



OPEN The ecological role of *Pholas dactylus* (Mollusca, Bivalvia) empty burrows

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The study of biological rhythms has been widely explored in terrestrial and marine systems. Time-lapse photography can document species behaviour, avoiding observer disturbance, and record abundance and interactions. The present work aims to assess the role of the rock-boring bivalve *Pholas dactylus* Linnaeus, 1758 as a habitat former in the Conero Riviera, documenting the behaviour of the species associated with the common piddock and its burrows. The scan method approach was used to record two behaviours along 6 days of recording: Burrow Interaction (BI) and No Interaction (NI). A total of 34 taxa belonging to 5 phyla were identified, each one represented by one class: Gastropoda, Polychaeta, Malacostraca, Echinoidea and Teleostei. BI data were mainly related to standing on top of burrows, entering or leaving the burrows, or digging to keep it clean, with Gastropoda, Malacostraca and Teleostei displaying distinct activity patterns. The use of video monitoring enabled the analysis of species activity across diel cycles, highlighting the ecological value of the burrows created by *P. dactylus* and its role as an ecosystem engineer. This also provided new insights into the behavioural dynamics of benthic organisms associated with cryptic habitats.

Keywords Time-lapse, Allogenic engineer, Bioerosion, Biodiversity, Habitat complexity, North Adriatic

Ecosystem engineers play a fundamental role in shaping marine habitats by modifying physical structures and creating mosaics of complex frameworks, thus enhancing spatial heterogeneity and in turn influencing the species composition and abundance of surrounding communities¹. These organisms can be categorised into two main types: autogenic engineers, which build and maintain three-dimensional structures using their own living or dead tissues, and allogenic engineers, which transform materials from one physical state to another^{2,3}. Through a balance of constructive and bioerosion processes, ecosystem engineers drive community dynamics across a range of environments from polar to tropical ecosystems, including temperate areas^{4–6}. A notable example in the temperate Mediterranean Sea is the coralligenous assemblage where millennia of balanced bioconstruction and bio-erosion processes have created multilayered calcareous structures rich in biodiversity^{7,8}.

Bioeroders such as boring microorganisms, clonoid sponges, and bivalves act as key allogenic engineers, transforming living or non-living environmental material from one physical state to another². In particular, the Mediterranean rock-boring bivalves *Lithophaga lithophaga* (Linnaeus, 1758) and *Pholas dactylus* Linnaeus, 1758 significantly increase spatial heterogeneity by creating cryptic habitats, refugia, and niches. These structures facilitate species recruitment, offer protection against predators and hydrodynamic forces, and help reduce interspecific competition^{9,10}. Such modifications can influence biogeochemical cycles, affecting ecosystem stability, and overall, ecosystem resilience^{11–14}. However, this crucial ecological role is increasingly threatened by both direct and indirect anthropogenic pressures. Climate change and overharvesting are already disrupting the delicate equilibrium between bioconstruction and bioerosion¹⁵, and specifically for perforating bivalves, impacts led to the destruction of habitat complexity, the loss of macroalgal and zoobenthic cover, and in some cases, the desertification of entire coral and rocky reefs^{10,16–18}.

Understanding the interaction between organisms and their environment is central in ecology, and behavioural ecology has become a crucial component of the animal sciences. Biological rhythms, have been extensively studied in both terrestrial and marine ecosystems, revealing how behavioural and life cycle patterns align with environmental fluctuations over multiple temporal scales^{19–21}. Today, ecology is entering a “next-generation”

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phase, where quantifying species behaviour across spatio-temporal gradients is essential to understanding ecosystem functioning and productivity (e.g., energy and carbon transfer rates). This shift is supported by innovative tools and customised monitoring system hardware and software designed to collect behavioural and ecological data^{21–23}. In this context, time-lapse photography provides a non-destructive method for observing marine species in action, documenting their diversity and abundance, and revealing their interactions^{24,25}. These data are crucial for identifying the cascading ecological effects that may result from the loss of key species²⁶.

In this context, and for conservation purposes, it is crucial to understand the role of bioeroders in: (i) biological processes and interspecific interactions, (ii) species dynamics and temporal patterns, (iii) filter-feeders' rhythms, (iv) predation pressure on the benthic fauna, and (v) nutrient cycling through bioturbation. Such knowledge will improve our ability to track energy transfer from pelagic to benthic zones and to design tailored management strategies, in line with international objectives, such as the EU Biodiversity Strategy 2030 (COM/2011/0244).

In this study, we aim to explore the role of the common piddock, the bivalve *P. dactylus* as habitat former, and to investigate community-level behavioural responses to the structural complexity generated by these organisms across diel cycles. We use time-lapse photography as a non-invasive tool to capture interspecific interactions and to provide new insights into the ecological relevance of bioeroders.

Results

Image analyses

A total of 2,661 pictures were retrieved, corresponding to more than 130 h of recording. From the image analyses, a total of 34 taxa belonging to 5 phyla were identified, each one represented by one class: Gastropoda, Polychaeta, Malacostraca, Echinoidea and Teleostei (Supplementary Table 1). Among the 5 classes, Gastropoda, Malacostraca and Teleostei showed the highest occurrences: 6,892 (40.5%), 8,756 (51.5%) and 1,020 respectively (6%). For Gastropoda, BI (Burrow Interaction) data (42.5%) were mainly related to standing on top of the burrows, while NI (No Interaction) was related to their movement around the area (57.5%). Malacostraca data varied more: BI (50.5%) was related to crustaceans entering or leaving the burrows, standing on the edge of the burrow or digging to keep it clean (e.g., *Pilumnus* sp., *Xantho* sp., *Galathea* sp., *Palaemon* sp.), while NI data (49.5%) were related to events of movement or brief appearance. On the other hand, Teleostei were mostly looking out of burrows (24.9%), e.g. *Parablennius rouxi* (Cocco, 1833), or lying on top of them, e.g. *Parablennius gattorugine* (Linnaeus 1758) and *Gobius* sp., whereas NI data (75.1%) were related to short appearances while swimming around (e.g., *Serranus hepatus*, *Boops boops*, *Diplodus vulgaris*).

The results of the PERMANOVA showed a complex scenario in the burrows use of the observed organisms. More specifically, Gastropoda mainly changed behaviour along the recorded period (factor “days”, $p \approx 0.001$; Supplementary Table 2), showing an NI behaviour mainly during day 1 and 2, and BI in the following days (a posteriori pairwise, $p \approx 0.005$), with the species *Hexaplex trunculus* mostly contributing to the observed dissimilarities (Supplementary Table 3). Interestingly, in some cases, *H. trunculus* was seen interacting not only with empty burrows but also with burrows with living *P. dactylus* individuals, standing on them for several minutes. Conversely to Gastropoda, Teleostei showed differences in the interaction with holes only among timeslots (PERMANOVA, $p \approx 0.001$; Supplementary Table 2), more specifically between EN (Early Night) and D (Dawn), and LN (Late Night) and D (a posteriori pairwise, $p \approx 0.005$; SIMPER, dissimilarity 83.10% and 82.62%, respectively). These differences were mainly related to NI behaviour of *Serranus hepatus* (36.26% EN vs. D and 36.10% LN vs. D), *Parablennius rouxi* (21.48% EN vs. D and 19.38% LN vs. D) and unidentified fish during D compared to EN (12.82%), and BI behaviour of *P. rouxi* (13.58%) during LN (Supplementary Tables 2, 3). The analyses of Malacostraca revealed significant differences between days and timeslots (PERMANOVA, $p \approx 0.001$; Supplementary Table 2). However, pairwise comparison did not detect significant differences between days. In contrast, the same a posteriori tests identified differences between A (Afternoon) and EN, and A (Afternoon) and LN (a posteriori pairwise, $p < 0.05$; SIMPER, dissimilarity 77.07% and 78.94%, respectively). This difference recorded was mainly due to the taxa *Pilumnus* sp. and *Galathea* sp., which were observed mostly interacting with burrows (BI) during A, and the same species observed just moving around burrows during EN and LN (Supplementary Table 3). The most common taxa are reported in Fig. 1.

Visualisation of the circadian community's behavioural patterns with the nMDS is shown in Fig. 2. When considering Gastropoda (Fig. 2a), there was no clear separation among timeslots in the nMDS space, indicating similar patterns of occurrence across the day. Most observations were classified as NI, as reflected by the dominant red semicircles in the bubble plots. Unlike the general Gastropoda group, *H. trunculus* displayed a more dynamic temporal pattern, with higher levels of BI behavior during D, E, and EN. This is evidenced by the greater proportion of blue in the bubble plots and the wider separation of timeslots in the nMDS ordination. For Malacostraca (Fig. 2b), activity varied across timeslots, with higher occurrences recorded during night (EN to D). However, there was no clear predominance of either BI or NI behavior, as shown by the similar proportions of red and blue in the bubble plots. Regarding the class of Teleostei, higher occurrences are observed during day timeslots while the differences were found between BI and NI, as shown in Fig. 2c, with BI mainly represented in the night timeslots. Among Teleostei, *P. rouxi* follow the general pattern observed for the group while *S. hepatus* displayed majority of the data during the diurnal timeslots, especially during D.

Discussion

The present study provides novel insights into the behavioural dynamics of Gastropoda, Malacostraca, and Teleostei associated with *Pholas dactylus* habitats and their empty burrows in the Conero Riviera (North Adriatic Sea). The diel variation and habitat interactions observed across these taxa highlight the multifunctional ecological roles of these cryptic and neglected environments.

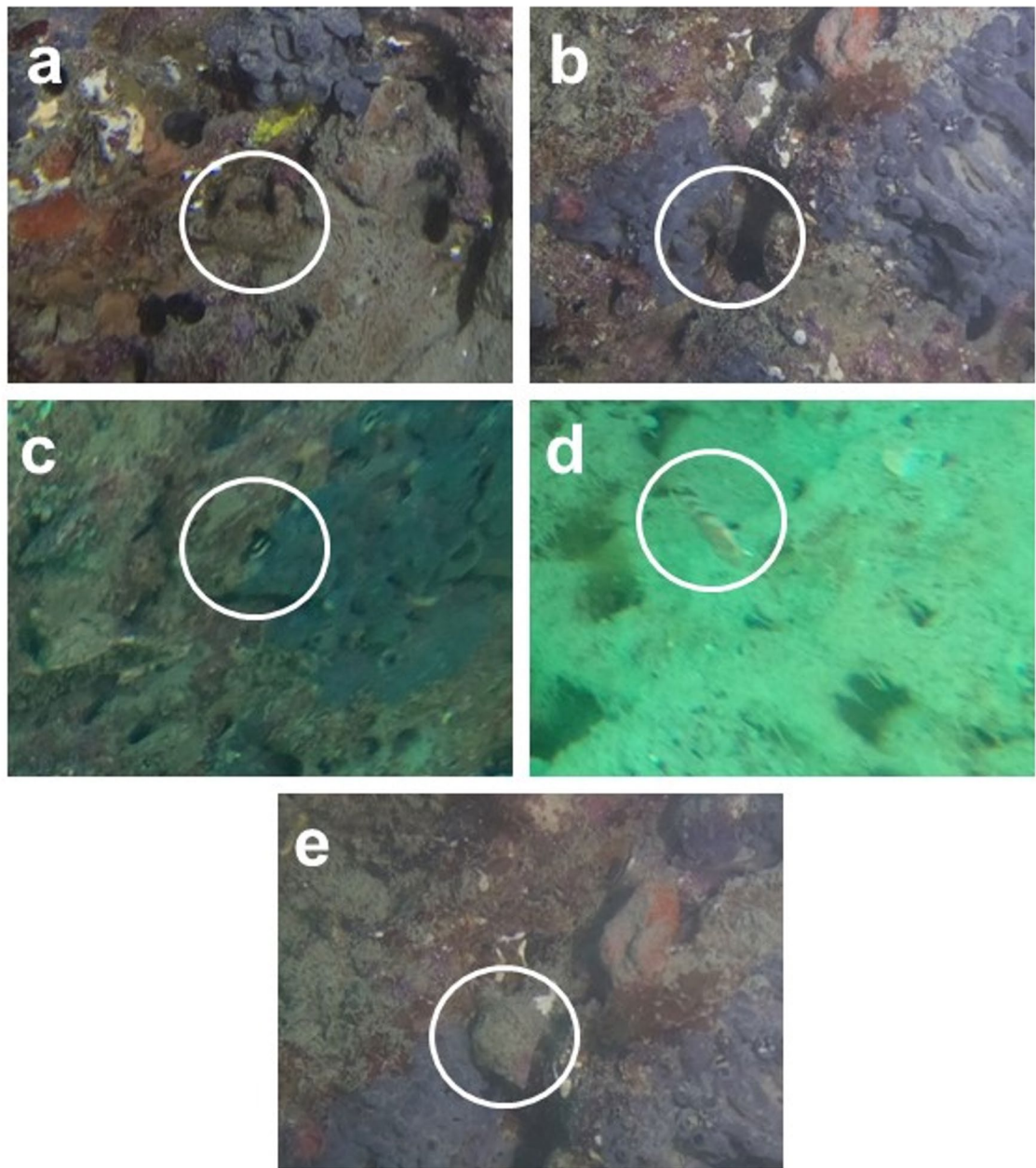


Fig. 1. Most common species recorded in the pictures: white circles indicate, (a) *Pilumnus* sp. in front of a burrow; (b) *Galathea* sp. on the edge of a burrow, (c) *Parablennius rouxi* emerging from a burrow, (d) *Serranus hepatus* swimming around the area, (e) *Hexaplex trunculus* moving around the area.

Gastropods, represented mainly by *Hexaplex trunculus*, exhibited no significant diel differences, with most occurrences classified as NI (No Interaction) (Fig. 2a). This result may derive from the fact that *H. trunculus* is a known predator, primarily targeting mussel populations by drilling through shells and extracting soft tissues using its muscular proboscis, influencing their community structure and dynamics^{27–30}. It is therefore plausible that the presence of *H. trunculus* around or interacting with empty burrows is related to a potential foraging behaviour. In fact, its prolonged feeding periods, which can last several days^{31,32}, likely explain the absence of discernible temporal variation for the BI (Burrow Interaction) behaviour, as individuals may remain stationary or intermittently present during extended feeding events.

In contrast, Malacostraca, notably represented by *Galathea* and *Pilumnus* species, demonstrated clear nocturnal activity, aligning with existing knowledge on crustacean trophic roles and their generally nocturnal foraging behaviour, from predators to filter feeders, grazers, and scavengers, contributing to the regulation of larval and phytoplankton populations, while also serving as prey for other invertebrates and fish^{33–35}. More specifically, considering the two main contributors to the group, *Galathea* sp. did not differ significantly between interaction with burrows and NI behaviours (Fig. 2b1), while *Pilumnus* sp. showed increased BI behaviour specifically during night-time (Fig. 2b2), likely related to reproductive dynamics. Specifically, increased evening

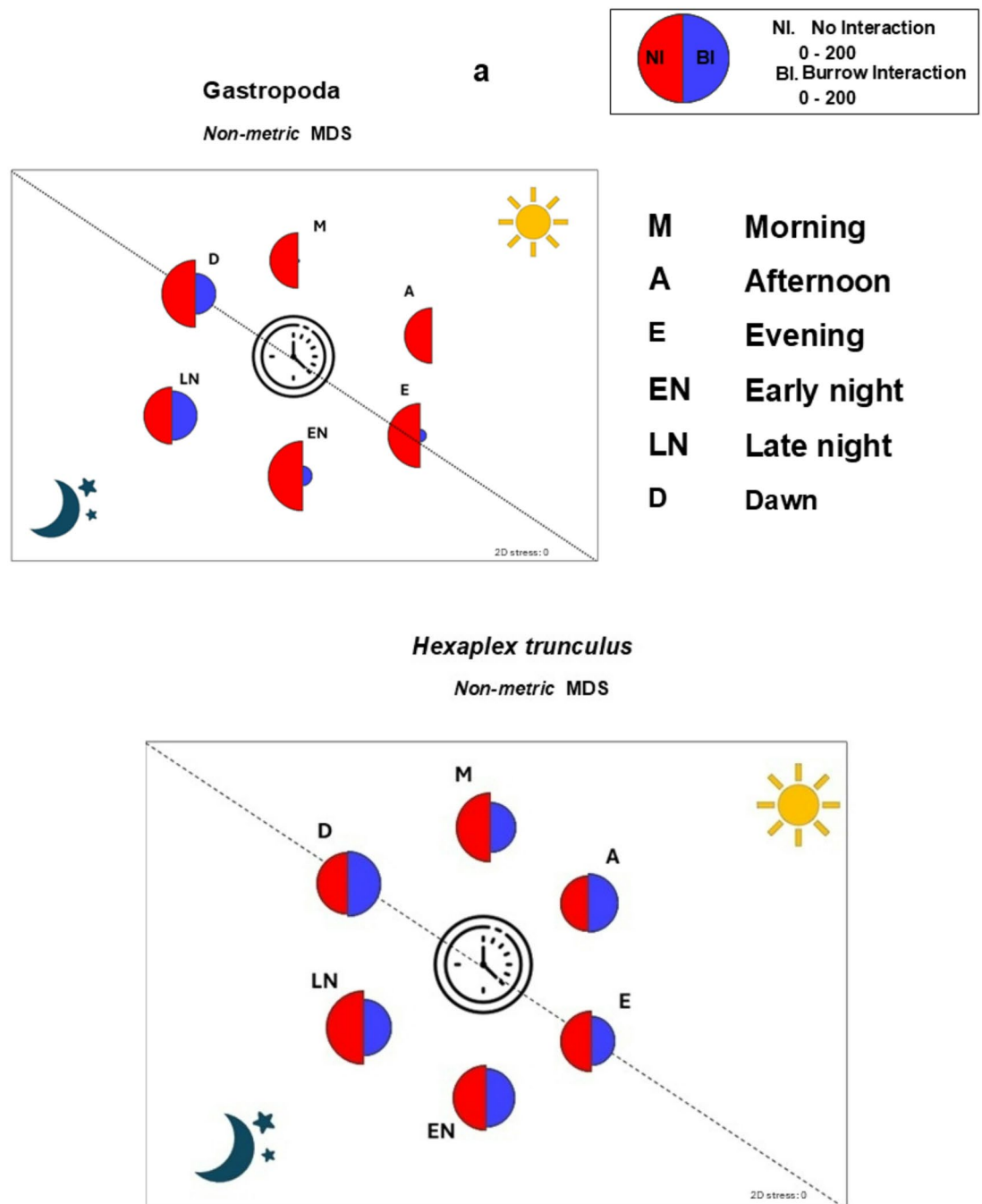


Fig. 2. Non-metric multidimensional scaling (nMDS) plot: bubble plots highlighting the distribution of relative abundance of behavioural data among timeslots for Gastropoda (**a**) with *Hexaplex trunculus*, Malacostraca (**b**) with *Pilumnus* sp. (**b1**) and *Galathea* sp. (**b2**), Teleostei (**c**) with *Parablennius rouxi* (**c1**) and *Serranus hepatus* (**c2**). No Interaction (NI) are shown as red bubbles, while interaction data are shown as blue (BI).

and reduced dawn activities match previously documented feeding patterns and reproductive behaviours in Pilumnidae, where females shelter in burrows during breeding periods, prompting male interactions at entrances, outlining the BI behaviour^{36,38,39}. On the other hand, NI data may reflect males browsing nearby. Conversely, the absence of behavioural differentiation in *Galathea* sp. may reflect ontogenetic shifts in habitat preference and cryptic behaviour patterns documented in juveniles compared to adults, which are described to be found at the burrow entrances^{40–42}.

Regarding Teleostei, *Parablennius rouxi* and *Serranus hepatus* displayed distinct activity patterns. These were described as diurnal, and our data showed that the activity peak was concentrated within the M (08:00–11:59) and A timeslots (12:00–15:59) (Fig. 2c). Blennids were predominantly diurnal yet demonstrated peak habitat

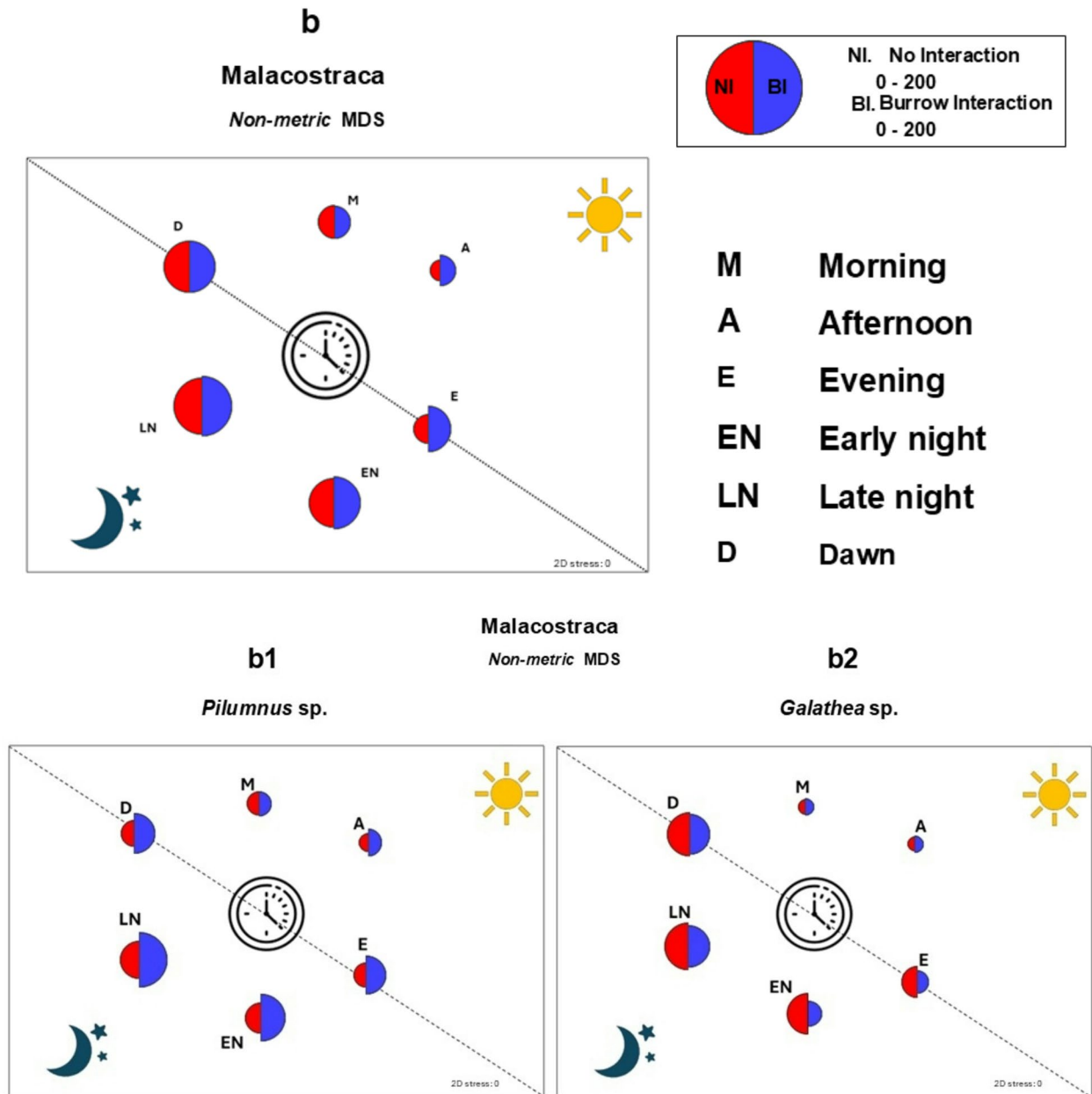


Fig. 2. (continued)

interactions (BI) at night, consistent with their known site fidelity and nesting behaviours within burrows and crevices^{43,44}. Their mating behaviour is closely tied to availability of burrows, often those eroded by endolithic bivalves. Males guard nests in small cavities and invite females to lay eggs, which they fertilise and protect, while satellite males patrol the area to opportunistically participate in fertilisation. Breeding periods occurs from May to July, which corresponds with the period of our study^{45–49}. Serranids, conversely, were exclusively diurnal, predominantly in the D time slot and showing no differences between BI and NI behaviours. The wandering behaviour of Teleostei could explain the lack of differences observed between days, suggesting that their presence is not necessarily related to empty burrows. However, the nesting behaviour of *P. rouxi* and the foraging behaviour of *S. hepatus* likely reflects broader ecological interactions and spatial distribution related to their diet and habitat use^{50–53}. These behaviours overlap considerably with benthic crustaceans, highlighting the crucial role of *P. dactylus* habitat.

Overall, the burrows created by *P. dactylus* function as critical multifunctional habitats, supporting various species through feeding, reproductive activities, and refuge provision across different life stages. Additionally, these bioengineered structures enhance environmental conditions by mitigating hydrodynamic stress, promoting sediment accumulation, and facilitating the coexistence of soft bottom with hard bottom fauna^{10,14}. As ecosystem engineers, bioeroding bivalves significantly contribute to biodiversity enhancement across multiple ecological scales, potentially explaining the peculiar biodiversity of the Conero area. Burrows can maintain their

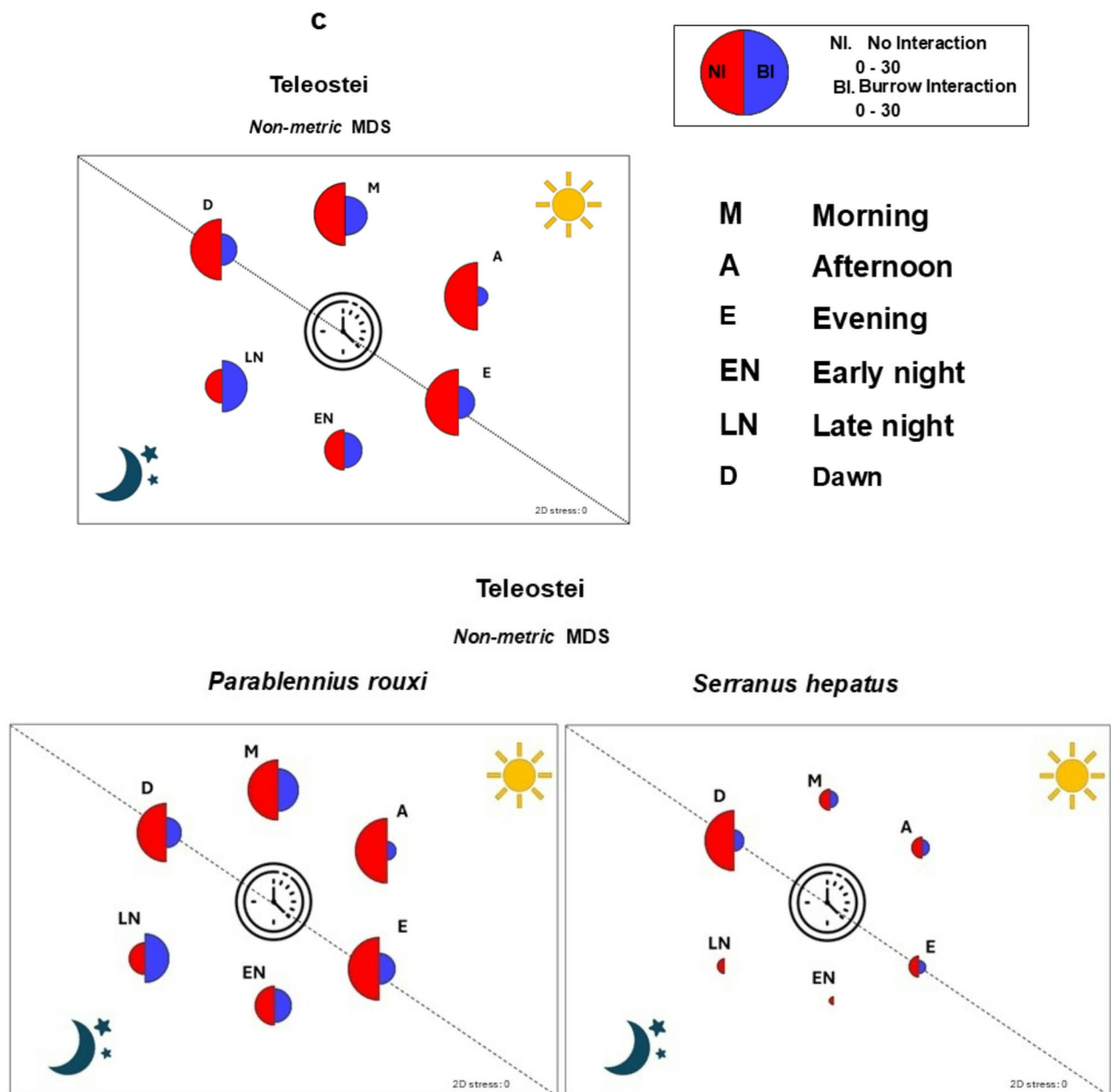


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ecological functions also in places where anthropic activities are intensive, a function rapidly lost in habitats where 3-dimensional species are the main responsible for habitat complexity and for the maintenance of local biodiversity.

Materials and methods

A time-lapse underwater camera was deployed by SCUBA divers at 7 m of depth in June 2022 in the Passetto area (43°37'01.0"N, 13°32'06.5"E; Conero Riviera, Ancona, Italy), to investigate the behavioural response and refuge selection of the taxa associated with habitats created by the bioeroding bivalve *Pholas dactylus*. The recording device consisted of a custom GoPro 8 mounted on a motherboard with an Atmel® ATmega 4809 microcontroller, data logger and DIP switch controller for different recording settings; a sensor for light (lumens) and temperature (°C) profiling was also present. The time-lapse system was equipped with a light system synchronised with the photo acquisition. The whole system was charged by an external battery pack (25Ah) connected by a wet-mate cable. Both the device and the battery pack were designed in stainless steel (AISI 316) and polyoxymethylene copolymer (POM-C) composite housings with a maximum operating depth of ~ 100 m (Fig. 3). The time-lapse system was developed by Ingenious Solutions SRLS.

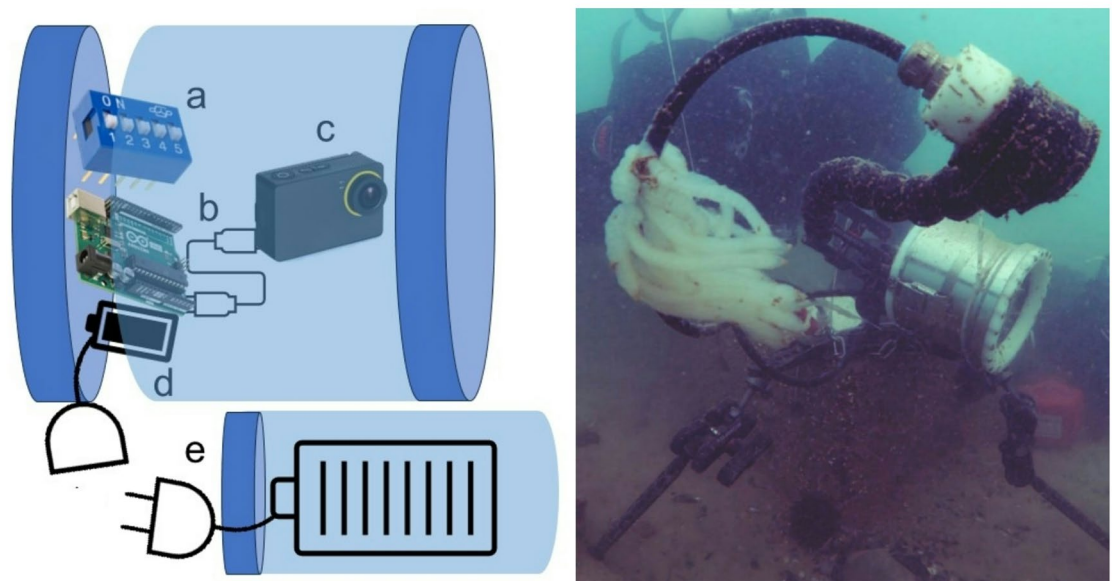


Fig. 3. Diagram of the time-lapse box recorder, Ingenious Solutions SRLS (Left). In the left picture dark blue and light blue represent the POM-C and stainless-steel parts respectively. **a** DIP switch controller to set different recording intervals by different button combinations (e.g. 3; 5; 8 min). **b** Microcontroller to program the different parts of the whole system (e.g. DIP switch controller, turning the camera and sensors on and off at the right moment, storing the data log of the images). **c** Custom GoPro 8 mounted on the motherboard. **d** Backup battery and wet-mate connector. **e**: External battery pack and wet-mate connector. Underwater picture of the time-lapse camera (Right), installed at the Passetto Area (Ancona, Italy).

The time-lapse camera was positioned on the seafloor framing a substrate with live specimens of *P. dactylus* to record the community associated with its cryptic habitat. The field of view was approximately 50 × 50 cm, and the camera was programmed to take an image every 3 min for 6 days (Fig. 3).

Image analyses

The scan method approach (i.e., the observation time divided in regular intervals and the behaviour of all visible animals recorded at the sample points, typically the instant at the end of each interval;^{54–56}) was used and adapted as standardised methodology to analyse behavioural data recording. All spotted organisms were identified at the lowest possible taxonomic level and the behaviour adopted associated with empty burrows was reported^{42,57,58}. Two main behaviour categories were defined a priori to describe the occurrence (or not), in a specific moment of the day, of an interaction among an organism and the burrows. Any target animal that interacted with the burrows, whether directly or not (e.g. partially emerging from the burrow, digging, standing on the edge of the burrow) was defined as BI (Burrow Interaction). Contrarily, if no interaction was detected (e.g. swimming or standing far from the burrows) the datum was recorded as NI (No Interaction). In case of low visibility (e.g. turbidity or sedimentation) obscuring the view of one or multiple burrows, data for that specific burrows were reported as NV (Non-Visible). For each organism and burrow, only one of the three events (BI, NI, NV) was recorded per frame (i.e. instantaneous sampling⁵⁴). An example of the retrieved picture is showed in Fig. 4.

To identify temporal patterns in faunal behaviour, six timeslots were identified within each day: Dawn (D) (04:00–07:59); Morning (M) (08:00–11:59); Afternoon (A) (12:00–15:59); Evening (E) (16:00–19:59); Early Night (EN) (20:00–23:59); and Late Night (LN) (24:00–03:59) following Enrichetti et al.²⁰. Each frame was therefore characterized in terms of the individual performing one of the behaviours mentioned above, in a specific burrow of the picture, in the relative timeslot (e.g. time 09:07, frame t1, burrow 1 and behaviour BI).

Statistical analyses

Patterns of change in mobile benthic communities' behaviour through time were analysed considering a two crossed factors design: days (random, 6 levels) and timeslots (fixed, 6 levels). Due to the low number of occurrences of some of the identified groups of organisms, only data on Gastropoda, Malacostraca and Teleostei were considered for further analysis. Each dataset was square root-transformed and dissimilarity matrixes based on the Bray-Curtis dissimilarity index were computed. Using these matrixes, a permutational multivariate analyses of variance (PERMANOVA;⁵⁹) with 9,999 permutations was performed per class. A posteriori pairwise comparisons were run in case of statistically significant differences in the main test. Analysis of similarity percentages (SIMPER;⁶⁰) were used to determine taxa mostly contributing to the dissimilarities within each class. Additionally, data were visualized using non-metric multi-dimensional scaling (nMDS) on averaged data of taxa and timeslot and then distances among relevant centroids were performed. Finally, the 'bubble' plot option was used to better represent timeslot and behaviours groups. All statistical analyses were performed with PRIMER 7 with the PERMANOVA + add-on package⁶¹ and a 95% confidence interval.

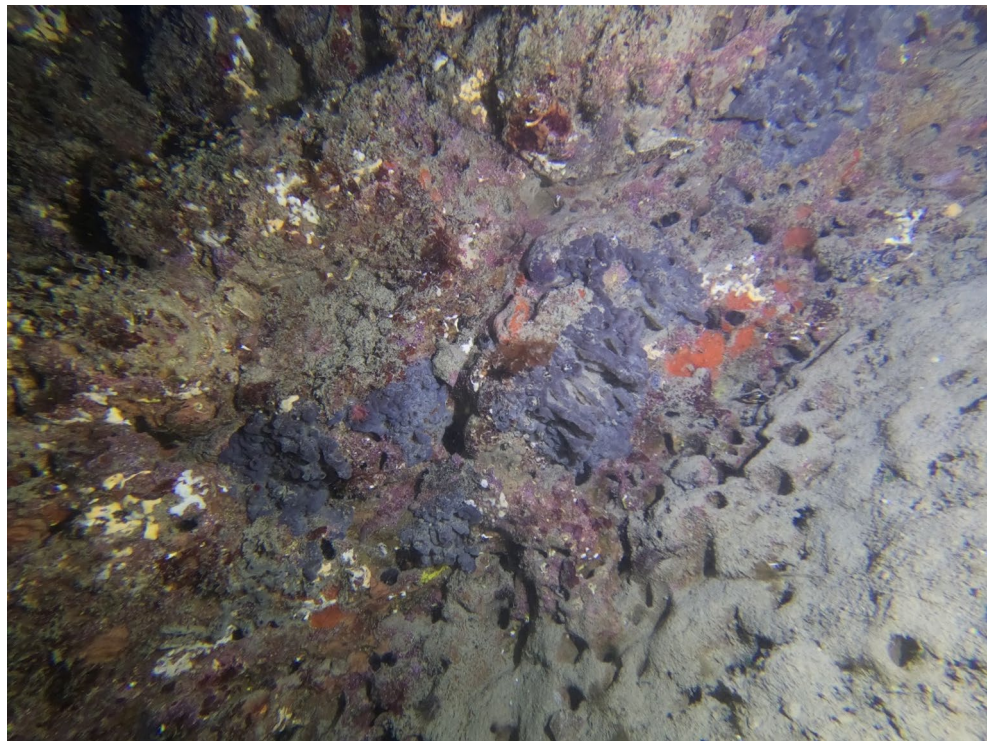


Fig. 4. Example of one of the frames obtained with the time-lapse device.

Data availability

Data is provided within the manuscript or supplementary information files.

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Author contributions

Study Design and Methodology, all authors; Experiment, T.M., C.C., B.C. and S.P. Data Treatment, T.M.; Interpretation, T.M., C.C., B.C. and S.P.; Original Draft Writing, T.M. and M.C.; Manuscript Review and Editing, all authors; Funding acquisition, C.C. and S.P. All authors contributed critically to the drafts and gave final approval for publication.

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Declarations

Competing interests

The authors declare no competing interests.

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