	0.064 ± 0.07	0.49	100–110°N

Table 1. Oceanographic records for temperature (T), salinity (S), current velocity (C) and direction registered by sensors mounted on mooring BB and EE.

The actual onset of settlement and skeletal growth may therefore have occurred later, implying that the one-year growth estimate might be conservative and possibly underestimated.

The *in situ* growth rates measured for *D. dianthus* in our study exceed most values previously reported for the species but they fall within the range documented for other scleractinian CWCs in the Mediterranean[24]. The temperature and salinity values recorded by the moorings fall within the typical range of the Levantine Intermediate Water, indicating favorable but not exceptional conditions for CWCs growth, and suggesting that hydrodynamic may play a more significant role. During the studied periods, current velocity reached up to 0.49 m s^{-1} at EE, while at BB a maximum velocity of 0.21 m s^{-1}, both predominantly oriented along the canyon axis (120° and 290° N). These peak values reflect the existence of energetic hydrodynamic events characteristic of the area[37,44], with intensity varying from year to year. Such events likely enhance food availability by resuspending and advecting organic particles downslope, while reducing sediment deposition. This combination of sustained particle fluxes and low sediment stress provides an energetically favorable environment that could sustain observed coral growth.

These findings have several implications for deep-sea restoration science. First, they provide rare, time-bounded data on CWCs growth and colonization under natural conditions, which can inform realistic recovery targets and timeframes for restoration planning. Secondly, the successful colonization observed on a scientific mooring provides additional evidence that artificial structures, when thoughtfully designed and strategically placed, can serve as effective substrates for coral recruitment. This supports the inclusion of engineered structures or modified infrastructure in restoration strategies.

Although caution is necessary when interpreting findings from a single case study, the data presented here represent valuable information for guiding the establishment of realistic restoration targets. Moreover, these insights are fundamental for the effective monitoring and evaluation of restoration interventions already underway. By providing concrete, time-bound evidence of growth and colonization dynamics in cold-water coral habitats, this study offers a valuable reference point for both planning and adaptive management in deep-sea restoration initiatives.

Methods

Oceanographic mooring EE and BB

Two fixed-point oceanographic moorings, EE and BB, have been operating for over a decade in the southern Adriatic Sea to collect data for detecting trends and variability in ocean conditions, supporting regional climate models, and enhancing our understanding of ecosystem dynamics in semi-enclosed basins[37]. Mooring BB, first installed in 2010 at 600 m depth in the Bari Canyon (41°20.46′ N 17°11.64′ E[45]), is part of the EMSO ERIC infrastructure and provides continuous, high-resolution time series essential for long-term ocean monitoring, while mooring EE, firstly deployed in 2012 at 1,194 m depth in the South Adriatic Pit (41°37.88′ N, 17°37.23′ E[45]), contributes complementary observations from deeper in the basin. EE was deployed in June 2020 but failed to respond to acoustic release commands during the planned recovery in February 2021. While the upper section detached and washed ashore near Brindisi in February 2023, a Remotely Operated Vehicle (ROV) survey in April 2024 revealed that the lower section remained upright in its original location, extending ~ 20 m above the seabed. Mooring BB was redeployed in April 2024 and successfully recovered in May 2025 for maintenance of instruments. Both moorings were operated following standardized protocols for calibration, deployment, and data quality control to ensure data reliability and comparability across long-term observations. Both moorings are equipped with current meter which measures intensity and direction of currents and also with CTD probes. Two types of current meters are installed on BB and EE moorings. On BB, an Acoustic Doppler Current Profiler (ADCP) of the type RDI Workhorse II Sentinel 300 kHz (Teledyne RD Instruments USA, Poway, California) was used, and details about the configuration is the same as reported in Paladini de Mendoza et al.[37]. The single point current meter on EE is the type Aanderaa RCM9 installed at a mean nominal depth of 1186 m (EE) with sampling interval set to 3600 s. SBE 37 SMP-ODO and SBE 16plus V2 SeaCat were installed at approximately 10 m above the seabed on mooring BB and EE, respectively, to acquire thermohaline parameters. Both CTDs are high-accuracy recorders designed for moorings or other long-duration, fixed-site deployments. The probes are equipped with optional pump for bio-fouling protection and data of water conductivity were measured by sensor, with accuracy of 0.0005 S m^{-1} and resolution of 0.00005 S m^{-1}; the water temperature by means of a thermometer, with accuracy of 0.005 °C and resolution of 0.0001 °C; and the water pressure by means of a pressure strain gauge sensor, with an accuracy of 0.002% of full-scale range.

ROV video collection, analysis and specimens sampling

During the ECOREST expedition (March-April 2024) onboard R/V *Gaia Blu*, a ROV dive was performed in the last known site of mooring EE using a SubAtlantic Tomahawk ROV, outfitted with a 4 K-resolution video system for high-precision observation. The ROV was equipped with a Kongsberg cNODE MiniS 31–180 USBL positioning system, integrating a pressure sensor to provide accurate geospatial and depth data at 1-second intervals. Laser scaling devices ensured consistent spatial reference across transects.

Information on macrofauna colonizing the mooring was derived either from annotations conducted in real time during dive and through post-dive analyses of ROV video footage. Following the methodology outlined in Castellan et al.[46], frames were systematically extracted from video every second using script developed in R software. Images were analyzed for taxonomic identification and specimens of *D. dianthus* were counted. When needed, these frames were cross-referenced with the corresponding high-definition video segments to enhance species identification accuracy.

During cruise EMSO-SA2025 onboard R/V *Gaia Blu* in 2025, organisms found on mooring BB components were collected, focusing primarily on corals. Samples were handled with clean gloves and sterilized tools, preserved in ethanol 99%, labeled with site and depth information, and stored at 4 °C. Taxonomical identification of individuals was performed using a ZEISS Stemi 305 stereomicroscope.

Megafauna size estimation

Video frames were subsampled to retain only those in which megafaunal organisms were clearly visible, with minimal motion blur or displacement. Selected images were subsequently processed in R using the ImageR package. Calibration was performed by defining known reference dimensions within each frame. When visible, the fixed distance between laser beams (10 cm) served as the primary scale reference for size estimation of corals. In frames where the laser beams were not visible, the dimensions of the mooring components themselves were used as alternative scale references. In such cases, careful attention was given to selecting portions of the mooring structure that appeared as close as possible to a planar view, to minimize distortion due to perspective.

The linear dimensions of corals, intended as length from the base to distal point of the calyx, were annotated for all usable frames, with each specimen measured three times. Mean values were then calculated for every individual within each mooring section, to enable comparisons of organism size across different depth intervals and the mooring structure.

Linear length of physical samples of *D. dianthus* colonizing mooring BB were measured using a caliper and photos of the individuals were collected using the Zeiss © Axiocam 208 color mounted on a ZEISS Stemi 305 stereomicroscope.

Data availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Declarations

Competing interests
The authors declare no competing interests.

Additional information
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