

RESEARCH ARTICLE

Restoration of animal forests: a novel transplantation method for coastal octocorals in the NE Atlantic

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Octocorals are among the main habitat-engineering species, generating complex three-dimensional ecosystems of unquestioned importance. Despite their importance, octocoral habitats have dramatically declined in the last decades due to several stressors. Consequently, octocoral gardens are internationally recognized as Vulnerable Marine Ecosystems. In the last decade, several octocoral restoration methodologies were the object of study, yet long-term success was sparsely achieved or lacked assessment. To reverse the actual scenario, it is important to develop cost-efficient methodologies to recover impacted, endangered octocoral habitats. In this 4-year study, we developed and tested the Direct Substrate Attachment (DSA) method. This novel octocoral transplant method was trialed with two size classes of the species *Paramuricea grayi* and extended with a third class (20–40 cm) using *Leptogorgia sarmentosa*. With a recorded 95% attachment success, yearly annual positive growth, and a survival of 75% after 4 years, we prove the suitability of the DSA methodology in habitat restoration. Moreover, transplant size did not influence success; all transplants had verifiable holdfast and growth rates of up to 8.34 ± 1.7 cm. Seasonal growth and health status were monitored and compared to further assess the success of the transplant. The transplant performed with the DSA method is to date the first successful octocoral transplant in the Atlantic temperate seas with proven long-term success. The results achieved are especially important in a moment where ecological degradation and mitigation efforts are a hot topic among decision-makers. Using the DSA methodology, octocoral transplantation is possible and should be considered in conservation and restoration efforts.

Key words: ecosystem restoration, gorgonian, *Leptogorgia sarmentosa*, octocoral growth, *Paramuricea grayi*, transplant methods, transplantation success

Implications for Practice

- The Direct Substrate Attachment (DSA) methodology is the first and longest octocoral study (4 years) reporting transplantation success considering attachment success, high survival, yearly positive growth, and occurrence of natural reattachment.
- With the DSA methodology, the attachment of octocorals of several sizes is possible, from less than 10 cm up to 40 cm.
- More research is needed to verify the response of other octocoral species to transplantation.
- Large-scale studies are necessary, where the outcome of transplantation is verified through ecological impact and natural repopulation studies.
- Replication of the “Stick” methodology was not successful.

Introduction

Octocorals (Class Octocorallia), commonly known as gorgonians, soft corals, and sea fans, are long-lived sessile ecosystem engineering species that can live for centuries (Cerrano et al. 2010; Martinez-Dios et al. 2016). Dense aggregations of octocorals are commonly known as “Coral Gardens,”

“Gorgonian Forests,” or “Animal Forests” (Rossi et al. 2017). These intricate three-dimensional communities are extremely important in coastal waters, where they increase landscape heterogeneity, fuel the local carbon cycle (Coppari et al. 2019), and contribute to increasing species richness (Cerrano et al. 2010; Carvalho et al. 2014; Sini et al. 2019). In turn, the health and delicate balance of these communities depend on the population stability of these species (Ponti et al. 2016). Most octocorals exhibit slow growth rates, low recruitment, and low fecundity—characteristics that explain their slow population dynamics (Coma et al. 1995; Santangelo et al. 2003). These characteristics render octocorals highly vulnerable to

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rapid and long-lasting biological and anthropogenic disturbances (Garrabou et al. 2009; Cúrdia et al. 2013).

In recent decades, climate anomalies have increased, leading to widespread episodes of mass mortality in octocoral species (Turicchia et al. 2018; Garrabou et al. 2021). These anomalies are accompanied by direct and indirect anthropogenic pressures in coastal areas, including algal blooms and viral infections (Mistri & Ceccherelli 1996; Bally & Garrabou 2007), pollution (Chan et al. 2012), fishing (Dias et al. 2020), and leisure activities (Waters 2015; Ferrigno et al. 2016). These impacts partially explain the recent population declines reported by several studies (Fava et al. 2010; Mokhtar-Jamaï et al. 2011; Gómez-Gras et al. 2021), thus emphasizing the need for protection. Consequently, octocoral gardens have been internationally recognized as Vulnerable Marine Ecosystems (OSPAR Commission 2010; Fabri et al. 2014). Coastal ecosystems are also subject to various EU policy legislations, such as the Habitats Directive (92/43/EEC) and Marine Strategy Framework Directive (EC 2008), aimed at promoting sustainable natural resource use and improving the status of marine ecosystems. However, ecological restoration efforts are often necessary to recover impacted habitats (Goreau 2010). Consequently, restoration has been recognized by policymakers and scientists as a critical measure to ensure the continued provision of ecosystem services (Duarte et al. 2020; Saunders et al. 2020). This importance is further underscored by the United Nations' Sustainable Development Goal 14, which emphasizes the necessity of underwater restoration within the broader framework of the "Decade of Restoration" initiative.

Transplantation of live colony fragments is one of the strategies used to recover octocoral populations (Rinkevich 2014). Increasing the number of colonies through transplantation aims to enhance recruitment and population persistence (Linares et al. 2008; Montseny et al. 2019). These methods have shown promising results, but they also face significant challenges. Among the many difficulties, the attachment of the colony is reported as one of the most challenging steps in octocoral transplantation, being critical and directly linked to survival (Villechanoux et al. 2022; Topçu et al. 2023). Various methods have been tested over the past decades (Kumagai et al. 2004), with the most successful involving the scraping of the substrate and adhering the octocoral using an adhesive putty, such as epoxy or cement (Casoli et al. 2022). However, this attachment method, often with slight variations, has encountered long-term issues, including adhesive detachment, breakage, and lack of holdfast formation, which ultimately lead to the loss of transplants (Linares et al. 2008; Villechanoux et al. 2022). Despite these hurdles, the potential success of transplantation has led to investment in research and the development of new methodologies (Montero-Serra et al. 2018; Montseny et al. 2020). Most efforts in octocoral transplantation methodologies focus on survival (Topçu et al. 2023), with limited research on long-term results (most up to 1 year) (Boström-Einarsson et al. 2020). Although survival is a key factor, it is difficult to assess the true success of the transplant without attaining positive growth and a healthy ecological status on a long-term scale (Montero-Serra et al. 2018). Recently, Casoli et al. (2022) reported high survival

and colony growth rates over a 2.5-year period. Despite this, the study raised questions about the influence of transplant size and the viability of transplanted fragments. Our 4-year study presents a novel transplantation method called Direct Substrate Attachment (DSA), which aims to promote the direct attachment of the octocoral to the substrate while stimulating the growth of a long-lasting holdfast. We assessed the feasibility and success of using the DSA method to transplant *Paramuricea grayi* (Johnson, 1861) octocoral fragments of two different size classes (>10 cm and 10–20 cm) by closely monitoring attachment success, survival, growth, holdfast formation, and health. Moreover, to further assess the attachment capacity of the method, the study was extended to include a third-size class (20–40 cm) where *Leptogorgia sarmentosa* (Esper, 1791) fragments were transplanted. This study provides valuable insights for political boards and managers involved in large-scale marine ecosystem restoration projects.

Methods

Study Site

This study was conducted from December 2017 to December 2021 in Sagres at the Baleeira harbor breakwaters (37°0'43.56"N, 8°55'27.17"W) (Fig. 1). The area is part of the marine reserve "Parque Natural do Sudoeste Alentejano e Costa Vicentina" (PNSACV). The breakwaters were built in 1978 using a mix of natural calcareous boulders, tetrapods, and H-interlocking concrete structures. The maximum depth ranges from –15 to –18 m, depending on the tide. At the very end of the breakwaters, between 15 and 18 m (at high tide), there is a healthy octocoral forest that extends for 60 m. In this area, the species *Eunicella labiata* (Thomson, 1927), *E. verrucosa* (Pallas, 1766), *E. gazella* (Studer, 1901), *Leptogorgia sarmentosa*, and *Paramuricea grayi* were recorded. The octocorals are mostly found over the rocky boulders and artificial concrete structures of the breakwaters, with a preference for vertical walls and overhangs. Octocoral species are mixed, and horizontal distribution was found to be continuous. The study area's limited accessibility and local laws that forbid recreational or fishing activities minimize human impacts, making it an excellent study site. As such, colony collection and transplantation were done in this area.

Sample Collection and Preparation

Octocoral (*P. grayi*) fragment collection occurred at the Sagres harbor breakwaters. All fragments were collected from healthy, necrosis-free colonies of *P. grayi* between –15 and –18 m, with each colony providing only one fragment to avoid a negative impact on the donor colony. The collected gorgonian fragments, each containing at least one apical branch of 8 cm, were stored in plastic zip-lock bags for transportation. Upon collection, the fragments were transported to the laboratory and maintained in aquaria at 16°C, matching the ambient temperature recorded on the day of collection. The colonies were fed locally cultivated *Artemia* twice a week and categorized into two size classes: less than 10 cm (up to 10 cm tall) and 10–20 cm (from 10 to 20 cm

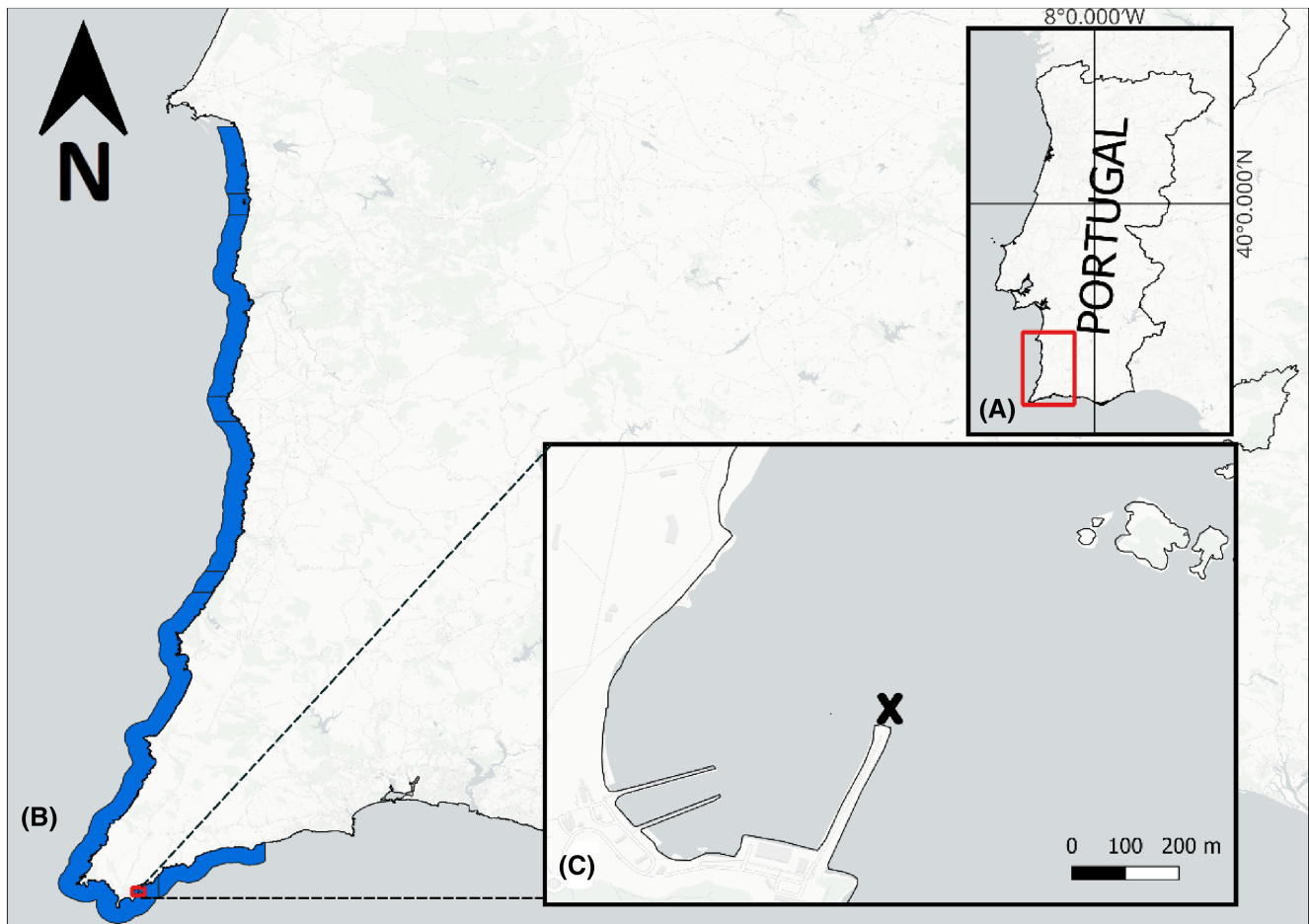


Figure 1. (A) Location of the Parque Natural do Sudoeste Alentejano e Costa Vicentina (PNSACV) regarding the Portuguese continental territory. (B) The map of PNSACV, with the MPA marked in blue. (C) Map of Sagres' Baleeira harbor, where the breakwaters can be seen. The study site is marked with a "X."

tall), excluding the 2 cm base. On the transplantation day (2 weeks after collection), the base of the fragments was scraped and cleaned of side branches, exposing the skeleton (Fig. 2). The average width of the bare skeletons was measured to be 2 mm. This measurement was used to determine the appropriate drill bit size for creating holes for the transplants, as the ideal drill bit should be 2 mm larger in diameter than the base of the octocoral. Due to unexpected events, the study on methodology attachment success was expanded to include a third-size class. The study initially only considered two size classes, but the discovery of large octocoral colonies (up to 50 cm in height) on the beach after a series of storms on Portugal's south coast provided an opportunity to test the methodology further. The available biomass, combined with the apparent success of the transplants for the smaller size classes, made it possible to test the methodology attachment capacity for larger fragments with a third-size class (20–40 cm) using *L. sarmentosa*.

DSA Methodology

The DSA method is designed to promote the direct attachment of octocoral transplants to the substrate. The approach creates

conditions for the octocoral to overgrow the adhesive (fixating material), such as epoxy glue, and establish a holdfast on the substrate. This method aims to minimize the risk of skeletal breakage or detachment, which are common causes of transplant loss in other methodologies (Villechanoux et al. 2022). In the present study, successful transplant attachment to the natural substrate was considered achieved when a complete holdfast, including tissue and gorgonin (the octocoral's skeleton), was observed.

The proposed process was implemented as follows: a hole 2 cm deep was opened by using an underwater drill (Nemo Divers Hammer Drill), approximately at a 20° angle with the vertical axis (Fig. 2). After removing the resulting particles from the hole, a small amount of epoxy glue (Splash Zone A-788) was inserted and pushed strongly inward with an extra drilling bit of the same size. The epoxy was verified to be compact, and the octocoral fragment was carefully inserted, making sure the living tissue was left touching the substrate (Fig. 2). Any excess epoxy glue was removed, leaving the natural substrate clean and with as little residue of epoxy as possible. The fragments were all transplanted in a row at the same depth, at roughly 1 m distance, considering the preferred habitat characteristics

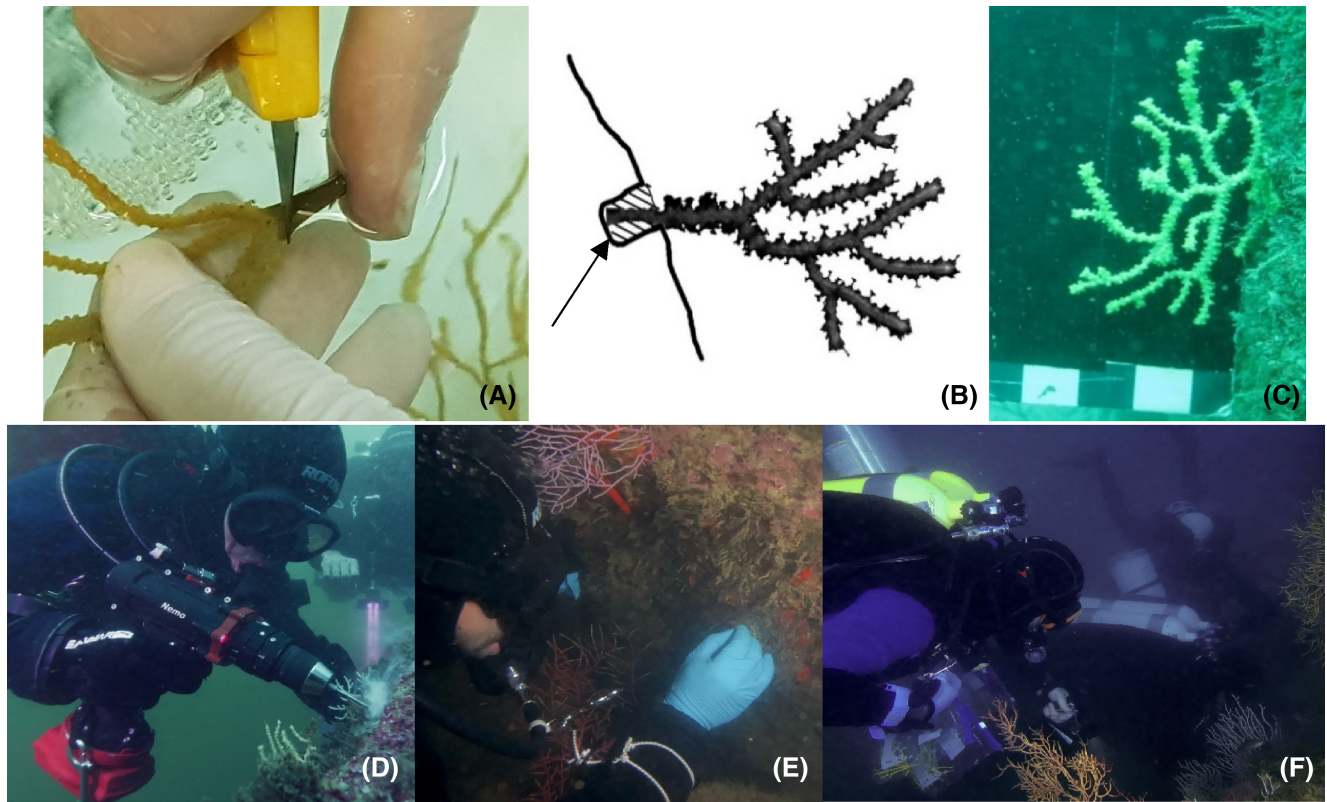


Figure 2. (A) *Paramuricea grayi* fragment being prepared for the transplant. The first 2 cm of the base was scrapped out of the living tissue, exposing the skeleton. (B) Sketch of an octocoral transplant done with DSA methodology. The solid line represents the substrate, and the stripped area is the glue material. The arrow places in evidence that the living tissue is touching the substrate. (C) *P. grayi* transplant being monitored. The scaled plate behind the octocoral provides a perfect contrast, facilitating future image analysis. (D) A hole in the substrate is opened using an underwater driller. (E) The octocoral fragment is inserted in the hole already filled with epoxy. (F) The team can be seen working in the transplantation process at 18 m of depth.

of the transplanted species in the area, such as depth (15–18 m), orientation (preference for vertical walls), and light incidence (area not directly exposed to light). Size classes were alternated to decrease possible environmental heterogeneity bias. This transplant disposition was selected as it mimics the distribution of the octocorals in the area.

In total, 70 octocoral fragments were transplanted: 58 of *P. grayi* (30 of <10 cm and 28 of 10–20 cm) and 12 of *L. sarmentosa*. The fragments were divided into three size classes, for a total of three different treatments.

Preliminary Assay

A preliminary experiment was conducted to compare the attachment success of the DSA method with the established “Raw” and “Stick” methods (Linares et al. 2008; Casoli et al. 2022). The goal was to assess whether the DSA method could match or surpass the attachment efficiency of the “Stick” method, which had previously reported 70% survival after 1 year. The least successful was the “Raw” methodology with a 30% survival rate. For the smaller size class (<10 cm), the “Stick” method achieved 100% attachment success, but it was less efficient on 10–20 cm fragments. During transplantation, many transplants fell due to water flow or fish collisions; after

3 months, only 20% of the colonies remained in place, and all were dead.

In contrast, the DSA method resulted in 100% success for both size classes the day after the transplant, and 97% of the colonies were alive and healthy after 3 months.

Monitoring

Monitoring was conducted daily for the first 2 days, monthly for the first 3 months after the transplant (until March 2018), and every 6 months until the end of the study. Several parameters were used to establish a baseline for growth and health status, with the monitoring schedule designed to be frequent in the early stages and more spaced out later. During monthly monitoring events, survival, attachment (adhesive bonding), presence of holdfasts, and health status were recorded. In addition to these parameters, growth was assessed at the 6-month monitoring for the first 2 years, which was enough to observe temporal growth changes over consecutive years. The immediate methodology’s success was evaluated by assessing the presence or absence of the transplanted colonies (survival) and their firm attachment to the substrate. Attachment was considered successful only if it was established for at least 3 months, providing sufficient time to identify attachment issues not apparent in the

early stages. To confirm the development of a full holdfast (living tissue and gorgonin growing over the substrate), the presence of gorgonin was verified by scraping small portions of living tissue from the base of the coral. The colonies' immediate adaptation was assessed by observing polyp activity (Fava et al. 2010). Colony size was assessed through scaled photography. The photographs were taken with a Canon G16 without flashes along a fixed transect with markings, ensuring all colonies were consistently assessed in the same order. The health state of the octocoral was determined by monitoring for signs of necrosis, bare skeleton, discoloration, or epiphytes.

Photograph Pre-Processing

Using Paintshop Pro software, the photographs taken during the monitoring events were pre-processed. The images' background was removed, leaving only the image of the gorgonian in black and white (Fig. 3). The images were then processed with ImageJ software, with which the total branch length (TBL) (Fava et al. 2010) and the height of the transplanted octocorals were measured. The TBL measures the length of all octocoral branches, while height was measured from the holdfast (substrate level) to the highest point of the colony. This data allowed us to estimate colony size (in cm) and growth in between monitoring events using both methods.

Data Processing and Statistical Analyses

After picture pre-processing using ImageJ software, the data were pooled regarding several descriptors to have a finer integrated analysis of the temporal evolution of the response parameters.

Size of the transplants was computed for all monitoring events regarding their height and TBL. Net growth was calculated by subtracting the initial size (day after transplant day) from the size of the octocoral fragment in monitoring events post-transplant. Data was analyzed regarding height and TBL.

The growth rate was calculated by determining the difference in size between the most recent monitoring event and the previous monitoring event. This approach effectively measures the relative

size increment or decrement between successive monitoring events. Both positive and negative growth rates were considered in this analysis. The monthly growth rate was determined by dividing the growth increments observed between successive monitoring events by the number of months between these events. Additionally, the annual growth rate was calculated by subtracting the initial size at the beginning of the year from the size recorded at the last monitoring event of the same year (e.g. December 2019 size minus January 2019 size). Growth data was treated regarding height and TBL. Health status was assessed regarding the presence or absence of epiphytes, discoloration, polyp release, and necrosis. The percentage of transplants affected was recorded regarding the total area of the colony. The results were then fitted into a class: 1 = 0–10%; 2 = 10–25%; 3 = 26–50%; 4 = 51–75%, and 5 = 76–100% of the colony impacted, following a modification of Francour & Koukouras (2000) methodology, where up to 10% coverage is considered a healthy octocoral. Results are reported as mean \pm standard error (SE). Statistical analyses and graphical outputs were performed using open-source R software version 3.4.3 (R Core Team 2017). The effects of size factors (size classes <10 and 10–20 cm) on response variables of attachment, survival, size, growth, holdfast formation, and health status along time (monitoring event) were tested. Data normality was checked via a Shapiro–Wilk test. A fit-Distr function (Spiess 2018) was run on all non-normal distribution subsets to supply a Generalized Linear Model (GLM) with the best-fitting distribution. Analyses were performed using GLMs with the package *glm2* (Marschner et al. 2018), using the best-fitting family for each response variable; attachment, survival, holdfast formation, and health status used the binomial family, growth rate the Gaussian family, and size the gamma (height) and inverse gamma (TBL) families.

Results

Survival

Transplant survival, monitored for 4 years from December 2017 until December 2021, revealed that survival was influenced by

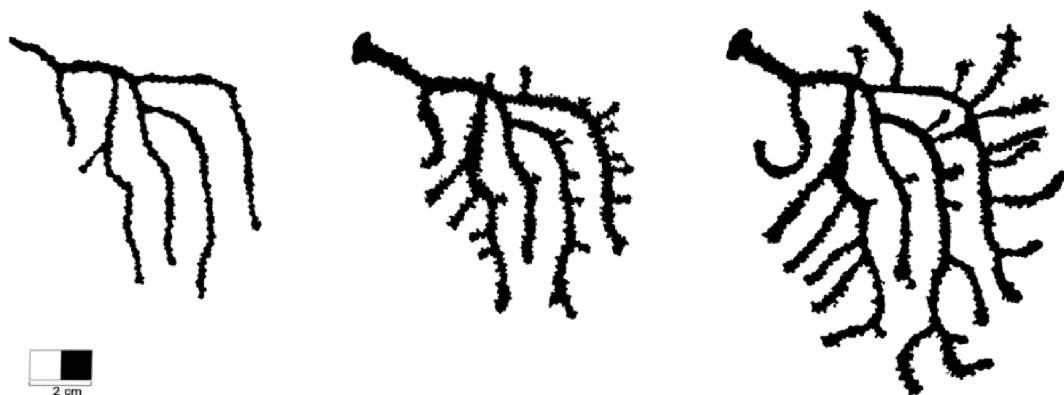


Figure 3. Octocoral transplant images of the same *Paramuricea grayi* colony after being processed using PaintshopPro software. The background was removed and the octocoral was colored in black. In the image from left to right, the colony on the transplant day, in the middle 1 year monitoring, and on the right 2 years monitoring can be observed.

transplant technique failure (attachment success of each method), natural mortality, and anthropogenic impacts.

The DSA technique of attachment (adhesive bonding) using epoxy glue was 100% successful in both size classes on the day after the transplant. After 3 months, survival was 97% on small fragments (size <10 cm), and 93% on medium-sized fragments (size 10–20 cm). There were no significant differences in survival due to attachment success between size classes (GLM, $p = 1.000$), nor between the transplant event and the monitoring in March 2018 (GLM, $p = 0.993$). Overall, attachment success was 95% after 3 months (Fig. 4). The third class, tested with bigger fragments of *Leptogorgia sarmentosa* (20–40 cm), had a success rate of 100% the day after the transplant and 75% 3 months later.

Size had no influence on the transplant's survival (GLM, $p = 0.100$), whereas time significantly influenced survival when comparing the start and end of the trial (GLM, $p < 0.001$). After 2 years, the less than 10 cm size class had 70% survival, and the 10–20 cm transplants had 68% survival, while by the end of the trial, after 4 years, survival was 66.7% and 64.3%, respectively (Fig. 4). Out of 58 colonies transplanted, 9 fragments were lost in the 10–20 cm size class, of which 33.3% were associated with natural events, 22.2% were lost due to technique failure, and 45.5% were due to observable anthropogenic impacts (such as fishing nets, lines, litter, and others). In the smaller transplants (<10 cm), nine fragments were lost, with 77.7% associated with natural events, 11.1% due to technique failure, and 11.1% due to anthropogenic impacts. Overall, 50% of the mortality was considered to be associated with natural events since it could not be associated with anthropogenic impacts. Anthropogenic impacts leading to the death of the transplanted colony were observed in 8.6% of the total transplanted colonies. Despite that, there are differences concerning survival between the first and following years of the study. When comparing the transplant moment and the 1-year monitoring (December 2018), survival changed significantly (GLM, $p = 0.010$). Yet, in the second year, comparing the first and last monitoring events, it did not (GLM, $p = 0.741$). The same is observed in the following years (2020 and 2021), where survival did not change significantly (GLM, $p = 1$). Although the third-size class (20–40 cm) was formerly planned to test attachment alone, survival was still monitored throughout the study. After 1 year, survival was 67%, and after 4 years it remained the same, a similar result when compared with the other size classes.

Holdfast Formation

All fragments remaining at the end of this experiment had a verifiable natural holdfast. There were differences between size classes when it concerned holdfast formation (GLM, $p = 0.009$). The first occurrences of holdfast formation were observed after 3 months. After 5 months, the 10–20 cm size class had 58.3% of colonies with a developed holdfast. From April 18 to May 18, significant holdfast growth occurred (GLM, $p < 0.001$), where the <10 cm class size treatment changed from 34.5 to 96.3% colonies with holdfast, and the 10–20 cm size class from 58.4 to 95.6% (Fig. 4B). After 1 year,

regardless of size class, all the transplants had created a holdfast. Until the end of the trial, no holdfast regressed.

Growth

Growth was monitored in the first 2 years of the trial, from December 2017 to December 2019. Concerning the colonies' total size evolution, both size classes depict a significant TBL increase over the 2 years (GLM, $p < 0.001$). The TBL total size for the less than 10 cm size class had a significant increase (GLM, $p = 0.044$) from an average of 9.28 ± 1.25 cm at transplant to 25.38 ± 3.67 cm after 2 years (Fig. 5A). The 10–20 cm size class also increased, growing from 33.98 ± 2.23 to 45.66 ± 5.23 cm in 2 years (Fig. 5A), but there were no significant differences between the initial and final values for this size class ($p = 0.499$). The annual growth rate concerning TBL in the less than 10 cm treatment was 8.34 ± 1.7 cm in the first and 8.42 ± 1.7 cm in the second year of the trial. In the 10–20 cm treatment, annual growth rates were 6.22 ± 3.4 and 5.1 ± 2.7 cm for the first and second years, respectively. TBL net growth showed a positive trend over the 2-year trial, with the smaller class (>10 cm) achieving a net growth of 170% (16.51 ± 3.66 cm) and the 10–20 cm class growing 30% (12.02 ± 6.3 cm). Net growth was not significantly different between size classes at the end of the study. Growth rates were positive in both treatments yearly and by month, apart from the 1.5-year monitoring event in summer (Table 1). No differences were found between monthly growth rates in TBL (GML, $p = 0.66$), yet two distinct moments were identified: the 6-month and 1.5-year monitoring events (both in the summer season). At the 6-month monitoring event, both classes showed a lower growth rate of 0.39 ± 0.3 cm (>10 cm) and 0.48 ± 0.64 cm (10–20 cm) in comparison with the 1-year monitoring (winter season) with rates of 1.11 ± 0.27 and 1.39 ± 0.64 cm for the less than 10 cm and 10–20 cm treatments, respectively (Table 1).

There were no significant differences in total height when comparing the start and end of the experimental trial. Overall, height had no significant changes in both size classes, although the less than 10 cm size class had a slight increase in height and the 10–20 cm size class had a decrease. There were also no significant differences in the annual growth rate of the monthly height in any of the treatments (Table 2). Overall, height's growth rate was nonexistent and did not change significantly during the whole trial. In between the 6-month monitoring and the last monitoring 2 years later, there were also no significant differences (<10 cm: GLM, $p = 0.720$; 10–20 cm: GML, $p = 0.870$).

Health Status

The octocoral transplants' health did not change significantly in the duration of this study. Such is the case for both the less than 10 cm (GLM, $p = 0.999$) and 10–20 cm (GLM, $p = 0.983$) size classes. Moreover, all transplanted fragments had open polyps and were feeding in the first two monitoring events. Still, there were significant differences between size classes

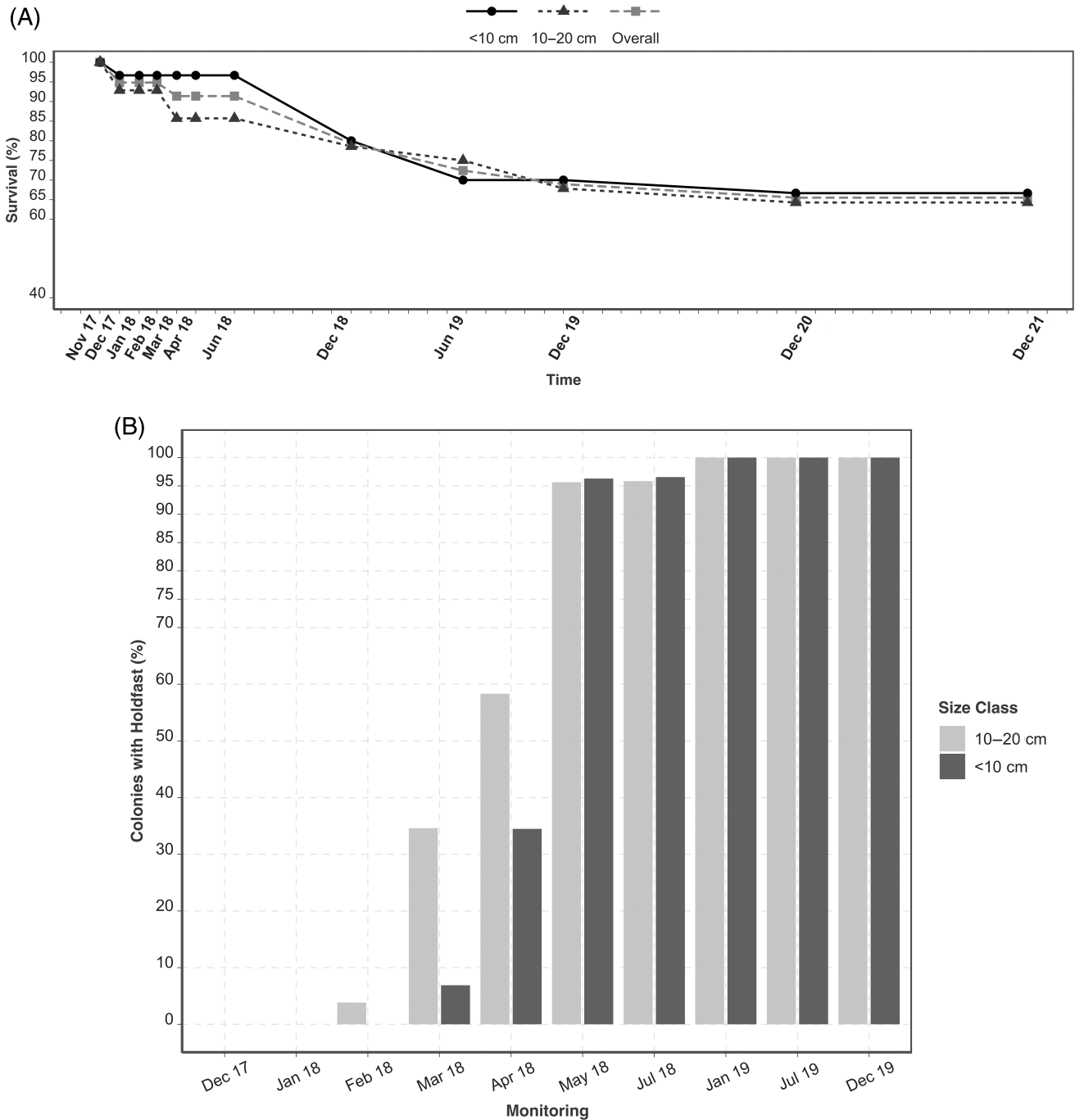
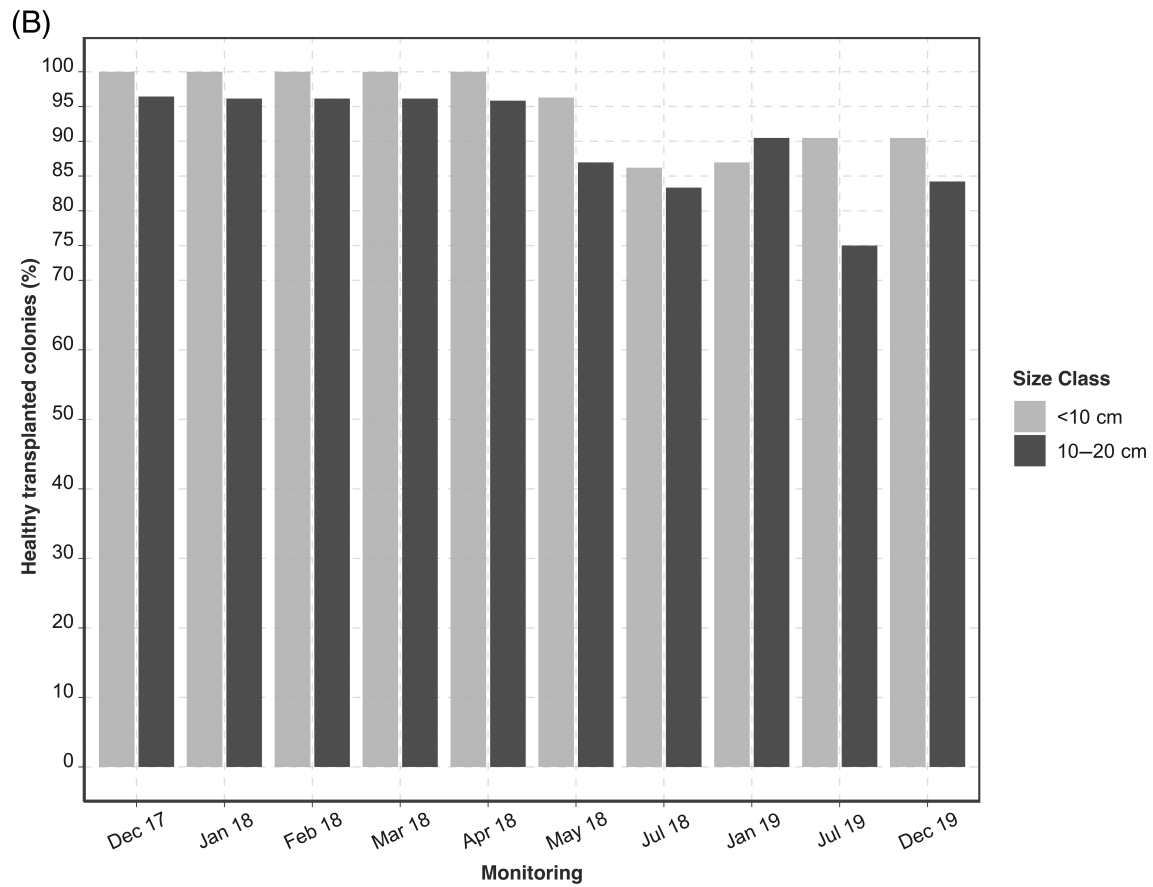
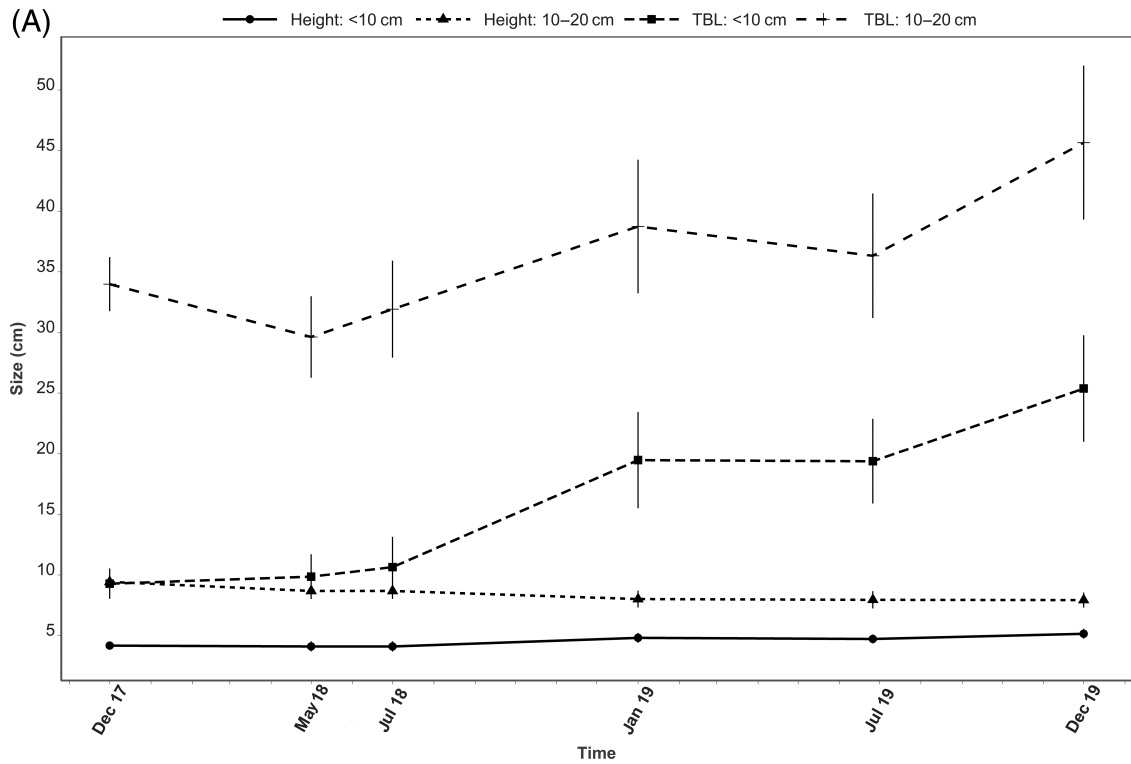


Figure 4. (A) Survival (%) of *Paramuricea grayi* transplants done using the DSA method for the different monitoring events for the duration of the trial. Survival was monitored monthly in the first 3 months and then every 6 months, by verifying the presence of the colony and if it was alive. Survival is reported, including methodology and anthropogenic losses. (B) Percentage of *P. grayi*'s transplanted colonies that have developed a natural holdfast during the study period. Both size classes are represented for each monitoring event.

(GLM, $p = 0.021$). By the end of the 2 years of monitoring, 90% of the small fragments and 84% of the medium-sized transplants were healthy with no signs of disease, necrosis, or epiphytes, and had an overall healthy condition (Fig. 5B). The colonies found to have been impacted only showed small epiphytes in extremities or exposed branch tips.

Discussion

In the present study, we demonstrate that the novel DSA transplantation methodology is a successful and viable long-term restoration tool when used with *Paramuricea grayi*. Such was shown by not only the positive results achieved but also because this gorgonian restoration study is likely the longest followed up



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Table 1. Monthly total branch length's (TBL) growth rate (average \pm SE) in cm, of both *Paramuricea grayi* transplant treatments (<10 cm and 10–20 cm). Growth rates calculated every 6 months, from the transplant monitoring until the end of the experiment. Growth rates are presented with their standard error (95% CI).

	Size < 10 cm	Size 10–20 cm
0.5 Year	0.39 \pm 0.3	0.48 \pm 0.64
1 Year	1.11 \pm 0.27	1.39 \pm 0.64
1.5 Years	0.41 \pm 0.14	–0.64 \pm 0.33
2 Years	1 \pm 0.23	1.17 \pm 0.3

Table 2. Monthly height's growth rate in cm (average \pm SE), of both *Paramuricea grayi* transplant treatments (<10 cm and 10–20 cm), in intervals of 6 months, through the experiment duration. Growth rates are presented with their standard error (95% CI).

	Size < 10 cm	Size 10–20 cm
0.5 Year	0.09 \pm 0.07	0 \pm 0.16
1 Year	0.09 \pm 0.07	0 \pm 0.11
1.5 Years	–0.05 \pm 0.06	–0.05 \pm 0.07
2 Years	0.07 \pm 0.03	–0.07 \pm 0.04

to date (4 years). Longer monitoring studies are necessary and should be considered in modern restoration attempts (Montero-Serra et al. 2018).

Attachment and Holdfast Formation

The DSA methodology achieved an initial attachment success rate of 95% after 3 months. Additionally, the method demonstrated considerable flexibility in accommodating colonies of various sizes, maintaining a 75% success rate for fragments measuring 20–40 cm. To our knowledge, this study on octocoral restoration reports one of the highest attachment success rates. The limited use of epoxy adhesive facilitated long-term attachment, enabling the octocoral transplants to develop a natural holdfast over the substrate. One-year post-transplantation, all samples had formed organic holdfasts over the substrate, fulfilling a primary objective of the DSA methodology and marking a significant achievement for long-term success.

Common issues in octocoral transplantation, such as colony detachment from the adhesive after curing, the inability to maintain colony position during the curing process, or adhesive detachment from the substrate while still holding the colony, are well-documented in the literature. For instance, the “Stick” methodology reported a 70% survival rate after 1 year but experienced over 40% transplant loss due to poor attachment (Linares

et al. 2008). The primary causes included epoxy breakage and the loss of supporting rods used for fragment fixation. In a more recent study utilizing the “Raw” methodology, 15% of the reported 18% mortality was attributed to technique failure (Casoli et al. 2022). Additionally, among the four common techniques, up to 70% of transplants were lost due to detachment or technique failure within 2–4 years (Villechanoux et al. 2022).

In contrast to the previous reports, the DSA methodology achieved an attachment success rate of 97% for fragments smaller than 10 cm and an overall success rate of 95%, demonstrating its high efficacy in securing transplanted colonies despite being more time-consuming. The method's resilience to displacement is due to the drilled hole in the substrate being only slightly larger than the octocoral skeleton, which, when subjected to force, ensures the fragment remains immobile while the epoxy hardens.

Resulting from technique attachment, holdfast growth was also a success. In the 10–20 cm treatment, living tissue began to cover and extend over the natural substrata within 1-month post-transplantation. Conversely, no evidence of holdfast formation was observed in the less than 10 cm treatment within the same timeframe. Although gorgonin was not observed in any treatment during this monitoring period, the early extension of living tissue in the 10–20 cm transplants suggests these corals allocated resources to reattachment earlier than the smaller, less than 10 cm transplants. Furthermore, the 10–20 cm transplants developed observable organic holdfasts, including gorgonin growth, sooner than the smaller class. These findings indicate that larger transplants have a higher and faster capacity to reattach to the substrate. Nevertheless, within 6 months to 1 year, smaller transplants (<10 cm) also developed verifiable holdfasts. Our results support the notion that for long-term restoration, transplant attachment success should include the colony's natural adherence to the substrate, resulting in what can be described as organic attachment (Edwards & Gomez 2007; Montseny et al. 2019). This contrasts with the growth of holdfasts solely over the material used to secure the transplants (Linares et al. 2008; Casoli et al. 2022; Villechanoux et al. 2022).

The plasticity of the DSA methodology in accommodating varying transplant sizes is crucial for long-term habitat restoration, particularly concerning reproduction. The capability to effectively secure both small and large transplants offers managers and decision-makers greater flexibility in defining restoration goals. Such goals are often limited by methodological constraints and the availability of biomass for transplantation. Octocoral reproductive maturity is size-dependent and species-specific; moreover, larger colonies typically exhibit higher fecundity, thereby increasing the likelihood of successful reproduction and recruitment (Coma et al. 1995; Rossi & Gili 2009).

(Figure legend continued from previous page.)

Figure 5. (A) *Paramuricea grayi*'s mean transplants' total branch length \pm SE (TBL) and height, for both treatments (<10 cm and 10–20 cm) in all monitoring events performed in the 2-year growth experimental trial. Size is presented with its standard error and a 95% CI. (B) Transplanted *P. grayi* colonies treatments' (<10 cm and 10–20 cm) health status. Percentage of transplants that had no visible impacts (disease, discoloration, polyp release, exposed skeleton, or epiphytes) through the duration of the experiment. No significant differences were found between the start and end of the trial (95% CI).

Consequently, transplanting larger fragments can potentially expedite the recolonization of an area through enhanced reproductive output. This is an aspect this study was not able to address, and that requires more research. Another usual limitation is biomass availability. In such cases, dividing the available colonies into smaller fragments allows for a greater number of transplants, which may delay recolonization in the short term but results in more individual colonies. These factors must be considered when establishing restoration goals and determining the number and size of transplants.

Despite the critical role of attachment in transplant efforts, the definition of a successful transplant attachment has remained vague. In this study, we define “technique attachment success” as the successful fixation of the transplant in place and “transplant’s successful attachment” as the direct growth of an organic holdfast on the available substrate post-plantation. This growth step is essential in the coral’s life history, requiring successful larval settlement and subsequent development (Zelli et al. 2020). For coral restoration to achieve long-term success, the formation of a natural holdfast is crucial; without it, transplants are likely to break or loosen over time (Edwards & Gomez 2007; Linares et al. 2008; Villechanoux et al. 2022). The initial segment of the transplant’s skeleton and its artificial base (adhesive) endure significant stress, which intensifies as the coral grows and interacts with water currents and local fauna. Furthermore, the size of octocorals is proportional to their holdfast, with larger colonies exhibiting correspondingly larger holdfast areas and greater detachment strengths to support their structure (Sponaugle & LaBarbera 1991). Thus, without continuous enlargement, strengthening, and organic recovery of the attachment point—similar to natural colonies—transplants are prone to eventual detachment and loss. The DSA methodology addresses this issue, as all transplants developed an organic holdfast over the substrate.

Regarding substrate differences, although not a primary goal of this study, it was observed that holdfasts grew on both natural and artificial blocks of the breakwaters used for transplantation. This suggests that concrete substrates may also be suitable for restoration efforts, an important consideration for future projects.

Survival. In the present study, transplants demonstrated a high survival rate of 74.5% after 4 years, considering all treatments and excluding losses from anthropogenic impacts (fishing nets, lines, litter, and others). Notably, transplant size had no direct impact on survival, allowing other factors to be prioritized in restoration projects involving *P. grayi*. This is an encouraging outcome, especially given that the average annual observed survival for several octocoral species is 48% (Montseny et al. 2020), with specific 1-year survival rates of 35–45% for *Eunicella singularis* (Esper, 1791), 30% for *E. verrucosa*, and 35–50% for *P. clavata* (Risso, 1827) (Linares et al. 2008; Fava et al. 2010; Montero-Serra et al. 2018).

The survival rates obtained with the DSA methodology are comparable to the highest rates reported in the literature, such as the recent study at the Costa Concordia wreck site, which

reported an 82.1% survival rate after 2.5 years, excluding anthropogenic losses (Casoli et al. 2022). In a similar timeframe and excluding anthropogenic losses, the DSA methodology achieved a 79.2% survival rate for 10–20 cm transplants. Despite selecting a site with restricted anthropogenic activity, approximately 8.6% of transplanted colonies in this study were lost due to illegal sport fishing, with fishing gear and lines causing physical damage to the colonies. Transplant size has also been identified as a potentially relevant factor in survival (Linares et al. 2008). Most published restoration studies focus on a single size class, typically small sizes (up to 10 cm). Some studies have attempted to transplant larger sizes (>10 cm), but results were either unsuccessful or inconclusive (Casoli et al. 2022). This indicates a knowledge gap in the field. Our study demonstrates that with *P. grayi*, transplant size did not significantly impact survival. Moreover, transplant survival was particularly notable given the multiple severe storms that impacted the Portuguese coastline during the experiment (IPMA; Padrão N, 2018, University of Algarve, personal observation). Despite waves reaching heights of 5–6 m, no transplant losses were recorded during post-storm monitoring. Seasonal changes are a critical factor often inadequately assessed due to the short duration of most studies. The lack of long-term studies (over 2 years) can create a bias toward positive results (Bayraktarov et al. 2015; Montero-Serra et al. 2018). Our study, which presents 4-year monitoring results, demonstrates that transplant survival using the DSA methodology with *P. grayi* exceeds the average survival rates reported in the literature. Moreover, it is, to our knowledge, the longest octocoral restoration research conducted to date, significantly contributing to the validation of long-term restoration success.

Growth. This study demonstrates that *P. grayi*, transplanted using the DSA methodology, achieved yearly positive net growth in both treatment size classes (<10 and 10–20 cm) over a 2-year monitoring period. Notably, the less than 10 cm treatment exhibited greater growth than the 10–20 cm treatment, which aligns with the established understanding that colonial organisms, particularly octocorals, tend to decrease growth rate with increasing size (Lasker et al. 2003). While net growth results indicated negligible annual growth in height, positive growth was observed when considering TBL. This highlights the importance of monitoring TBL to accurately determine growth in explants, as height measurements alone can lead to misleading interpretations of experimental outcomes (Palma et al. 2018).

The lack of growth in height underscores the necessity of considering octocoral growth dynamics, particularly during transplantation (Montero-Serra et al. 2018). Explants, collected from whole octocoral colonies and trimmed closer to the base before insertion into the adhesive material (e.g. epoxy glue), might redirect resources toward growth in different sections of the colony, thereby altering typical growth dynamics (Matsumoto 2004). This resource allocation affects height increases while promoting the formation and growth of other branches. Additionally, restoration efforts must account for the

trade-off between vertical growth and holdfast formation. We observed that smaller transplants exhibited higher growth rates but developed their holdfasts later, whereas larger transplants grew slower but reattached faster, consistent with findings that octocoral apical sections allocate energy toward branch growth, while secondary branches focus on other needs such as reproduction and reattachment (Brazeau & Lasker 1992).

Despite achieving positive annual growth, transplant growth rates were not consistent throughout the year, showing an inverse relationship with increasing water temperatures during the summer, indicative of seasonal variability. Both treatments experienced higher growth rates (above 1 cm/month) during winter, while summer growth rates dropped significantly, with the 10–20 cm treatment even showing negative growth rates. These dynamics are consistent with other studies (Gómez-Gras et al. 2021; Casoli et al. 2022), suggesting that Atlantic populations also respond, like Mediterranean populations, to seasonal temperature and food availability fluctuations (Ribes et al. 2003; Gori et al. 2013). Stressful phases linked to warmer conditions have been previously reported (Matsumoto 2004; Fava et al. 2010). While negative growth has been documented in both tropical (Brazeau & Lasker 1992) and temperate octocorals (Rossi et al. 2011), it is attributed to various factors including predation, fragmentation, environmental adaptations, damage, or disease (Lasker et al. 2003; Rossi et al. 2011; Serrano et al. 2018). It is important to emphasize negative growth associated with high temperatures (Rossi et al. 2011; Roveta et al. 2023), particularly when climate change is a major concern. Negative growth in response to high temperatures further emphasizes the need to incorporate this parameter in restoration analyses to avoid overlooking seasonal stress or reproductive strategies that affect size, thereby introducing potential positive biases in growth assessments.

Seasonal growth variability and stress phases are crucial considerations when selecting the timing for octocoral transplantation. Transplanting during the summer, a naturally less favorable period, combined with manipulation-induced stress, could lead to unsuccessful outcomes. Therefore, understanding and accounting for these seasonal dynamics is essential for optimizing transplantation success.

Health Status

The transplanted colonies, encompassing both treatment size classes (<10 and 10–20 cm), maintained healthy conditions throughout the 2-year monitoring period. This aligns with expectations, as observations of the surrounding area revealed a minimal number of impacted natural colonies (Padrão N, 2019, University of Algarve, personal observation). The few impacted colonies exhibited less than 5% of their total area affected, with minor epiphyte presence on branch extremities. Such minor impacts are typical in healthy octocoral gardens, attributable to natural disturbances like predation or temperature shifts (Cerrano & Bavestrello 2008; Sini et al. 2015; Topçu & Öztürk 2015). Consequently, colonies with less than 5% impact are often considered healthy (Francour & Koukouras 2000).

Importantly, there was no significant degradation in the health of the transplants immediately post-transplantation. This conclusion is supported by the observed health status in the initial months and the immediate post-transplant conditions. Notably, polyps were open, and colonies were feeding the day after transplantation, indicating that *P. grayi* is a resilient species, capable of withstanding the stress associated with transplantation. Additionally, there was no evidence of negative interactions between the epoxy material and the living tissue, as no degradation was observed in the base branches or holdfast areas of the transplants. These findings underscore the suitability of *P. grayi* for transplantation procedures and highlight the species' resilience and compatibility with epoxy materials used in the process.

Transplant Cost and Limitations. When implementing restoration projects, one of the primary constraints is funding limitations. Restoration initiatives are estimated to cost up to U.S.\$ 75 M/ha, with an average cost of around U.S.\$ 4.8 M/ha (Van Dover et al. 2014). Therefore, it is essential to provide detailed information regarding the costs and limitations of methodologies when developing or testing new techniques. Recent studies have begun to address this issue by highlighting the need for cost-effective restoration actions and publishing methodologies with lower costs (around U.S.\$ 170,000 ha⁻¹) (Montseny et al. 2021).

When implementing the transplant procedure using the DSA methodology, our team of two divers was able to transplant 60 colonies in 82 minutes. The amount of epoxy required was approximately 0.15 L, equivalent to €10 of material. Considering the local economy in Portugal at the time of the study, the cost of allocating two technicians, highway tolls, and gasoline was estimated at €170 per day. Given that the transplant area could be accessed without a vessel, the cost per transplant was roughly €3, with epoxy material costing €0.17 and the remainder covering human resources and logistics.

Despite the low cost, this method may present limitations for research groups aiming to implement it at depths below 30 m (recreational diving depths) or those unaccustomed to using underwater tools such as drills. Nonetheless, if the procedure is simplified to the point where citizens can participate in the transplant effort, the DSA methodology becomes an effective and inexpensive option. This concept is currently being tested in collaboration with a local dive center and is expected to become a reality soon.

Restoration and mitigation efforts are often constrained by funding limitations, making cost-efficiency a crucial factor for decision-makers when selecting transplantation methodologies. This consideration has gained even greater importance following the United Nations' designation of the current decade as the "Decade of Restoration," which includes underwater restoration as a Sustainable Development Goal (Goal 14). Consequently, realistic cost estimations should be openly shared among peers to properly assess the viability of projects, taking into account financial constraints and diverse economic realities worldwide.

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LITERATURE CITED

- Bally M, Garrabou J (2007) Thermodependent bacterial pathogens and mass mortalities in temperate benthic communities: a new case of emerging disease linked to climate change. *Global Change Biology* 13:2078–2088. <https://doi.org/10.1111/j.1365-2486.2007.01423.x>
- Bayraktarov E, Saunders MI, Abdullah S, Mills M, Behr J, Possingham HP, Mumby PJ, Lovelock CE (2015) The cost and feasibility of marine coastal restoration. *Ecological Applications* 26:1055–1074. <https://doi.org/10.1890/15-1077>
- Boström-Einarsson L, Babcock RC, Bayraktarov E, Ceccarelli D, Cook N, Ferse SC, et al. (2020) Coral restoration – a systematic review of current methods, successes, failures and future directions. *PLoS One* 15:e0226631. <https://doi.org/10.1371/journal.pone.0226631>
- Brazeau DA, Lasker HR (1992) Growth rates and growth strategy in a clonal marine invertebrate, the Caribbean octocoral *Briareum asbestinum*. *Biological Bulletin* 183:269–277. <https://doi.org/10.2307/1542214>
- Carvalho S, Cúrdia J, Pereira F, Guerra-García JM, Santos MN, Cunha MR (2014) Biodiversity patterns of epifaunal assemblages associated with the gorgonians *Eunicella gazella* and *Leptogorgia lusitanica* in response to host, space and time. *Journal of Sea Research* 85:37–47. <https://doi.org/10.1016/j.seares.2013.10.001>
- Casoli E, Ventura D, Mancini G, Cardone S, Farina F, Donnini L, Pace DS, Shaul R, Belluscio A, Ardizzone G (2022) Rehabilitation of Mediterranean animal forests using gorgonians from fisheries by-catch. *Restoration Ecology* 30:1–10. <https://doi.org/10.1111/rec.13465>
- Cerrano C, Bavestrello G (2008) Medium-term effects of die-off of rocky benthos in the Ligurian Sea. What can we learn from gorgonians? *Chemistry and Ecology* 24:73–82. <https://doi.org/10.1080/02757540801979648>
- Cerrano C, Danovaro R, Gambi C, Pusceddu A, Riva A, Schiaparelli S (2010) Gold coral (*Savalia savaglia*) and gorgonian forests enhance benthic biodiversity and ecosystem functioning in the mesophotic zone. *Biodiversity and Conservation* 19:153–167. <https://doi.org/10.1007/s10531-009-9712-5>
- Chan I, Tseng LC, Kâ S, Chang CF, Hwang JS (2012) An experimental study of the response of the gorgonian coral *Subergorgia suberosa* to polluted seawater from a former coastal mining site in Taiwan. *Zoological Studies* 51:27–37. https://www.researchgate.net/publication/279675728_An_Experimental_Study_of_the_Response_of_the_Gorgonian_Coral_Subergorgia_suberosa_to_Polluted_Seawater_from_a_Former_Coastal_Mining_Site_in_Taiwan
- Coma R, Ribes M, Zabala M, Gili JM (1995) Reproduction and cycle of gonadal development in the Mediterranean gorgonian *Paramuricea clavata*. *Marine Ecology Progress Series* 117:173–184. <https://doi.org/10.3354/meps117173>
- Coppari M, Zanella C, Rossi S (2019) The importance of coastal gorgonians in the blue carbon budget. *Scientific Reports* 9:1–12. <https://doi.org/10.1038/s41598-019-49797-4>
- Cúrdia J, Monteiro P, Afonso CML, Santos MN, Cunha MR, Gonçalves JMS (2013) Spatial and depth-associated distribution patterns of shallow gorgonians in the Algarve coast (Portugal, NE Atlantic). *Helgolander Marine Research* 67:521–534. <https://doi.org/10.1007/s10152-012-0340-1>
- Dias V, Oliveira F, Boavida J, Serrão EA, Gonçalves JMS, Coelho MAG (2020) High coral bycatch in bottom-set gillnet coastal fisheries reveals rich coral habitats in southern Portugal. *Frontiers in Marine Science* 7:1–16. <https://doi.org/10.3389/fmars.2020.603438>
- Duarte CM, Agusti S, Barbier E, Britten GL, Castilla JC, Gattuso JP, et al. (2020) Rebuilding marine life. *Nature* 580:39–51. <https://doi.org/10.1038/s41586-020-2146-7>
- Edwards AJ, Gomez ED (2007) Biological restoration. Pages 13–19. In: Edwards AJ, Gomez ED (eds) Reef restoration concepts and guidelines: making sensible management choices in the face of uncertainty. The Coral Reef Targeted Research & Capacity Building for Management Program, St. Lucia, Australia
- Fabri MC, Pedel L, Beuck L, Galgani F, Hebbeln D, Freiwald A (2014) Megafauna of vulnerable marine ecosystems in French mediterranean submarine canyons: spatial distribution and anthropogenic impacts. *Deep-Sea Research Part II: Topical Studies in Oceanography* 104:184–207. <https://doi.org/10.1016/j.dsr2.2013.06.016>
- Fava F, Bavestrello G, Valisano L, Cerrano C (2010) Survival, growth and regeneration in explants of four temperate gorgonian species in the Mediterranean Sea. *Italian Journal of Zoology* 77:44–52. <https://doi.org/10.1080/11250000902769680>
- Ferrigno F, Bianchi CN, Lasagna R, Morri C, Russo GF, Sandulli R (2016) Corals in high diversity reefs resist human impact. *Ecological Indicators* 70:106–113. <https://doi.org/10.1016/j.ecolind.2016.05.050>
- Francour P, Koukouras A (2000) Methods for studying the impact of diver frequentation and mooring on coralligenous communities. Pages 69–74 In: Goñi R, Badalamenti F, Le Diréac L, (eds) Introductory guide to methods for selected ecological studies in marine reserves. GIS Posidonie Publication, Marseille, France
- Garrabou J, Coma R, Bensoussan N, Bally M, Chevaldonné P, Cigliano M, et al. (2009) Mass mortality in northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. *Global Change Biology* 15:1090–1103. <https://doi.org/10.1111/j.1365-2486.2008.01823.x>
- Garrabou J, Ledoux J-B, Bensoussan N, Gómez-Gras D, Linares C (2021) Sliding toward the collapse of Mediterranean coastal marine rocky ecosystems. Pages 291–324. In: Canadell JG, Jackson RB (eds) Ecosystem collapse and climate change. *Ecological studies*. Vol 241. Springer, Cham, Switzerland. https://doi.org/10.1007/978-3-030-71330-0_11
- Gómez-Gras D, Linares C, López-Sanz A, Amate R, Ledoux JB, Bensoussan N, et al. (2021) Population collapse of habitat-forming species in the Mediterranean: a long-term study of gorgonian populations affected by recurrent marine heatwaves. *Proceedings of the Royal Society B: Biological Sciences* 288:20212384. <https://doi.org/10.1098/rspb.2021.2384>
- Goreau TJ (2010) Coral reef and fisheries habitat restoration in the coral triangle: the key to sustainable reef management. In: *Proceedings of the Coral Reef Management Symposium on the Coral Triangle Area, Manado, Sulawesi, Indonesia*.
- Gori A, Linares C, Viladrich N, Clavero A, Orejas C, Fiorillo I, Ambroso S, Gili JM, Rossi S (2013) Effects of food availability on the sexual reproduction and biochemical composition of the Mediterranean gorgonian *Paramuricea clavata*. *Journal of Experimental Marine Biology and Ecology* 444:38–45. <https://doi.org/10.1016/j.jembe.2013.03.009>
- Kumagai NH, Shinagawa H, Sato T, Tsuchiya Y, Aoki MN (2004) Transplantation of gorgonian octocorals for in situ experimental manipulations. *Benthos Research* 59:11–19. https://doi.org/10.5179/benthos1996.59.1_11
- Lasker HR, Boller ML, Castanaro J, Sánchez JA (2003) Determinate growth and modularity in a gorgonian octocoral. *Biological Bulletin* 205:319–330. <https://doi.org/10.2307/1543295>
- Linares C, Coma R, Zabala M (2008) Restoration of threatened red gorgonian populations: an experimental and modelling approach. *Biological Conservation* 141:427–437. <https://doi.org/10.1016/j.biocon.2007.10.012>

- Marschner I, Donoghoe MW, Donoghoe MM (2018) Package ‘glm2’ 1.2.1. <https://doi.org/10.32614/CRAN.package.glm2>
- Martinez-Dios A, Dominguez-Carrió C, Zapata-Guardiola R, Gili JM (2016) New insights on Antarctic gorgonians’ age, growth and their potential as paleorecords. Deep-Sea Research Part I: Oceanographic Research Papers 112:57–67. <https://doi.org/10.1016/j.dsr.2016.03.007>
- Matsumoto AK (2004) Heterogeneous and compensatory growth in *Melithaea flabellifera* (Octocorallia: Melithaeidae) in Japan. Hydrobiologia 530–531:389–397. <https://doi.org/10.1007/s10750-004-2673-5>
- Mistri M, Ceccherelli VU (1996) Effects of a mucilage event on the Mediterranean gorgonian *Paramuricea clavata*. I – short term impacts at the population and colony levels. Italian Journal of Zoology 63:221–230. <https://doi.org/10.1080/11250009609356137>
- Mokhtar-Jamaï K, Pascual M, Ledoux JB, Coma R, Féral JP, Garrabou J, Aurelle D (2011) From global to local genetic structuring in the red gorgonian *Paramuricea clavata*: the interplay between oceanographic conditions and limited larval dispersal. Molecular Ecology 20:3291–3305. <https://doi.org/10.1111/j.1365-294X.2011.05176.x>
- Montero-Serra I, Garrabou J, Doak DF, Figuerola L, Hereu B, Ledoux JB, Linares C (2018) Accounting for life-history strategies and timescales in marine restoration. Conservation Letters 11:1–9. <https://doi.org/10.1111/conl.12341>
- Montseny M, Linares C, Carreiro-Silva M, Henry LA, Billett D, Cordes EE, et al. (2021) Active ecological restoration of cold-water corals: techniques, challenges, costs and future directions. Frontiers in Marine Science 8:1–21. <https://doi.org/10.3389/fmars.2021.621151>
- Montseny M, Linares C, Viladrich N, Capdevila P, Ambroso S, Díaz D, Gili JM, Gori A (2020) A new large-scale and cost-effective restoration method for cold-water coral gardens. Aquatic Conservation: Marine and Freshwater Ecosystems 30:977–987. <https://doi.org/10.1002/aqc.3303>
- Montseny M, Linares C, Viladrich N, Olariaga A, Carreras M, Palomeras N, et al. (2019) First attempts towards the restoration of gorgonian populations on the Mediterranean continental shelf. Aquatic Conservation: Marine and Freshwater Ecosystems 29:1278–1284. <https://doi.org/10.1002/aqc.3118>
- OSPAR Commission (2010) Quality status report 2010. OSPAR Commission, London, United Kingdom
- Palma M, Casado MR, Pantaleo U, Pavoni G, Pica D, Cerrano C (2018) SfM-based method to assess gorgonian forests (*Paramuricea clavata* [Cnidaria, Octocorallia]). Remote Sensing 10:1–21. <https://doi.org/10.3390/rs10071154>
- Ponti M, Grech D, Mori M, Perlini RA, Ventra V, Panzalis PA, Cerrano C (2016) The role of gorgonians on the diversity of vagile benthic fauna in Mediterranean rocky habitats. Marine Biology 163:1–14. <https://doi.org/10.1007/s00227-016-2897-8>
- R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Ribes M, Coma R, Rossi S (2003) Natural feeding of the temperate asymbiotic octocoral-gorgonian *Leptogorgia sarmentosa* (Cnidaria: Octocorallia). Marine Ecology Progress Series 254:141–150. <https://doi.org/10.3354/meps254141>
- Rinkevich B (2014) Rebuilding coral reefs: does active reef restoration lead to sustainable reefs? Current Opinion in Environmental Sustainability 7:28–36. <https://doi.org/10.1016/j.cosust.2013.11.018>
- Rossi S, Bramanti L, Gori A, Orejas C (2017) Marine animal forests. In: Rossi S (ed) The ecology of benthic biodiversity hotspots. Springer International Publishing, Cham, Switzerland. <https://doi.org/10.1007/978-3-319-21012-4>
- Rossi S, Gili JM (2009) Reproductive features and gonad development cycle of the soft bottom-gravel gorgonian *Leptogorgia sarmentosa* (Esper, 1791) in the NW Mediterranean Sea. Invertebrate Reproduction and Development 53:175–190. <https://doi.org/10.1080/07924259.2009.9652304>
- Rossi S, Gili JM, Garrofé X (2011) Net negative growth detected in a population of *Leptogorgia sarmentosa*: quantifying the biomass loss in a benthic soft bottom-gravel gorgonian. Marine Biology 158:1631–1643. <https://doi.org/10.1007/s00227-011-1675-x>
- Roveta C, Pulido Mantas T, Bierwirth J, Calcinaï B, Coppari M, Di Camillo CG, Puce S, Villechanoux J, Cerrano C (2023) Can colony resizing represent a strategy for octocorals to face climate warming? The case of the precious red coral *Corallium rubrum*. Coral Reefs 42:535–549. <https://doi.org/10.1007/s00338-023-02365-9>
- Santangelo G, Carletti E, Maggi E, Bramanti L (2003) Reproduction and population sexual structure of the overexploited Mediterranean red coral *Corallium rubrum*. Marine Ecology Progress Series 248:99–108.
- Saunders MI, Doropoulos C, Bayraktarov E, Babcock RC, Gorman D, Eger AM, et al. (2020) Bright spots in coastal marine ecosystem restoration. Current Biology 30:R1500–R1510. <https://doi.org/10.1016/j.cub.2020.10.056>
- Serrano E, Coma R, Inostroza K, Serrano O (2018) Polyp bail-out by the coral *Astroides calycularis* (Scleractinia, Dendrophylliidae). Marine Biodiversity 48:1661–1665. <https://doi.org/10.1007/s12526-017-0647-x>
- Sini M, Garrabou J, Trygonis V, Koutsoubas D (2019) Coralligenous formations dominated by *Eunicella cavolini* (Koch, 1887) in the NE Mediterranean: biodiversity and structure. Mediterranean Marine Science 20:174–188. <https://doi.org/10.12681/mms.18590>
- Sini M, Kipson S, Linares C, Koutsoubas D, Garrabou J (2015) The yellow gorgonian *Eunicella cavolini*: demography and disturbance levels across the Mediterranean Sea. PLoS One 10:e0126253. <https://doi.org/10.1371/journal.pone.0126253>
- Spieß A (2018) Propagate: Propagation of uncertainty. R package version 1.0-6. <https://CRAN.R-project.org/package=propagate>
- Sponaugle S, LaBarbera M (1991) Drag-induced deformation: a functional feeding strategy in two species of gorgonians. Journal of Experimental Marine Biology and Ecology 148:121–134. [https://doi.org/10.1016/0022-0981\(91\)90151-L](https://doi.org/10.1016/0022-0981(91)90151-L)
- Topçu EN, Öztürk B (2015) Composition and abundance of octocorals in the Sea of Marmara, where the Mediterranean meets the Black Sea. Scientia Marina 79:125–135. <https://doi.org/10.3989/scimar.04120.09A>
- Topçu NE, Yılmaz IN, Saraçoğlu C, Barraud T, Öztürk B (2023) Size matters when it comes to the survival of transplanted yellow gorgonian fragments. Journal for Nature Conservation 71:126326. <https://doi.org/10.1016/j.jnc.2022.126326>
- Turicchia E, Abbiati M, Sweet M, Ponti M (2018) Mass mortality hits gorgonian forests at Montecristo Island. Diseases of Aquatic Organisms 131:79–85. <https://doi.org/10.3354/dao03284>
- Van Dover CL, Aronson J, Pendleton L, Smith S, Arnaud-Haond S, Moreno-Mateos D, et al. (2014) Ecological restoration in the deep sea: Desiderata. Marine Policy 44:98–106. <https://doi.org/10.1016/j.marpol.2013.07.006>
- Villechanoux J, Bierwirth J, Mantas TP, Cerrano C (2022) Testing transplantation techniques for the red coral *Corallium rubrum*. Water 14:1–19. <https://doi.org/10.3390/w14071071>
- Waters L (2015) Acute and chronic effects of large-vessel anchoring on coral reef communities inside a designated commercial anchorage. Master’s thesis. Nova Southeastern University, Fort Lauderdale, Florida.
- Zelli E, Quéré G, Lago N, Di Franco G, Costantini F, Rossi S, Bramanti L (2020) Settlement dynamics and recruitment responses of Mediterranean gorgonians larvae to different crustose coralline algae species. Journal of Experimental Marine Biology and Ecology 530–531:151427. <https://doi.org/10.1016/j.jembe.2020.151427>

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