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***In situ* observation of circadian rhythm of polyps' opening and closing of the coral *Dendrophyllia ramea* (Linnaeus, 1758)**

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Abstract

A widespread population of the coral *Dendrophyllia ramea* has been revealed southeast of Syracuse (East Sicily, Italy) at around 75 m depth. *Dendrophyllia ramea* is an arborescent scleractinian coral, classified as “Vulnerable” in the Mediterranean IUCN Red List and listed in Annex B of the Barcelona Convention. It is considered rare because it is seldom recorded on the Mediterranean seabed. *In situ* observations of two selected colonies were carried out over three months using a custom-made underwater video recording system to increase knowledge about the ecology of the species, specifically its circadian rhythm. The area was also surveyed using a special navigation system integrated into a diver propulsion vehicle to map the colonies' position and distribution. The rhythms of the opening and closing of *Dendrophyllia ramea*'s polyps during the day were studied and linked to environmental factors, such as temperature, water flow, and direction.

The results show that *Dendrophyllia ramea* opens and closes its polyps according to its circadian rhythm and water flow in analogy with other anthozoans in different environments. The opening/closing frequency analysis showed that both colonies closed at least once daily with different periodicity; one colony closed on average a few hours earlier. This project gathered important information on *D. ramea*'s circadian rhythm, which is relevant for improving knowledge about the ecology of this species since it provides insights into its feeding behavior, reproduction seasonality, response to environmental changes, interactions with other species, and conservation needs.

Keywords: Scleractinian corals; time-lapse; polyp's rhythm; Ionian Sea; Global Underwater Explorers; East Sicily.

Introduction

The temperate mesophotic zone is the middle layer of oceans, usually found between 40 and 120 m below the surface, but it can extend down to about 200 m (Cerrano *et al.*, 2019). This region receives limited sunlight, resulting in diminished visibility but enough light for photosynthetic organisms to survive. Its depth interval varies depending on sunlight penetration, primarily due to solar radiation incidence and water clarity (Castellan *et al.*, 2022). The temperate mesophotic zone is a transition zone between surface waters strongly influenced by light, seasonal temperature variations, and wave motion, and deep-sea characterized by the constant absence of light and a more stable temperature. The exploration of mesophotic and deep-sea areas has shed light on the presence of rich benthic communities mainly characterized by Por-

ifera and Cnidaria (Idan *et al.*, 2021); these communities represent a hot spot of biodiversity, with an important role in structuring communities (Lesser *et al.*, 2018).

Dendrophyllia ramea (Linnaeus, 1758) is a colonial scleractinian, only reported in the temperate mesophotic zone, characterized by an orange-yellow arborescent skeleton with large white polyps whose colonies can reach 1 m in height and form structures and communities in a few areas of the Mediterranean Sea (Zibrowius, 1980; Salomidi *et al.*, 2010; Orejas *et al.*, 2017, 2019a, b; Salvati *et al.*, 2021). It and *Dendrophyllia cornigera* (Lamarck, 1816) are the largest species of Mediterranean colonial Dendrophylliidae corals. According to Zibrowius (1980), the two species differ in geographical and depth distribution and are not ecologically equivalent; in particular, *D. ramea* is a shallower species mainly encountered in the lower circalittoral zone. *Dendrophyllia ramea* is

present in the southern Mediterranean Sea, the Levantine area, and Atlantic waters and is of conservation interest (IUCN Red List, Annex B of Barcelona Convention). Its scattered distribution has not favored the acquisition of useful data to understand this species's ecology. Despite the large quantity of biological data derived from oceanographic survey campaigns and image acquisition using ROV (remote operated vehicle), data related to this species still needs to be improved (Orejas *et al.*, 2017). The start of technical diving and rebreathers has allowed us to discover and observe this species at various sites beyond the 40 m depth limit (Salvati *et al.*, 2021).

This coral, being a passive suspension feeder, is mainly concentrated on ridges where strong currents enhance food accessibility (Roberts *et al.*, 2006; Thiem *et al.*, 2006), making the capture rates dependent on water flow (Purser *et al.*, 2014; Gori *et al.*, 2015). Passive suspension feeders benefit from strong water flow to capture nutrition, limiting the energy necessary to feed; conversely, active suspension feeders are independent of water flow but require a large metabolic outlay to generate water flow. Therefore, the behavior of passive suspension feeders forces them to live in exposed positions in microhabitats with appropriate flow characteristics, making them maintain a low resistance filtering structure (La Barbera, 1984; Boero *et al.*, 1991; Wildish & Kristmanson, 1997; Wijgerde *et al.*, 2012).

Our knowledge about the ecology and biology of *D. ramea* is deficient and scattered, coming from colonies at different depths and on diverse substrates (Orejas *et al.*, 2019a). Only in recent years has there been an increase in studies relating to the physiology and ecology of *Dendrophyllia* spp., mostly laboratory studies (e.g., Reynaud & Ferrier-Pagès, 2019; Reynaud *et al.*, 2021). The few *in situ* studies on stable isotopes, lipid signatures, and other features of *D. ramea* have shown that they can feed on various food sources, including detritus, phytoplankton, and different size spectrum zooplankton (Orejas *et al.*, 2017). Analogous *in situ* observation on other temperate corals determined that certain factors are responsible for tentacle and polyp expansion, such as light, currents (flow), and prey availability (Bell *et al.*, 2006). Instead, laboratory experiments on the polyps' opening/closing rhythms in suspension feeders highlighted that despite measurements being more accurate and complex in controlled conditions, the filtration rate is overestimated, probably correlated to the food concentration, current speed, or light (Duchêne, 2017) which are different in the field.

On the other hand, in temperate corals, the stimuli that regulate the opening and closing of polyps are probably different since species containing algal symbionts are few, and those harboring symbionts may not be as dependent on the nutrients they provide as tropical species (Davy *et al.*, 1996). The alternating contraction and expansion of the polyps guarantees food acquisition, both by adhesion and direct capture, the removal of sediment, and the protection of soft tissues from predators. Most species contract during the day and expand at night, although intense currents favor the polyps opening even during daylight

hours. Several studies on polyps' motion helped to understand coral physiology in a changing environment in terms of light conditions, temperature, pH, oxygen, and other environmental variables and, consequently, how these variables play an essential role in feeding, competition, reproduction, and thus survival and fitness (Sebens & DeRiemer, 1977; Previati *et al.*, 2010; Li *et al.*, 2021; 2022). Previati *et al.* (2010) highlighted that above specific temperatures, oxygen consumption and polyp reactivity both decreased in all studied species, confirming reduced metabolic activity in Mediterranean gorgonians during periods of high temperature. Researchers have long agreed that most of the functions of living beings are regulated by circadian clocks, a molecular network that translates predictable environmental signals into organismal responses, including behavior and physiology (McFarland *et al.*, 1999; Aguzzi *et al.*, 2012; Sorek & Levy, 2012; Reitzel *et al.*, 2013). Studying the rhythmic regulation of coral's behavior would provide knowledge about the physiology of this key animal group (Oren *et al.*, 2015) and its response to environmental changes (Häfker *et al.*, 2023).

Time-lapse technology has been crucial in advancing research on coral polyps' rhythm and behavior because it allows the observation and analysis of slow processes or movements over an extended period, enabling the study of the polyps' daily activities and understanding how they interact with their environment over time. A similar approach was applied in a study of the occurrence and activity levels of macrozoobenthos in the Ross Sea, Antarctica, confirming its suitability as a tool for evaluating aspects of key macroinvertebrate foraging and behavior patterns in extreme environments such as marine caves (Cicogna & Pronzato, 1985) and polar habitats (Peirano *et al.*, 2016, 2023).

The present work aims to describe the polyp rhythms of *D. ramea* through *in situ* observations of two colonies found off Syracuse (East Sicily, Italy), using almost three months' worth of video recordings, taking environmental factors into consideration.

Material and Methods

Study area

The study site, known as Apollo Bank (36.9131° N, 15.194133° E), has a widespread *D. ramea* population discovered by local technical and rebreathers divers between 75 and 85 m depth. Apollo Bank is located on the northern border of the Malta Escarpment, representing the dominant morphological feature linking the deep Ionian basin to the east with the Hyblean carbonate platform to the west (Fig. 1). It is a 250 km-long underwater cliff that extends southwards from the eastern coast of Sicily towards the eastern coast of the Maltese islands and beyond (Argnani & Bonazzi, 2005). The sea bottom morphology is characterized by abrasion platforms carved on Miocene-Pleistocene carbonate succession and at least two paleo-cliffs of marine origin (Scicchitano &

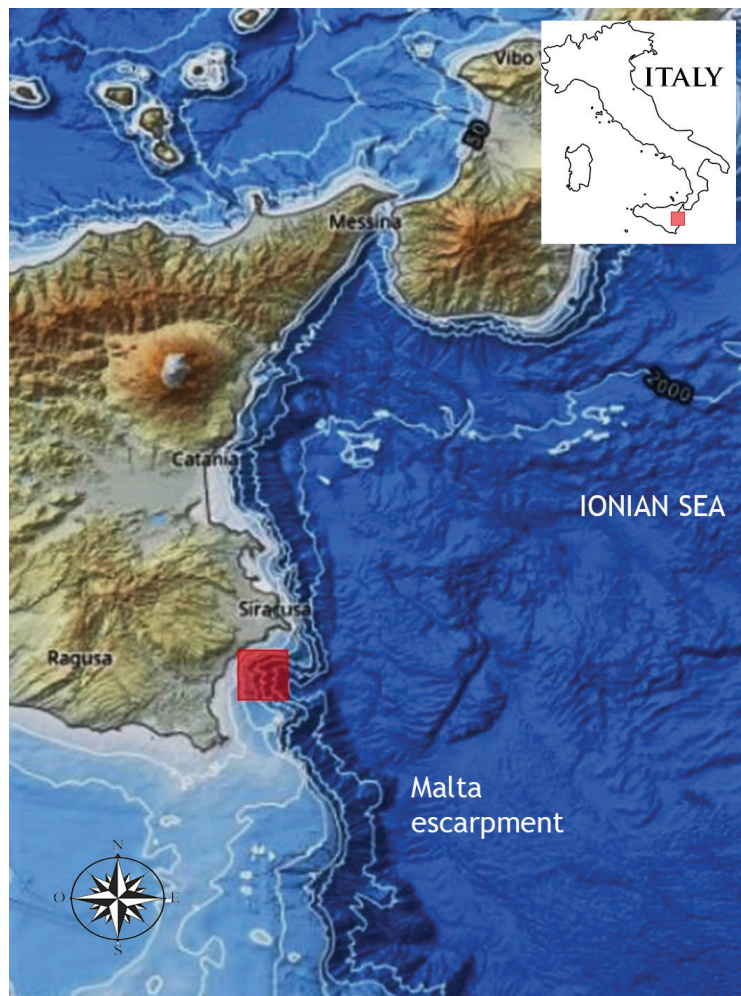


Fig. 1: The study area (red box) is located on the Malta Escarpment border. Map from EMODNET (<https://www.emodnet-bathymetry.eu/>).

Monaco, 2006). From a sedimentological point of view, due to its morphological and lithological characteristics and the absence of a fluvial sediment supply, the seabed mainly comprises hard rocky bottom (CONISMA, 2003). The study area is influenced by coastal currents that head south to the confluence of Capo Passero, where the impact of the front is determined by the meanders of the superficial Atlantic current that enters the Sicilian Channel. This results in a significant transport of suspended material and a fast mixing of coastal waters, which benefits the area's marine environment (CONISMA, 2003).

The sea bottom is mainly rock, fully covered by mostly soft sediment (fine sands/mud) with small rocky outcrops that, from 50 m depth, gently break up to a vertical step towards the open sea at 75 m water depth. The base, which forms a cliff, is about 83 m deep. The *D. ramea* population, according to local divers' descriptions, grows with different morphologies, either fan or cabbage shapes. The site was reported by technical divers in 2017, who also reported the presence of lost fishing gear on the sea bottom; this, together with the sale of *D. ramea* branches in local shops (Salvati *et al.*, 2021), suggests a strong fishing pressure in the area.

Time-lapse camera setup

A low-cost time-lapse video camera was specifically built by Blueresearch (<http://www.blueresearch.eu/>). The system comprises two Delrin™ housings with an external diameter of 7 cm and a length of 25 cm. One housing hosts a Mobius ActionCam (<https://www.mobius-cam.com/>) (full HD resolution 1920 x 1280 pixels) with a battery pack and control board. The other housing contains a 6-watt LED lamp with its battery pack. Every battery pack is composed of 14 AA NiMH cells. A wet pluggable sea cable connects the two cylinders to synchronize the camera with the light. The control board, which is composed of an Arduino Pro Mini single-board microcontroller, a DS3231 Real Time Clock module, a DC/DC converter, and two MOS-FETs, was set to switch on the light and camera and record a five-second video every hour for almost three months. A frame made of HDPE (high-density polyethylene) was produced to keep the camera and light housings at a relative distance of 25 cm and slightly convergent (10°). The two housings and the HDPE structure were fixed using inox steel Allen bolts to an adjustable stainless-steel tripod capable of keeping the camera and light 65 cm from the bottom (Fig. 2).

In addition, a stand-alone HOBO U24-002-C conductivity/salinity data logger (<https://www.hobodataloggers.com/>).

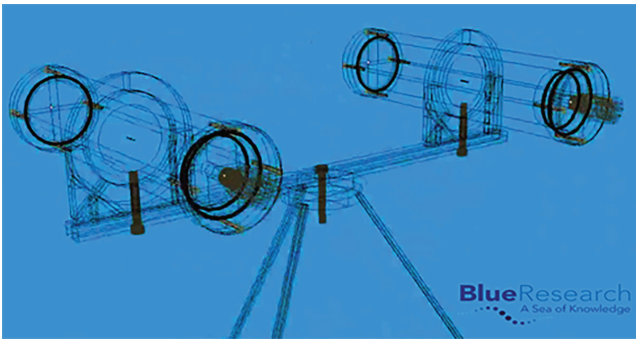


Fig. 2: Scheme of the time-lapse camera system.

com.au), set to record temperature and salinity every hour, was fixed to the metal tripod with two nylon cable ties.

Deployment of instruments

Considering the logistical difficulties of working at great depths, the support of specially trained technical and rebreather divers was essential. Divers from Global Underwater Explorers identified the most convenient area for positioning the time-lapse camera setup. The location was selected based on the presence of *D. ramea* colonies and the physical characteristics of the seabed to guarantee long-term stability, that is, the presence of a flat area close to the colonies to be monitored (Provenzani *et al.*, 2019). The instrumental setup was deployed on June 16th, 2018, by rebreather and open circuit divers at 75 m depth at a 95° compass direction from two colonies (identified as A and B). The colonies were each about 20 cm wide and 30 cm high. Colony A (60 polyps) is located on top of a rock boulder (around 25 cm from the bottom), and colony B (66 polyps) is closer to the seabed (around 10 cm from the bottom) (Fig. 3).

Once the camera setup was positioned pointing directly at the colonies at a 1 m distance, the instrument was ballasted using weights and secured with a string line to the surrounding rocks. Other *D. ramea* colonies in the same area were surveyed photographically within a 10 x 10 m grid to provide additional information on

the density around the monitored colonies. In addition, an exploratory path was carried out with the support of the SINAPSI navigation system for georeferencing the position of the surrounding colonies and getting an idea of their distribution in the site. Lastly, before ascending, the divers checked the camera's functionality and alignment. The procedure described here was documented on video, which is available on request.

The SINAPSI navigation system is a special tool equipped with sophisticated electronics and connected to a diver propulsion vehicle (DPV), specifically a SUEX DPV, which makes it possible to receive and process underwater navigation-acquired data (<https://www.suex.it/en/sinapsi/>). In particular, the system maintains constant orientation while diving, recording the route and fixing every target with a related georeferenced position. All colonies were documented photographically.

The same divers retrieved the camera system on October 28th, 2018. The camera was surfaced using a lift bag, assisted by divers in the first ascent phase, to ensure a constant slow ascent to prevent damage or flooding of the camera housings.

Data and statistical analysis

Video and photographs collected by divers during the exploratory path and the grid survey were analyzed to describe the site.

A total of 1374 videoclips (each 5 seconds long) were collected through time-lapse video and processed by image analysis. Each polyp from both colonies was counted and classified into two categories: open or closed. The movement and velocity of the suspended matter were used as a proxy for water flow and related direction; for this purpose, a fixed point of the frame was used as a reference for estimating the direction and intensity of the flow. Vagile animals surrounding the monitored colonies, such as fishes, crustaceans, and echinoderms were also documented.

The flow direction data was processed using the Kivi-

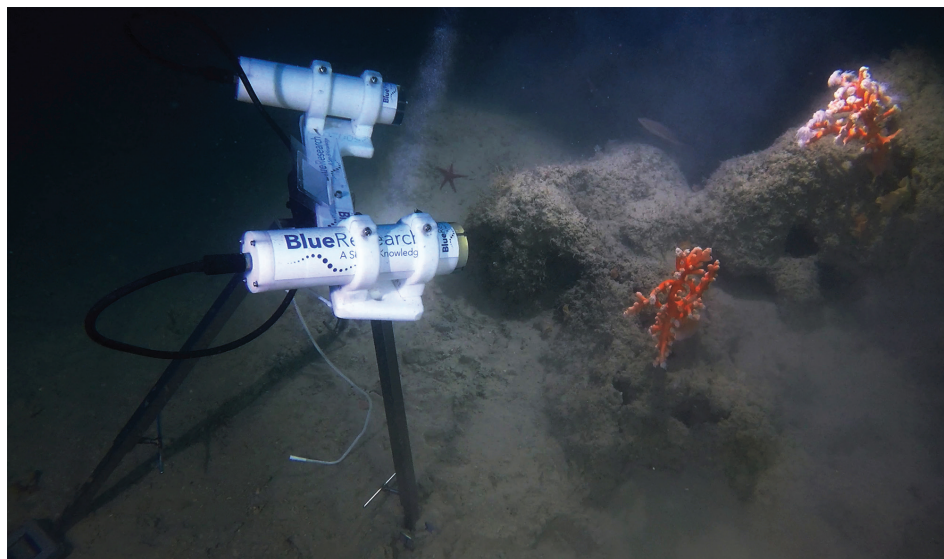


Fig. 3: Camera setup facing the two *Dendrophyllia ramea* colonies of the study (photo courtesy of Claudio Provenzani).

at diagram (Chambers *et al.*, 1983; Cleveland & McGill, 1984), a graphical method for showing data from multiple variables in a two-dimensional graph of three or more variables represented on axes with the same origin.

A regression analysis was applied to integer count data following the Poisson distribution,

$$Y \sim Poiss(\lambda_i) \text{ con } P(Y_i = k) = \frac{\exp(-\lambda_i)\lambda_i^k}{k!}$$

to study the following relation:

$$E(Y_i|\beta, X_i) = \exp(\beta_0 + \sum_{j=1}^p \beta_j X_j)$$

i.e., the dependence of the count variable on a set of explanatory variables X_i with $i: 1, 2, \dots, p$. If the response function is exponential, this facilitates the interpretation of the parameters.

β_i can be interpreted as the proportional change in the mean of opening/closing counts corresponding to a unit change in the variable X_i . Multiplied by 100, it can be interpreted as the percentage change in Y for a unit increase of X .

The following explanatory variables have been included in the model: temperature ($^{\circ}\text{C}$), observation time (0-23 h), and the flow's direction according to the various gradients from N to NW in the graphic (dummy variables 0-1 for each direction). Since the number of open polyps in each colony is complementary to that of the closed one, the model has been applied to the open polyps (colonies A and B).

Results

The general videos made by the divers during the exploratory path revealed an extensive area characterized by a sandy-silty bottom with rocky outcrops varying in size from pebbles (20-40 cm) to boulders or outcrops rising a few meters over the seafloor. On the muddy seabed, an extensive cover of hydroids was observed as well as red coralline algae, encrusting and submassive Porifera (*Axinella* sp.), tunicates [*Halocynthia papillosa* (Linnaeus, 1767)], bryozoans (*Reteporella* sp.), echinoderms [*Hacelia attenuata* Gray, 1840, *Peltaster placenta* (Müller & Trochel, 1842), and Cidaridae], and polychaetes (*Protu-*

la sp.). The red coral *Corallium rubrum* (Linnaeus, 1758) was particularly abundant in rocky outcrops, mainly in crevices or small vertical walls. Additionally, numerous pieces of lost fishing gear (ropes and lines) were observed. The SINAPSI survey showed that *Dendrophyllia ramea* colonies are mainly aligned in a direction perpendicular to the axis of the canyon (Fig. 4).

Colonies of *D. ramea* were mainly found on the outcrops. Overall, seven large *D. ramea* colonies (> 25 polyps), six small/medium-sized colonies (< 25 polyps), and three single corallites were counted within the 100 m² grid with an estimated density of 0.16 colonies m⁻². Two distinct coral morphologies were found in the study area: the largest colonies were fan-shaped (Fig. 5A), while the small ones had a more spherical, “cauliflower” shape (Fig. 5B). The fan-shaped colonies showed an opening/closing phase differentiated according to the side of exposure, for example, the closure of one side's polyps corresponded with the opening of the polyps on the opposite side. The small colonies, conversely, did not show this side-dependent opening/closing phase.

Counting the total daily hours in which the polyps were closed for each colony showed that both colonies had a similar trend, with colony B closing on average two hours earlier except for two occasions (July 25th-27th, 2018, and August 8th, 2018), while colony A had more hours of closure than colony B (Fig. 6). The two colonies closed at least once a day, with colony A remaining closed on average for 3.5 h while colony B remained closed for 2 h; both predominantly closed in the daytime (Fig. 7).

The recorded water temperature during the survey period ranged from 14.7 to 16.7 $^{\circ}\text{C}$ (Fig. 8). A comparison of the two colonies's total closures with the relative recorded temperatures did not show a specific relationship between closure and temperature values. The flow mainly came from the fourth and second quadrants. Temporal differences in the flow direction throughout the day were identified. The main direction of the flow was SE regardless of the period, while at night, it alternated with E and N currents. In the morning and afternoon, currents from the SE alternated mainly with currents from the N and NW, while in the evening, currents from the SE alternated with those from the NW, N, and E (Fig. 9).

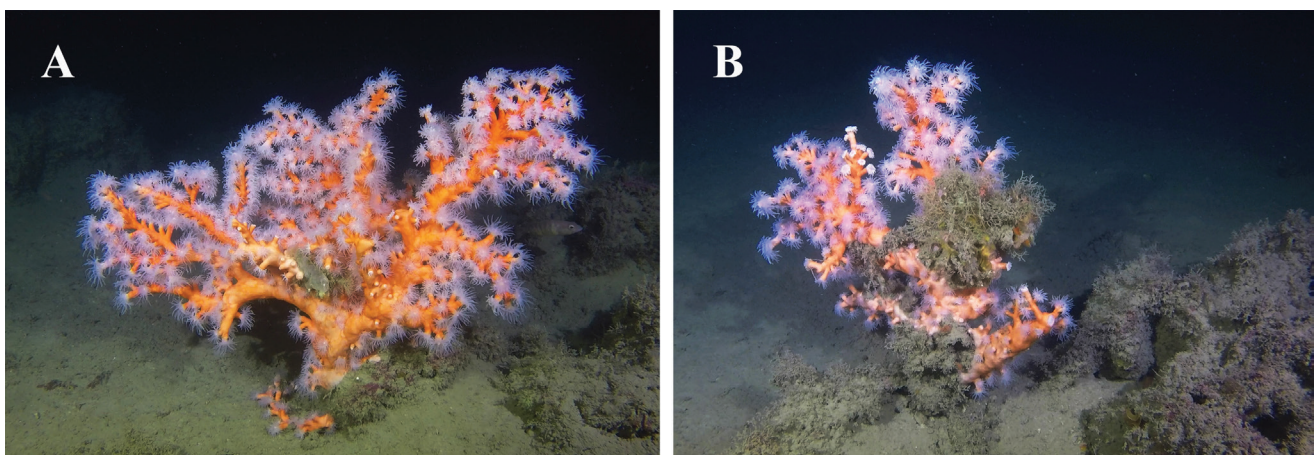


Fig. 4: Colonies of *Dendrophyllia ramea* exhibiting two different morphologies: Fan-shaped (A) and cauliflower (B) (photos courtesy of Claudio Provenzani).



Fig. 5: The survey by SINAPSI system. In the box is the positioning of the site respect of the escarpment. The yellow circle represents the position of *Dendrophyllia ramea* colony.

According to the results of Poisson regression model coefficients (Table 1), a temperature increase of one degree contributed to an increase of about 25% in colony A's polyps opening; between 11:00 and 18:00, a significant increase in closure was recorded (Table 1). At the same time, a clockwise flow from the N to S quadrants was associated with the openings of colony A's polyps,

increasing it from 7.7% (N) to 32.7% (S). Increased flow in the SW quadrant was associated with an increase in closures by 15.1% (Table 1).

Conversely, the temperature did not influence the number of open polyps in colony B. There was a significant increase in closed polyps from 7:00 to 20:00, a few hours earlier than colony A (Table 2). A significant increase in openings (5.01%) was observed only in correspondence with an easterly current; a decrease was recorded in correspondence with other current directions.

The video analysis allowed the identification of fish and crustaceans around the two colonies of *D. ramea*. Nine species of fish [*Anthias anthias* (Linnaeus, 1758), *Diplodus vulgaris* (Geoffroy Saint-Hilaire, 1817), *Diplodus sargus* (Linnaeus, 1758), *Muraena helena* Linnaeus, 1758, *Pagrus pagrus* (Linnaeus, 1758), *Phycis phycis* (Linnaeus, 1766), *Scorpaenodes arenai* Torchio, 1962, *Serranus cabrilla* (Linnaeus, 1758), *Zeus faber* Linnaeus, 1758], and four species of crustaceans, including *Palinurus elephas* (Fabricius, 1787) and *Scyllarides latus* (Latreille, 1803) were identified. Except for *D. vulgaris*, *S. cabrilla*, and *A. anthias*, whose presence was not associated with a recurring time interval, these species were observable during low light hours, from 17:20 to 06:20 (Fig. 10).

Two curious phenomena were observed: one specimen of the echinoderm *Peltaster placenta* (Müller & Troschel, 1842) was seen for six continuous days, and a school of fish, *Centracanthus cirrus* Rafinesque, 1810, moving very fast, was seen for one hour from 1:20 to 2:20 of July 7th, 2018.

Discussion

The study area, located on the break of the slope of the Malta escarpment, was revealed to be suitable for *D. ramea* corals. This study confirmed that this species prefers areas close to where a prevailing water flow comes from deeper areas. The flow analysis shows that the *D. ramea* community is well located in areas with strong water circulation, mainly by currents with a southward direction. The analysis also shows that large colonies modify their morphology in a planar growth perpendicular to the

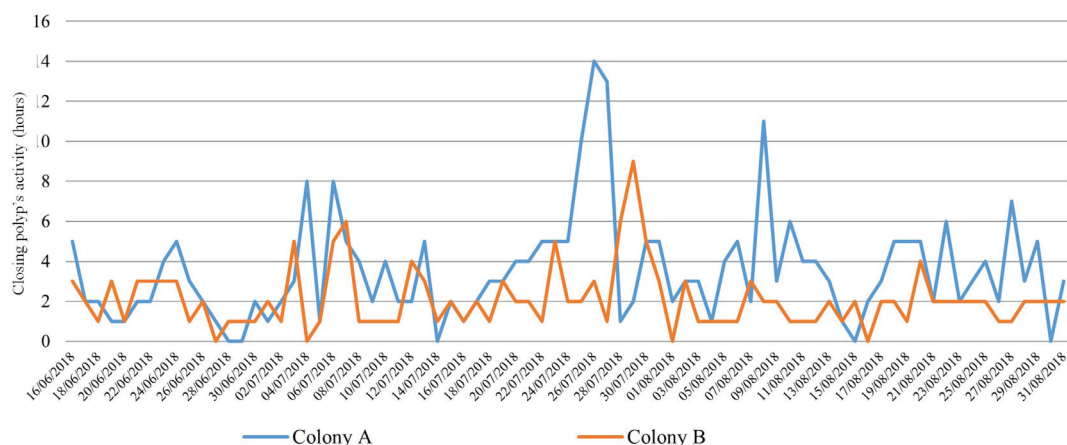


Fig. 6: Closing polyp's activity (hours) from 16th June 2018 to 31st August 2018.

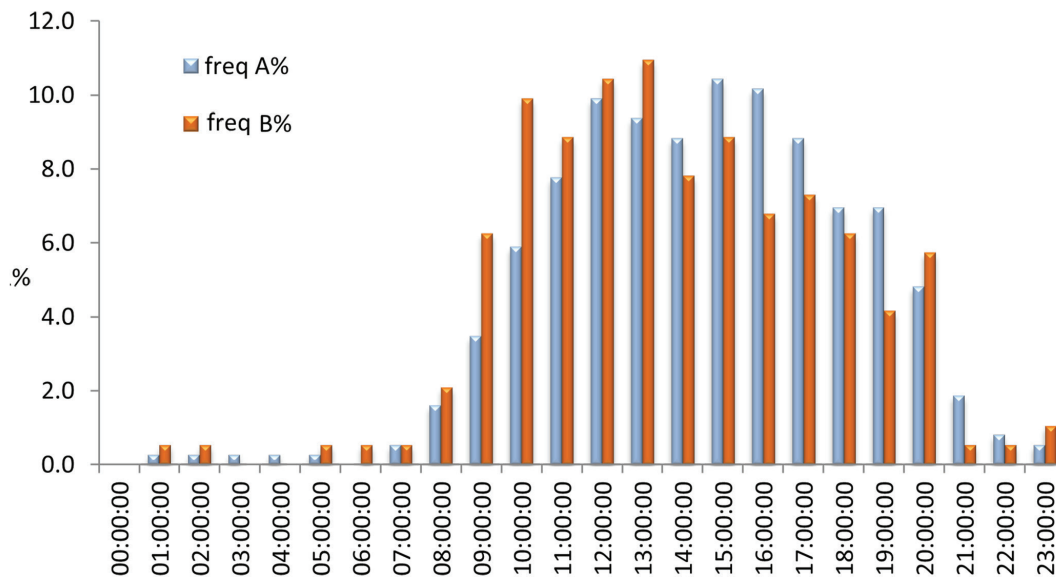


Fig. 7: Frequency (%) of closing polyps in the two colonies throughout the day.

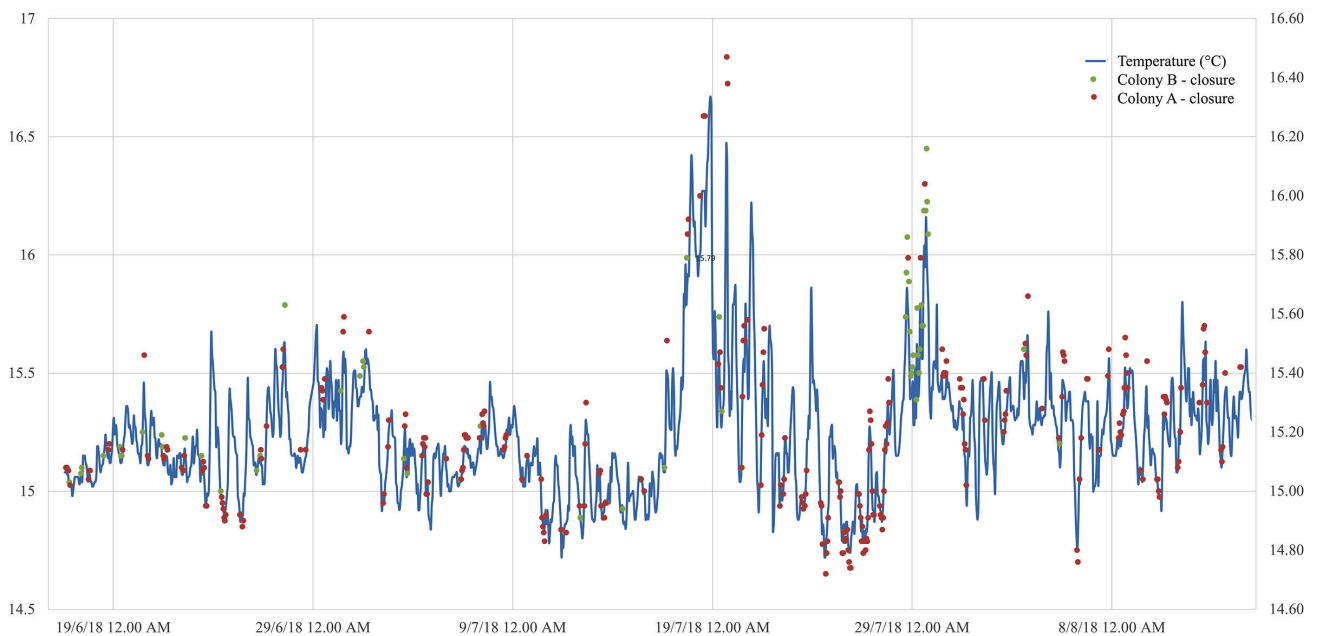


Fig. 8: Water temperature in relation with the total closure of colonies A and B, during the observation period (from 19th June to 12th August 2018).

dominant flow direction, analogously to the behavior of other corals (Riedl, 1971). Coral morphology and orientation in relation to flow and turbulence have been studied in tropical species (Johnson & Sebens, 1993; Kaandorp, 1999; Reidenbach *et al.*, 2006) and in the deepsea (Cyr *et al.*, 2016; De Clippele *et al.*, 2018; Sanna *et al.*, 2023). Indeed, suspension feeders need a strong enough flow to ensure the supply of food, nutrients, and oxygen, as well as the removal of waste and sediments, but not so strong to break the colony or mechanically distort the feeding structures (Helmuth & Sebens, 1993). *Dendrophyllia ramea* is a filter feeder that captures food during the expansion of its tentacles and alternates periods of expansion and feeding with periods of contraction and hypothetical inactivity (Robbins & Shick, 1980). As early as Parker (1919), it has been argued that flow is a stimulus for expansion; while the expanding polyp increases

its absorption of oxygen due to morphological changes to ensure a satisfactory amount of energy, its expansion in the presence of sustained currents would compensate the energy expenditure with a greater quantity of food-carrying filtered water per unit of time.

In many temperate waters and non-symbiotic tropical anthozoans, a circadian rhythm has been observed, with polyps opening at night and contracting during the day (Bell *et al.*, 2006). In our study, the circadian rhythm of the colonies manifested itself not as the total closure of all polyps but with an increase in the frequency of contracted polyps during the day; from 08:00 to 20:00, the percentage of contracted polyps rose by 15%. The continuous water movement recorded during observation suggested a positive energy balance despite the high percentage of opened polyps over the 24-hour cycle. This is further evidenced by the fact that during sporadic events

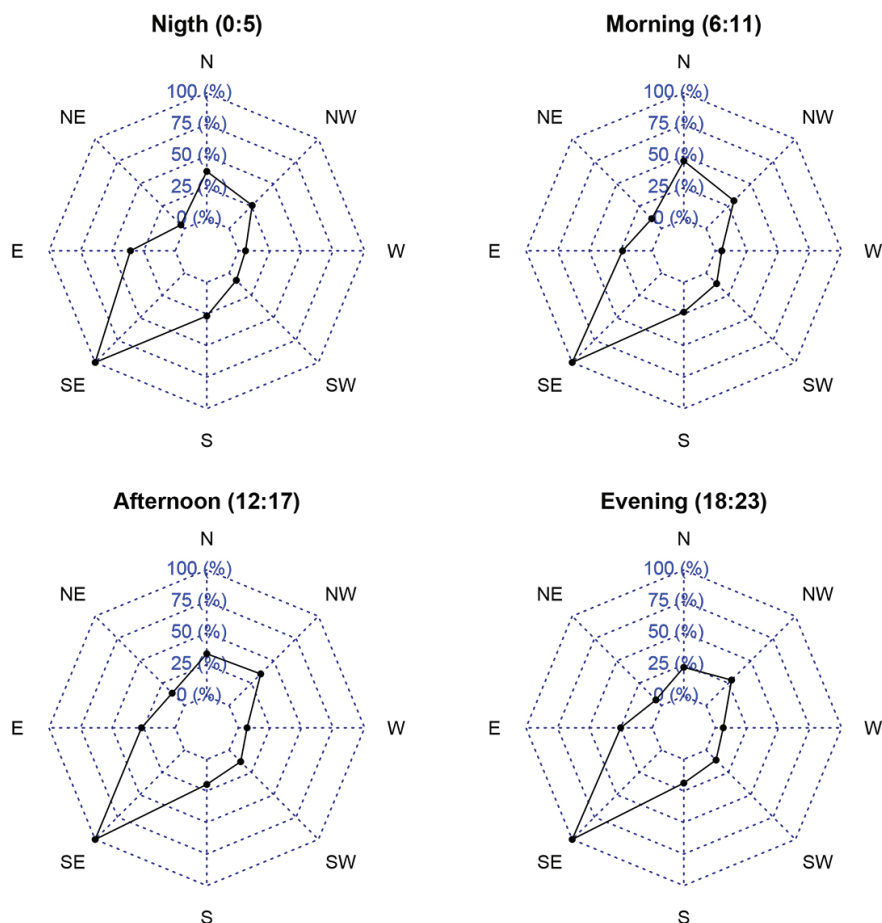


Fig. 9: Kiviatt chart of flow directions. The values inside the brackets represent the percentage of each direction on the total of the detected directions.

of strong diurnal current recorded during the study, the colony's polyps were sometimes completely open as if it were night, while during periods of nearly absent flow during the night, closing was sometimes brought forward by an hour.

The hypothesis that the current may be, for some cnidarians, a stimulus for the opening of the polyps is supported by an early study (Batham *et al.*, 1960), in which the extroflexion of an anemone's tentacles was noted due to current-induced deformation of the body wall and the stimulation of sensory cells concentrated in the parietal region of the mesentery.

Although the colony has a higher percentage of polyps closed during the day, it is interesting to know that a single polyp is closed only for a few hours at a time (3 h 30 mins). Understanding what regulates the closing time of a single polyp would be important in determining if the colony closed some of the polyps during the day as an effective strategy or if it is only a genetic inheritance. It would also be useful to understand whether contraction of the polyps is an energy-saving strategy or a precise physiological function attributable to "recovery".

Among the functions attributable to the contraction of polyps in non-symbiotic cnidarians, in addition to feeding and sediment removal, is protection against predators (Bell *et al.*, 2006). In our study, the greatest diversity of ichthyofauna around the colonies was concentrated at

night, and we did not record any fish predation on the two colonies. This was also the case with the echinoderm *P. placenta*; no interactions or evident predatory activities were observed despite the same individual having been in proximity to one of the two colonies for six consecutive days. This echinoderm is known in the literature as a predator of black corals, such as *Parantipathes larix* (Esper, 1788) (Bo *et al.*, 2019).

It is commonly known that some species can switch between passive and active modes depending on varying environmental conditions (Duchêne, 2017). Nevertheless, in this study, the polyps' behavior was constant. In three hours of recording, no movements attributable to active feeding were ever observed, although it was possible to recognize macrozooplankton (Euphausiacea or Mysida) in the vicinity of individual polyps. The lack of evidence for active feeding could lead to the hypothesis that the main diet of this species is particulate organic matter (POM), as Coppari *et al.* (2019) observed for the black coral *Antipathella subpinnata* (Ellis & Solander, 1786), a Mediterranean mesophotic species that lives in similar environmental conditions.

Although no literature provides information on the seasonality of *D. ramea*'s reproduction, neither gamete releases nor morphological alterations of the polyps were observed during the study period, which suggests a reproductive phase. This could be in accordance with what was

Table 1. Poisson regression applied to determined counts on opening data polyp colony A. The estimates of the model coefficients for each variable and their significance are reported.

Parameters	Estimate	Std.Error	Z value	Pr(> Z)
Temperature (°C)	0.247	0.015	16.03	<2e-16
Factor(hour) 0	0.076	0.237	0.318	n.s.
Factor(hour) 1	0.066	0.238	0.278	n.s.
Factor(hour) 2	0.076	0.236	0.320	n.s.
Factor(hour) 3	0.109	0.236	0.462	n.s.
Factor(hour) 4	0.134	0.236	0.575	n.s.
Factor(hour) 5	0.119	0.235	0.507	n.s.
Factor(hour) 6	0.057	0.235	0.321	n.s.
Factor(hour) 7	-0.014	0.235	-0.062	n.s.
Factor(hour) 8	-0.128	0.235	-0.544	n.s.
Factor(hour) 9	-0.309	0.235	-1.318	n.s.
Factor(hour) 10	-0.420	0.235	-1.787	n.s.
Factor(hour) 11	-0.604	0.235	-2.568	0.010
Factor(hour) 12	-0.584	0.235	-2.481	0.010
Factor(hour) 13	-0.624	0.236	-2.646	0.008
Factor(hour) 14	-0.691	0.236	-2.920	0.003
Factor(hour) 15	-0.650	0.237	-2.746	0.006
Factor(hour) 16	-0.707	0.237	-2.983	0.003
Factor(hour) 17	-0.571	0.237	-2.409	0.016
Factor(hour) 18	-0.499	0.237	-2.106	0.035
Factor(hour) 19	-0.337	0.237	-1.426	n.s.
Factor(hour) 20	-0.153	0.237	-0.649	n.s.
Factor(hour) 21	-0.014	0.237	-0.060	n.s.
Factor(hour) 22	0.066	0.237	0.279	n.s.
Factor(hour) 23	0.058	0.237	0.243	n.s.
Dummy (W. F. Direction) N	0.077	0.019	3.941	8.12e-05
Dummy (W. F. Direction) NE	0.098	0.030	3.273	0.001
Dummy (W. F. Direction) E	0.327	0.019	16.567	<2e-16
Dummy (W. F. Direction) SE	0.263	0.017	15.461	<2e-16
Dummy (W. F. Direction) S	0.229	0.021	10.854	<2e-16
Dummy (W. F. Direction) SW	-0.151	0.029	-5.093	3.52e-07
Dummy (W. F. Direction) W	-0.002	0.034	-0.049	n.s.
Dummy (W. F. Direction) NW	-0.021	0.021	-0.989	n.s.

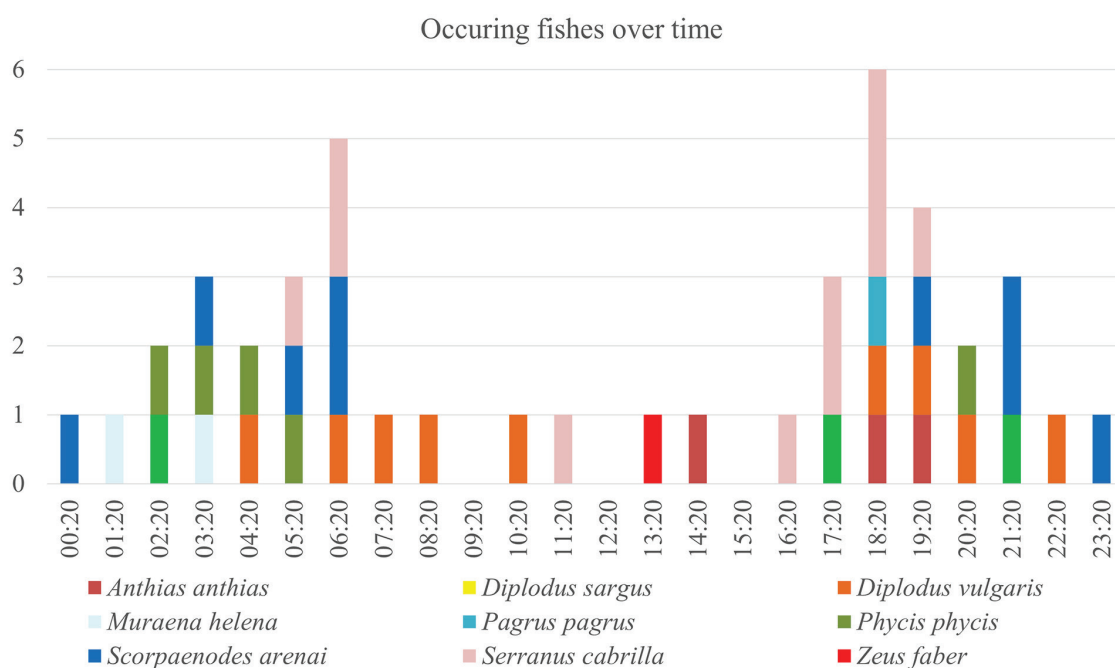


Fig. 10: The occurrence of fish species over 24 h of observation.

Table 2. Poisson regression applied to determined counts on opening data of polyp colony B. The estimates of the model coefficients for each variable and their significance are reported.

Parameters	Estimate	Std.Error	Z value	Pr(> Z)
Intercept	4.439	0.221	20.115	<2e-16
Temperature (°C)	-0.017	0.014	-1.209	n.s.
Factor(hour) 0	-0.016	0.023	-0.696	n.s.
Factor(hour) 1	-0.012	0.023	-0.438	n.s.
Factor(hour) 2	-0.009	0.024	-0.377	n.s.
Factor(hour) 3	0.006	0.024	0.259	n.s.
Factor(hour) 4	-0.010	0.024	-0.426	n.s.
Factor(hour) 5	0.006	0.024	0.236	n.s.
Factor(hour) 6	-0.012	0.024	-0.501	n.s.
Factor(hour) 7	-0.104	0.025	-4.236	2.28e-05
Factor(hour) 8	-0.316	0.026	-12.071	<2e-16
Factor(hour) 9	-0.499	0.028	-18.047	<2e-16
Factor(hour) 10	-0.509	0.028	-18.466	<2e-16
Factor(hour) 11	-0.569	0.028	-20.232	<2e-16
Factor(hour) 12	-0.568	0.028	-20.342	<2e-16
Factor(hour) 13	-0.555	0.028	-19.861	<2e-16
Factor(hour) 14	-0.493	0.027	-18.04	<2e-16
Factor(hour) 15	-0.415	0.027	-15.476	<2e-16
Factor(hour) 16	-0.371	0.027	-13.959	<2e-16
Factor(hour) 17	-0.336	0.026	-12.023	<2e-16
Factor(hour) 18	-0.263	0.026	-10.234	<2e-16
Factor(hour) 19	-0.186	0.025	-7.470	8.01e-14
Factor(hour) 20	-0.088	0.024	-3.639	0.0003
Factor(hour) 21	-0.033	0.024	-1.381	n.s.
Factor(hour) 22	-0.009	0.024	-0.370	n.s.
Factor(hour) 23	-0.004	0.024	-0.161	n.s.
Dummy (W. F. Direction) N	-0.003	0.017	-0.190	n.s.
Dummy (W. F. Direction) NE	-0.214	0.027	-7.883	3.19e-15
Dummy (W. F. Direction) E	0.050	0.017	2.937	0.003
Dummy (W. F. Direction) SE	0.026	0.014	1.846	n.s.
Dummy (W. F. Direction) S	-0.058	0.018	-3.121	0.002
Dummy (W. F. Direction) SW	-0.058	0.025	-10.958	<2e-16
Dummy (W. F. Direction) W	-0.055	0.028	-1.935	0.053
Dummy (W. F. Direction) NW	-0.074	0.017	-4.240	2.24e-05

observed for the congener *D. cornigera*, studied during the same period (spring/autumn) by other authors (León *et al.*, 2019). Their study did not detect larvae inside the polyps or evident reproductive events.

Conclusions

Conserving vulnerable coral species is a complex problem that requires an improved understanding of their biological and physiological functions. Their capability to contract, extend, and wave-movements influences how they feed, grow, and reproduce; consequently, all these aspects could play an important role in their adaptability and response to environmental stress.

This study is based on data collected *in situ* at the coral colonies' location over almost three months. The results show a clear circadian rhythm of partial opening and closing of the polyps despite being strongly influenced by the intensity of the current. This last aspect, of great interest for the ecology of this protected species, needs to be further investigated using current profilers to obtain

a quantitative estimate of the flow's intensity. With this data, more information is available on the feeding behavior of this species. Studying coral's circadian rhythms and their interconnection with environmental variables could make it possible to predict how various species will respond to environmental perturbations, including climate change.

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References

- Aguzzi, J., Company, J.B., Costa, C., Matabos, M., Azzurro, E. *et al.*, 2012. Challenges to the assessment of benthic populations and biodiversity as a result of rhythmic behavior: Video solutions from cabled observatories. *Oceanography and Marine Biology – An Annual Review*, 50, 235.
- Argnani, A., Bonazzi, C., 2005. Malta Escarpment fault zone offshore eastern Sicily: Pliocene-Quaternary tectonic evolution based on new multichannel seismic data. *Tectonics*, 24, TC4009.
- Batham, E.J., Pantin, C.F.A., Robson, E.A., 1960. The nerve-net of the sea anemone, *Metridium senile* (L.): the mesenteries and column. *Quarterly Journal of Microscopical Science*, 101, 487-510.
- Bell, J.J., Shaw, C., Turner, J.R., 2006. Factors controlling the tentacle and polyp expansion behavior of selected temperate Anthozoa. *Journal of the Marine Biological Association of the United Kingdom*, 86 (05), 977.
- Bo, M., Canese, S., Bavestrello, G., 2019. On the coral-feeding habit of the sea star *Peltaster placenta*. *Marine Biodiversity*, 49, 2009-2012.
- Boero, F., Cicogna, F., Pessani, D., Pronzato, R., 1991. *In situ* observations on contraction behavior and diel activity of *Halcampoides purpurea* var. *mediterranea* (Cnidaria, Anthozoa) in a marine cave. *Marine Ecology*, 12 (3), 185-192.
- Castellan, G., Angeletti, L., Montagna, P., Taviani, M., 2022. Drawing the borders of the mesophotic zone of the Mediterranean Sea using satellite data. *Scientific Reports*, 12 (1), 5585.
- Cerrano, A., Bastari, B., Calcinaï, C., Di Camillo, D., Pica, S. *et al.*, 2019. Temperate mesophotic ecosystems: gaps and perspectives of an emerging conservation challenge for the Mediterranean Sea. *The European Zoological Journal*, 86 (1), 370-388.
- Chambers, J., Cleveland, W., Kleiner, B., Tukey, P., 1983. *Graphical Methods for Data Analysis*. Wadsworth, 158-162.
- Cicogna, F., Pronzato, R., 1985. A time-lapse photography equipment for the investigation of macrozoobenthos survey. *Rapports et process-verbaux des reunion CIESM*, 29 (6), 183.
- Cleveland, W., McGill, R., 1984. Graphical Perception: Theory, Experimentation, and Application to the Development of Graphical Methods. *Journal of the American Statistical Association*, 79 (387), 531-554.
- CONISMA, 2003. *Studio di fattibilità propedeutico all'istituzione dell'area marina protetta "Penisola della Maddalena – Capo Murro di Porco" Siracusa*. Ministero dell'Ambiente & Comune di Siracusa Eds. Technical Report, 99 pp.
- Coppiari, M., Ferrier-Pagès, C., Castellano, M., Massa, F., Olivari, E. *et al.*, 2019. Seasonal variation of the stable C and N isotopic composition of the mesophotic black coral *Antipathella subpinnata* (Ellis & Solander, 1786). *Estuarine, Coastal and Shelf Science*, 106520.
- Cyr, F., van Haren, H., Mienis, F., Duineveld, G., Bourgault, D., 2016. On the influence of cold-water coral mound size on flow hydrodynamics, and vice versa. *Geophysical Research Letters*, 43 (2), 775-783.
- Davy, S.K., Lucas, I.A.N., Turner, J.R., 1996. Carbon budgets in temperate anthozoan-dinoflagellate symbiosis. *Marine Biology*, 126, 773-783.
- De Clippele, L.H., Huvenne, V.A., Orejas, C., Lundälv, T., Fox, A. *et al.*, 2018. The effect of local hydrodynamics on the spatial extent and morphology of cold-water coral habitats at Tisler Reef, Norway. *Coral Reefs*, 37, 253-266.
- Duchêne, J.C., 2017. Activity rhythm measurement in suspension feeders. p. 761-782. In: *Marine Animal Forests*. Rossi, S., Bramanti, L., Gori, A., Orejas, C. (Eds). Springer International Publishing, Cham.
- Gori, A., Reynaud, S., Orejas, C., Ferrier-Pagès, C., 2015. The influence of flow velocity and temperature on zooplankton capture rates by the cold-water coral *Dendrophyllia cornigera*. *Journal of Experimental Marine Biology and Ecology*, 466, 92-97.
- Häfker, N.S., Andreatta, G., Manzotti, A., Falcitore, A., Raible, F. *et al.*, 2023. Rhythms and clocks in marine organisms. *Annual Review of Marine Science*, 15, 509-538.
- Helmuth, B., Sebens, K., 1993. The influence of colony morphology and orientation to flow on particle capture by the scleractinian coral *Agaricia agaricites* (Linnaeus). *Journal of Experimental Marine Biology and Ecology*, 165 (2), 251-278.
- Johnson, A.S., Sebens, K.P., 1993. Consequences of a flattened morphology: effects of flow on feeding rates of the scleractinian coral *Meandrina meandrites*. *Marine Ecology Progress Series*, 99, 99-114.
- Kaandorp, J.A., 1999. Morphological analysis of growth forms of branching marine sessile organisms along environmental gradients. *Marine Biology*, 134, 295-306.
- Idan, T., Shefer, S., Feldstein, T., Ilan, M., 2021. New discoveries in Eastern Mediterranean mesophotic sponge grounds: updated checklist and description of three novel sponge species. *Mediterranean Marine Science*, 22 (2), 270-284.
- La Barbera, M., 1984. Feeding currents and particle capture mechanisms in suspension feeding animals. *American Zoologist*, 24, 71-84.
- León, A., Orejas, C., Veiga, A., Puerta, P., Lezzi, G. *et al.*, 2019. The reproductive biology of the cold-water coral scleractinian *Dendrophyllia cornigera* (NE Atlantic). In: *ATLAS 4th General Assembly, Mallorca (Spain), 1-5 April 2019*.
- Lesser, M.P., Slattery, M., Mobley, C.D., 2018. Biodiversity and functional ecology of mesophotic coral reefs. *Annual Review of Ecology, Evolution, and Systematics*, 49 (1), 49-71.
- Li, S., Roger, L.M., Kumar, L., Lewinski, N.A., Klein-Seetharaman, J. *et al.*, 2021. Digital image processing to detect subtle motion in stony coral. *Scientific Reports*, 11 (1), 1-9.
- Li, S., Roger, L.M., Klein-Seetharaman, J., Lewinski, N.A., Yang, J., 2022. Spatiotemporal dynamics of coral polyps on a fluidic platform. *Physical Review Applied*, 18 (2), 024078.

- McFarland, W., Wahl, C., Suchanek, T., McAlary, F., 1999. The behavior of animals around twilight with emphasis on coral reef communities. p. 583-628. In: *Adaptive mechanisms in the ecology of vision*. Archer, S.N., Djamgoz, M.B.A., Loew, E.R., Partridge, J.C., Vallerga, S. (Eds). Springer, Dordrecht.
- Orejas, C., Gori, A., Jiménez, C., Rivera, J., Iacono, C.L. *et al.*, 2017. First *in situ* documentation of a population of the coral *Dendrophyllia ramea* off Cyprus (Levantine Sea) and evidence of human impacts. *Galaxea, Journal of Coral Reef Studies*, 19 (1), 15-16.
- Orejas, C., Gori, A., Jiménez, C., Rivera, J., Kamidis, N. *et al.*, 2019a. Occurrence and distribution of the coral *Dendrophyllia ramea* in Cyprus insular shelf: Environmental setting and anthropogenic impacts. *Deep Sea Research Part II*, 164, 190-205.
- Orejas, C., Jiménez, C., Gori, A., Rivera, J., Lo Iacono, C. *et al.*, 2019b. Corals of Aphrodite: *Dendrophyllia ramea* - Populations of Cyprus. p. 257-260. In: *Mediterranean cold water corals: past, present and future*, cap. 23, Orejas, C. & Jiménez, C. (Eds). Springer, Cham.
- Oren, M., Tarrant, A.M., Alon, S., Simon-Blecher, N., Elbaz, I. *et al.*, 2015. Profiling molecular and behavioral circadian rhythms in the non-symbiotic sea anemone *Nematostella vectensis*. *Scientific Reports*, 5 (1), 1-15.
- Parker, G.H., 1919. *The Elementary Nervous System*. Lippincott, Philadelphia, 227 pp.
- Peirano, A., Bordone, A., Marini, S., Piazza, P., Schiaparelli, S., 2016. A simple time-lapse apparatus for monitoring macrozoobenthos activity in Antarctica. *Antarctic Science*, 28 (6), 473-474.
- Peirano, A., Bordone, A., Corgnati, L.P., Marini, S., 2023. Time-lapse recording of yearly activity of the sea star *Odontaster validus* and the sea urchin *Sterechinus neumayeri* in Tethys Bay (Ross Sea, Antarctica). *Antarctic Science*, 35 (1), 4-14.
- Previati, M., Scinto, A., Cerrano, C., Osinga, R., 2010. Oxygen consumption in Mediterranean octocorals under different temperatures. *Journal of Experimental Marine Biology and Ecology*, 390 (1), 39-48.
- Provenzani, C., Salvati, E., Santero, W., D'Ambrosi, A., Leonini, F. *et al.*, 2019. *In situ* long term observation of *Dendrophyllia ramea*. p. 48. In: *5th European Conference on Scientific Diving, Sopot (Poland), 24-27 April 2019*.
- Purser, A., Orejas, C., Moje, A., Thomsen, L., 2014. The influence of flow velocity and suspended particulate concentration on net prey capture rates by the scleractinian coral *Balanophyllia europaea* (Scleractinia: Dendrophylliidae). *Journal of the Marine Biological Association of the United Kingdom*, 94, 687-696.
- Reidenbach, M.A., Koseff, J.R., Monismith, S.G., Steinbuck, J.V., Genin, A. 2006. The effects of waves and morphology on mass transfer within branched reef corals. *Limnology and Oceanography*, 51 (2), 1134-1141
- Reitzel, A. M., Tarrant, A. M., Levy, O., 2013. Circadian clocks in the Cnidaria: environmental entrainment, molecular regulation, and organismal outputs. *Integrative and Comparative Biology*, 53 (1), 118-130.
- Reynaud, S., Ferrier-Pagès, C., 2019. Biology and Ecophysiology of Mediterranean Cold-Water Corals. In: *Mediterranean cold water corals: past, present and future*. p. 391-404. Orejas, C. & Jiménez, C. (Eds). Springer, Cham.
- Reynaud, S., Orejas, C., Campagnano, A., Rottier, C., Jemenez, C. *et al.*, 2021. Dendrophylliidae cold-water corals in a warm ocean: The effect of exposure duration on their physiological response. *Deep Sea Research Part II*, 193, 104962.
- Riedl, R., 1971. Water movement: General introduction. p. 1086-1088. In: *Marine Ecology*. O. Kinne (Ed.). J. Wiley & Sons, London.
- Roberts, J.M., Wheeler, A.J., Freiwald, A., 2006. Reefs of the deep: the biology and geology of cold-water coral ecosystems. *Science*, 312, 543-547.
- Robbins, R.E., Shick, J.M., 1980. Expansion-contraction behaviour in the sea anemone *Metridium senile*: environmental cues and energetic consequences. *Nutrition in the Lower Metazoa*, 101-116.
- Salomidi, M., Zibrowius, H., Issaris, Y., Milionis, K., 2010. *Dendrophyllia* in Greek waters, Mediterranean Sea, with the first record of *D. ramea* (Cnidaria, Scleractinia) from the area. *Mediterranean Marine Science*, 11 (1), 189-194.
- Salvati, E., Giusti, M., Canese, S., Esposito, V., Romeo, T. *et al.*, 2021. New contribution on the distribution and ecology of *Dendrophyllia ramea* (Linnaeus, 1758): abundance hotspots off north-eastern Sicilian waters. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 1-12.
- Sanna, G., Büscher, J. V., Freiwald, A., 2023. Cold-water coral framework architecture is selectively shaped by bottom current flow. *Coral Reefs*, 42 (2), 483-495.
- Scicchitano, G., Monaco, C., 2006. Grotte carsiche e linee di costa sommerse tra Capo Santa Panagia e Ognina (Siracusa, Sicilia sud-orientale). *Italian Journal of Quaternary Sciences*, 19 (2), 187-194.
- Sebens, K.P., DeRiemer, K., 1977. Diel cycles of expansion and contraction in coral reef anthozoans. *Marine Biology*, 43, 247-256.
- Sorek, M., Levy, O., 2012. The effect of temperature compensation on the circadian rhythmicity of photosynthesis in *Symbiodinium*, coral-symbiotic alga. *Scientific Reports*, 2 (1), 1-8.
- Thiem, Ø., Ravagnan, E., Fossa, J.H., Berntsen, J., 2006. Food supply mechanisms for cold-water corals along a continental shelf edge. *Journal of Marine System*, 26, 1481-1495.
- Wijgerde, T., Spijkers, P., Karruppanan, E., Verreth, J.A.J., Osinga, R., 2012. Water flow affects zooplankton feeding by the scleractinian coral *Galaxea fascicularis* on a polyp and colony level. *Journal of Marine Biology*, 854849.
- Wildish, D., Kristmanson, D., 1997. Benthic suspension feeders and flow. Cambridge University Press, Cambridge, 409.
- Zibrowius, H., 1980. Les Scléactiniaires de la Méditerranée et de l'Atlantique nord-oriental. *Memoires de l'Institut Oceanographique Fondation Albert 1er, Prince de Monaco*, 11 (1), 169-172.