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Environmental drivers and anthropogenic impacts influencing the presence probability and health status of *Isidella elongata* in the Ionian Sea.

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Abstract

The habitat-forming bamboo coral *Isidella elongata* creates structurally complex facies on bathyal muddy bottoms across the Mediterranean Sea and adjacent Atlantic waters. By enhancing benthic heterogeneity, these facies support diverse associated fauna, leading to their designation as Vulnerable Marine Ecosystems (VMEs) and Essential Fish Habitats (EFH). However, intense bottom trawling cause direct colony removal and sediment resuspension, resulting in drastic population declines and leading to the classification of *I. elongata* as Critically Endangered. We analyzed ROV video surveys from an active commercial fishing ground in the Ionian Sea to evaluate colony density and associated fauna, while assessing how anthropogenic pressure and environmental variables shape colony health and presence probability. Ordinal Logistic Regression (OLR) identified a significant relationship between cumulative trawling effort and colony damage. Crucially, Generalized Additive Models (GAMs) revealed that *I. elongata* presence is not simply restricted to flat muddy seabeds, but depends on specific geomorphological features, including pockmarks, alongside the pronounced negative effect of trawling. Our findings provide key ecological insights into habitat preferences while illustrating the severe impact of cumulative trawling activities, underscoring that science-informed spatial protection is urgently required to secure VMEs integrity and facilitate deep-sea recovery.

Introduction

The bamboo coral *Isidella elongata* (Esper, 1788) is a near-endemic, candelabrum-shaped octocoral that serves as a critical structural species on bathyal muddy bottoms throughout the Mediterranean Sea and adjacent Atlantic waters^{1–4}. Anchored by a root-like basal structure that penetrates soft sediments, *I. elongata* creates distinctive facies on compact muddy bottoms, where its colonies enhance the structural complexity of otherwise uniform soft sediments^{3,5,6}. These facies are primarily observed on flat or gently sloping sedimentary bottoms of the middle continental slope, typically between approximately 200 and 500 m depth, though the species may occur over a broader bathymetric range depending on regional environmental conditions and fishing pressure^{1,3,7–11}. By increasing habitat heterogeneity and providing three-dimensional biogenic structures, bamboo coral facies support local benthic biomass, promote benthopelagic coupling and offer refuge, feeding, nursery, and spawning opportunities for several species, including commercially valuable crustaceans and fishes^{3,4,6,7,10,12}. Thanks to its functional role, the structural complexity and the pronounced fragility, the General Fisheries Commission for the Mediterranean (GFCM) recognizes the compact mud facies associated with *I. elongata* as a Sensitive Habitat, a Vulnerable Marine Ecosystem (VME) and an Essential Fish Habitat (EFH)¹³.

Over the past decades, the technological expansion of commercial deep-sea fisheries has shifted bottom trawling pressure progressively down the continental slope to target valuable decapod crustaceans, such as the blue and red shrimp *Aristeus antennatus*, the giant red shrimp *Aristaeomorpha foliacea* and the Norway lobster *Nephrops norvegicus*^{14,15}. The spatial distribution of these target species frequently coincides with the muddy bottoms favored by *I. elongata*, resulting in significant and widespread degradation of these vulnerable and slow growth deep-sea facies due to bottom trawling^{3,4,11,16,17}. Bottom trawling affects *I. elongata* through both direct and indirect mechanisms. The mechanical action of towing nets, trawl doors, and ground gears can shatter, break, uproot, or fragment colonies, a vulnerability severely heightened by the poorly flexible structure of their calcareous skeleton^{17–20}. Colonies that are not completely removed could experience polyp damage, tissue necrosis, abrasion, and overgrowth by opportunistic secondary colonizers^{19–22}. The resulting turbid plumes clog delicate polyps, smother surviving benthos and settling larvae, and induce chronic physiological stress that elevates mortality among suspension feeders^{16,19,23–25}. *I. elongata* fields have experienced severe regression and fragmentation throughout much of their historical Mediterranean range, with habitat loss and reduced occurrence repeatedly associated to bottom trawling pressure^{4,7,11,16,22,25–27}. As result, *I. elongata* is designated as a species of high conservation priority, classified as Critically Endangered on the IUCN Red List of Mediterranean Anthozoans²⁸ and included in Annex II of the SPA/BD Protocol under the Barcelona Convention.

Due to the widespread decline, remaining well-developed aggregations are primarily documented in areas that provide some form of natural or indirect spatial protection^{3,8,10}. These isolated refuges include natural topographic features where trawling is physically challenging or unfeasible, such as steep submarine canyon flanks, deep rocky banks, and other complex

seabed morphologies^{8,22,25,26}. They also encompass accidental anthropogenic exclusion zones created around submarine cables, pipelines, or other seabed infrastructures^{3,10,29,30}.

However, not all remnant populations occur under such protective conditions, and evaluating the persistence of *I. elongata* within active bottom trawling fishing grounds is essential for developing effective conservation and management strategies.

In contrast to the paradigm of isolated and relatively undisturbed refugia, the aggregations investigated in this study are located within a heavily exploited commercial fishing ground subjected to ongoing bottom trawling. In this work, we used high-resolution acoustic mapping and ROV visual surveys to characterize *I. elongata* colonies persisting under continuous anthropogenic stress. The specific objectives were to: (1) assess the size structure and spatial density of *I. elongata* aggregations, (2) evaluate colony health status in relation to anthropogenic pressures, (3) characterize the associated fauna and host-epibiont interactions, and (4) quantify the relative influence of environmental predictors and human stressors on the species' probability of occurrence.

Material and methods

Data Collection

The study area is located in the Ionian Sea (central Mediterranean Sea), 21km off Punta Stilo in the southern Calabrian coast (Italy). It spans a total surface of 110 km², with depths ranging from 70 m to 1220 m. The area was explored during an oceanographic cruise for a feasibility study and environmental impact assessment aimed at the establishment of an offshore wind farm within the project "Enotria" by ACCIONA Energía. Acoustic surveys were conducted using the Multibeam Kongsberg EM712-MK2 echosounder and the Side Scan Sonar (SSS) "EdgeTech's 4125i Side Scan Sonar". The raw acoustic data were processed to generate, respectively, the Digital Elevation Model (DTM), with a spatial resolution of 10 m, and the SSS photomosaic with a resolution of 1 m pixels. A total of 36 video transects, each with an average linear length of 844 ± 304 m (s.d.), were conducted using a light-work class Sub Atlantic Tomahawk remotely operated vehicle (ROV). The ROV was equipped with an HD camera and a Z CAM E2-F6 Full Frame 6K Cinema Camera to capture ultra-high resolution video footage. Two laser pointers, mounted 10 cm apart, provided a reference scale for measurements. A Sea-Bird SBE37 MicroCAT multi-parameter probe was installed to record conductivity, temperature, partial pressure of oxygen (pO₂), sound velocity and pressure during the ROV-dives. The Ultra Short BaseLine (USBL) Kongsberg HiPAP acoustic positioning system was employed to determine the real-time georeferenced absolute position (latitude and longitude, WGS84) of the ROV, with one signal transmitted per second.

All research activities were carried out in accordance with the regulatory framework governing oceanographic research under Italian law. Because the campaign took place in waters not subject to site-specific environmental protections and no physical sampling of animal specimens was conducted, no additional specialized permits were required.

Video ROV analysis and biological data extraction

The Ocean Floor Observation Protocol software (OFOP; version 3.3.4) was used during the video survey transects to associate data, time, and coordinates with the presence of taxa, specimens, substrate types, and anthropogenic impacts. Each organism was identified at the lowest possible taxonomic level. Anthropogenic impacts were categorized as trawl marks, litter, or any source of Abandoned, Lost, or otherwise Discarded Fishing Gear (ALDFG). Each isolated trawl mark linked to a mud scar larger than 1 m was recorded as a single occurrence

^{22,31}.

For the target species, in addition to OFOP logging, videos documenting the presence of *I. elongata* were further analyzed to extract data on colony height (cm), percentage of necrotic tissue, presence of epibionts, and entanglement with ALDFGs. Tissue loss, defined as the percentage of exposed axial skeleton, was categorized into six classes, expanding upon the three damage classes proposed by Perez et al.³²: 0% (pristine colonies), 1-10%, 11-50%, 51-75%, 76-99%, 100% (colonies with full exposed axial skeleton). Colonies exhibiting fully

exposed root structures and lying on the seabed were classified as “Uprooted”. Colony height was measured using ImageJ software³³ with the two laser beams serving as a scale reference. To minimize positional noise, ROV tracks obtained via USBL positioning were manually cleaned in ArcGIS Pro³⁴ and then smoothed using a rolling average to reduce short-term fluctuations. Prior to spatial analyses, the coordinates were projected into the Universal Transverse Mercator (UTM) Zone 33N coordinate reference system (WGS 84 datum) to enable accurate distance- and area-based calculations.

The laser beam reference was used to estimate an average camera frame width of 2 m. This measurement was adopted as transect buffer width in accordance with established ROV video survey protocols^{35,36}. Observations within these buffers were rasterized at two different resolutions to standardize abundance data. A 1 m x 1 m grid, corresponding to the sample unit (SU) raster, was used to calculate the density (colonies/m²) of vital *I. elongata* specimens (tissue damage < 100%), providing a standardized measure of live coral abundance. Then, to maximize computational efficiency during covariate extractions and subsequent statistical modeling, a coarser 2 m x 2 m grid (matching the 2 m transect width) was used to create the final presence-absence dataset.

The Nearest Neighbor Distance (NND) method was applied to investigate the small-scale spatial structure of the colonies. The Euclidean distance between each colony and its closest neighbor was calculated using the function *nndist()* of the “spatstat” R.

The co-occurrence of *I. elongata* with other encountered taxa was analyzed using a 2 m radius buffer around each colony to extract data on associated species. All grids were built using the “terra” package³⁷ (Hijmans et al., 2026) in the R version 4.3.1³⁸ via the RStudio interface (Ver. 2023.06.2+561)³⁹.

Environmental, geomorphological and anthropogenic impact data

Temperature and pO₂ were extracted from the MicroCAT data records, which collected measurements at 30-seconds intervals. Neighborhood processing interpolation, employing a focal window of 3 x 3 pixels, was used to generate a raster for each buffer transect.

A DTM raster with a spatial resolution of 10m was used to derive six primary geomorphological features: slope, roughness, bathymetric position index (BPI), and the aspect components eastness and northness^{40,41}. The BPI was derived using neighborhood analysis, which calculates the relative topographic position of each pixel with respect to its neighboring pixels within a specified radius⁴¹. BPI was then computed using different radii of 15, 30, and 45 pixels, corresponding to 150 m, 300 m and 450 m respectively (BPI_15, BPI_30; BPI_45). All geomorphological features were estimated using “terra” and “MultiscaleDTM” R packages^{37,42}. Seafloor current velocity data were obtained from the Copernicus Marine Service Mediterranean Sea Physics Analysis and Forecast model⁴³. Bottom current speed (BCS) was calculated as the Euclidean norm of the eastward (uo) and northward (vo) velocity components ($BCS = \sqrt{vo^2 + uo^2}$), resulting in a raster with a spatial resolution of 1/24° (≈4.2 km). To assess the potential geochemical and physical influence of pockmarks^{44,45} on surrounding *I. elongata*

colonies, a raster-based Euclidean distance surface was generated from mapped pockmarks. The distance was log-transformed to account for the expected non-linear decline in pockmark influence with increasing distance and to reduce the influence of extreme values⁴⁶.

Estimated bottom-trawling hours were obtained from the Global Fishing Watch (GFW) portal⁴⁷. Estimates of trawling hours were extracted for the 2012 – 2023 period, spanning from the first year of GFW data availability to the year of the ROV survey. Data were cumulatively summed to generate the apparent fishing effort raster layer.

Finally, the spatial density of trawl marks identified during ROV video analysis was estimated using a bivariate Kernel Density Estimation (KDE) via the *density.ppp()* function in the R package *spatstat*⁴⁸. The smoothing bandwidth (σ) was set to 120 m, representing the area of influence for each detected mark, as this distance corresponds to the minimum dispersion distance for most sediment plume mass generated by trawling activities⁴⁹. All the extracted variable values were linked to *I. elongata* presence/absence dataset.

Statistical analysis

We fitted ordinal logistic regression (OLR) model under the proportional odds assumption^{50–52} to evaluate whether anthropogenic pressure contributes to the increase of tissue damage in *I. elongata* colonies. The cumulative logit formulation models the probability of assignment to progressively higher tissue damage categories while accounting for the ordinal nature of the response variable⁵¹. To improve the reliability of maximum likelihood estimation⁵², the original tissue damage classes were consolidated into three broader ordinal categories: No Damage (0%), Low/Medium Damage (1–50%), and High Damage/Dead (51–100%).

As the cumulative trawling hours and trawling mark density exhibited low collinearity (Pearson's correlation coefficient: $|r| = 0.20$), they were considered together in the same model. The OLR model was estimated using the *polr()* function in the MASS package for R⁵².

Concurrently, a Generalized Additive Model (GAM) was estimated to investigate the influence of geomorphological, environmental and anthropogenic drivers on *I. elongata* occurrence. The probability of occurrence was modeled using a binomial distribution and a logit link function via the *mgcv* package in R⁵³. Multicollinearity among the covariates was avoided by retaining only variables with a Pearson's correlation coefficient of $|r| < 0.70$. For both modeling frameworks, Akaike's Information Criterion (AIC) was used to compare candidate model structures and verify final model parsimony⁵⁴. Statistical significance for all analyses was set at $\alpha = 0.05$.

Results

Geomorphological features and anthropogenic impacts of the study area

The study area was characterized by bathyal muddy bottoms interspersed with scattered boulders. A large pockmark field extended across the central region between 400 and 820 m depth (Figs. 1a,b), increasing the topographic complexity of the soft-sediment seabed. The highest density of large pockmarks was observed near transects CRO_T07, CRO_T32a, and CRO_T32 (Fig. 1b). The central region contained a gently sloping soft bottom that rose above the surrounding seabed, with a steeper eastward-facing slope beginning at approximately 480 m depth and reaching 1020 m at the outer margins of the acoustic survey (Fig 1b).

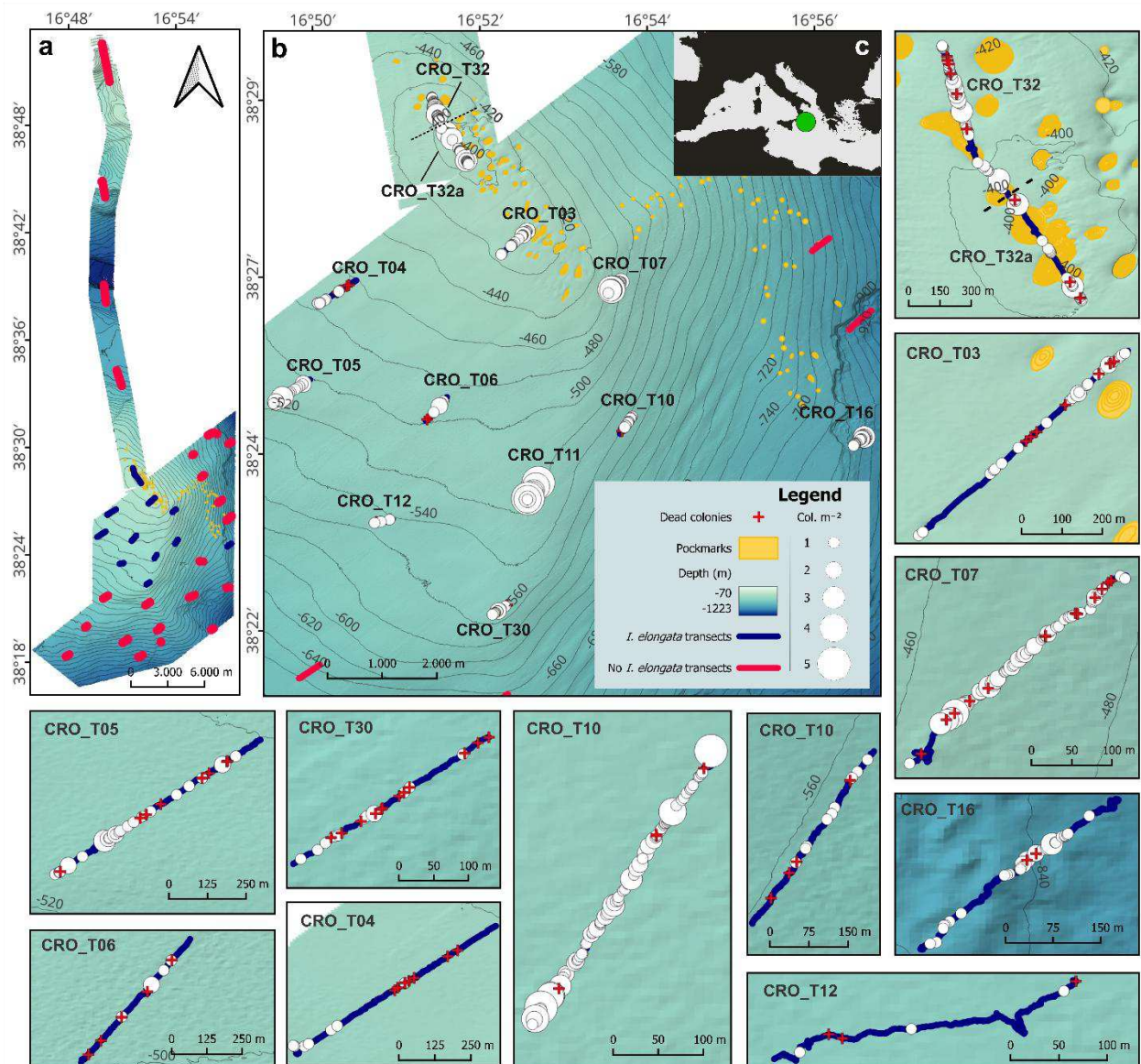


Figure 1 Map of the investigated area with *Isidella elongata* density values and dead colonies. **a)** Overview map with bathymetric contours displaying all ROV transects carried out; **b)** central study area characterized by *I. elongata* aggregations and pockmark fields (orange polygons); **c)** inset map of the Mediterranean Sea with the green dot indicating the study area location. Sub-panels display close-ups of individual transects where *I. elongata* was observed (labels correspond to transect IDs). White proportional circles represent live colony density (1–5 colonies m⁻²), red crosses indicate observed dead colonies, blue lines mark transects with *I. elongata*, and red lines denote transects where the target species was absent.

Multiple anthropogenic impacts were documented throughout the study area, including 42 Lost or Otherwise Discarded Fishing Gears (LDFGs; Fig 2c) and 311 trawl marks (Figs. 2a-d). Estimated cumulative fishing trawling activity averaged 54.48 ± 78.95 h (range: 0 – 545.39 h). An extensive zone of intense trawling activity (trawling hours > 96 h; Fig 2a) was identified in the north of the study area and near the northeastern edges of the shallow central region. Within this zone, the side-scan sonar (SSS) mosaic and ROV video footage revealed numerous distinct linear trawl scars, particularly in the northern sector (Figs. 2a,b,d,e; S1). Additional linear trawl scars were also observed across the broader study area, including zones where no ROV dives were conducted (Figs. 2d,e).

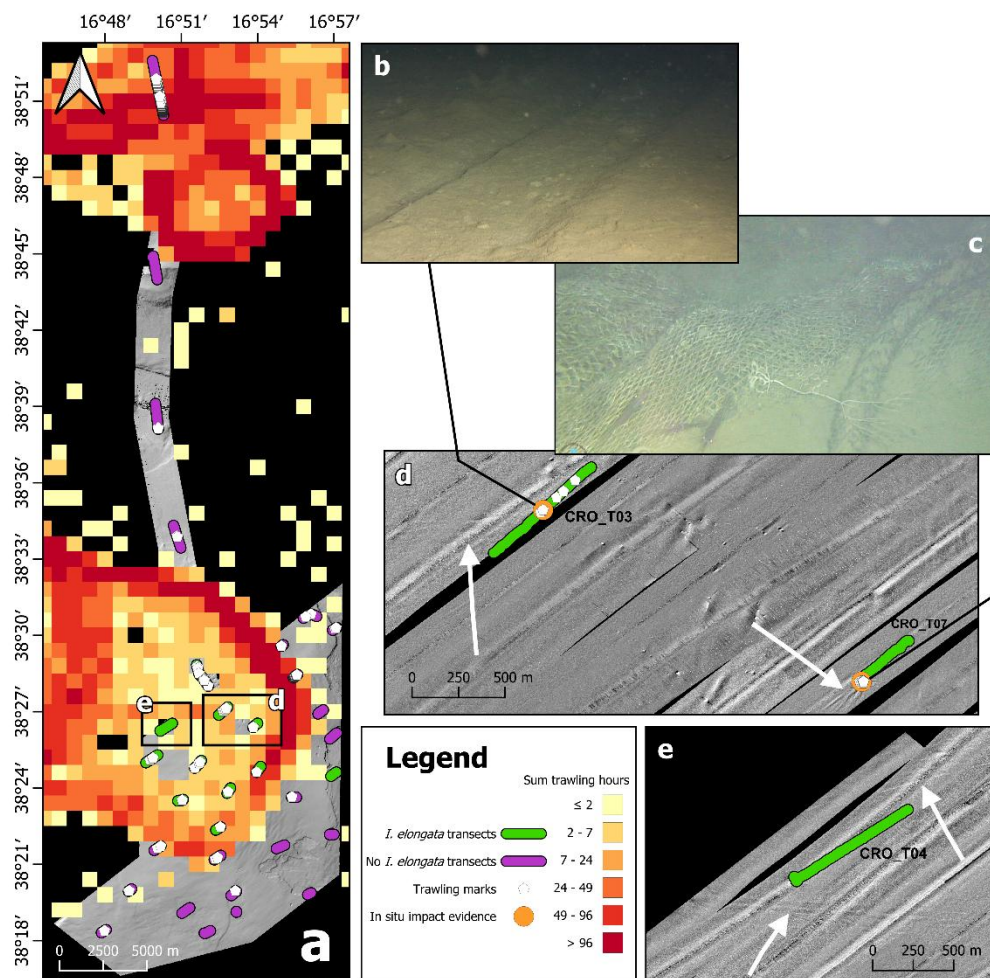


Figure 2. Spatial distribution of fishing pressure and in situ evidence of trawling impacts. Overview map of study area trawling effort displaying cumulative trawling hours (yellow-to-red raster gradient), ROV transects with *Isidella elongata* presence (green lines) and absence (purple lines), trawling marks identified by video (white pentagons) and the black boxes identifying the two inset areas showed in d) and e); b) ROV video frame showing a trawling mark in the muddy seabed; c) Large lost trawl net with an entangled colony of *I. elongata* and shrimps specimens belonging to the genus *Plesionika*; d) SSS photomosaic close up showing seabed trawling marks (white arrow) and the position (orange point) of the impact evidences shown in b) and c) along the transect CRO_T03 and CRO_T07. e) SSS photomosaic close-up near transect CRO_T04 displaying further acoustic evidence of trawling scars (white arrows).

Characterization of *I. elongata* facies and health status

A total of 159 hours of video footage was analyzed across the 36 transects, spanning a depth range of 151 to 1203 m and covering an overall area of 72,228 m². The presence of *I. elongata* was recorded in 12 transects with a total of 545 colonies identified at depths between 397 and 851 m (mean $\pm$ SD: 501 $\pm$ 105 m; Fig. 1). Of these, 463 were live colonies, with 370 classified as pristine (67.9%; see Figs. 3a,b and 4a) and 93 fell in the four category of tissue damage (1-10%: 3.9%; 11-50%: 9.0%; 51-75%: 2.4%; 76-99: 1.8%; Fig. 4a). An additional 67 colonies were dead (12.3%; Fig. 3b; 4a) and 15 colonies (2.8%; Fig. 3c) were uprooted and lying on the mud substrate with exposed roots (Fig. 3c). One uprooted specimen was even found still entangled

in the discarded fishing net (Fig. 2c). A high proportion of dead colonies was observed in transects with lower number of individuals ($n \text{ col.} < 10$), with CRO_T30 exhibiting the highest proportion ($n = 13$; 52.0%; tab 1). Several of these transects overlapped with intense bottom-trawling activity. For example, CRO_T10 transect, showed low colony abundance ($n = 9$) and a high percentage of dead colonies (30.8%; Tab. 1). This site was located within an area of high trawling pressure, as indicated by both high cumulative trawling hours and prominent trawl scars clearly visible on SSS imagery (Fig. S1).

Considering only live colonies, the lowest mean density was encountered in CRO_T12, with $0.003 \pm 0.054 \text{ col. /m}^2$ and the highest density was recorded in CRO_T11 with $0.128 \pm 0.488 \text{ col./m}^2$ (Tab. 1). CRO_T11 also exhibited the highest abundance values per sampling unit, reaching 5 individuals per square meter (Tab. 1). The presence coverage, defined as the spatial occupancy within SUs with at least 1 specimen, remains remarkably low across all surveyed transects. The highest spatial coverage was observed at CRO_T11 and CRO_T07 transects, which yield occupancy rates of 8.88% and 6.29%, respectively (Tab. 1). For the remaining monitored transects, occurrence values were uniformly low, closely hovering between 0.22% and 1.93% of the total sampled area (Tab. 1).

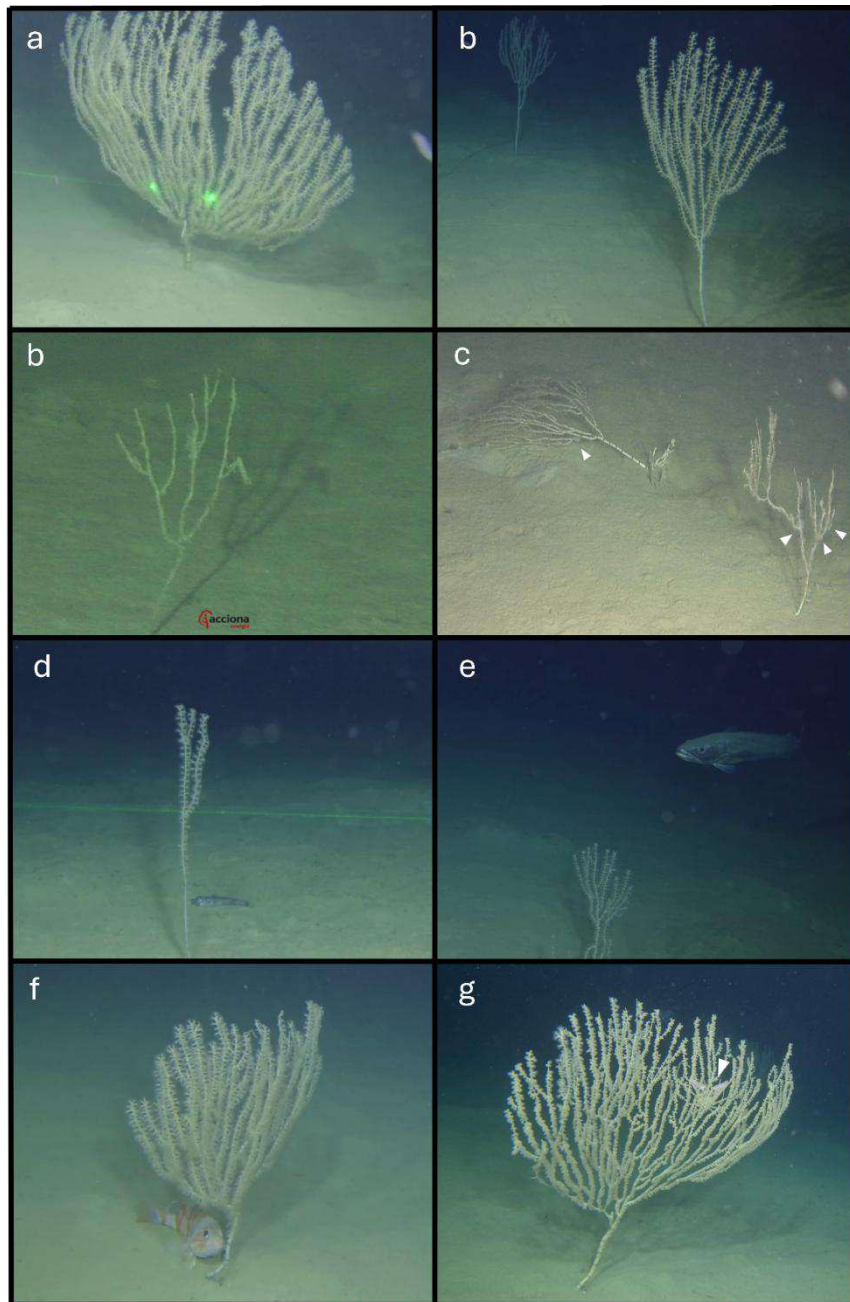


Figure 1. a) Large colony (class 40-50 cm) with no signs of damage (tissue class = 0); b) *I. elongata* facies formed by pristine specimens; c) Dead colony of *I. elongata*; d) Uprooted colony of *I. elongata* near an highly damaged specimen. The white triangle indicates polyps of *Amphianthus dohrnii*; e) *Chlorophthalmus agassizi* near a *I. elongata* colony; f) *Merluccius merluccius* swimming around a colony; g) *Helicolenus dactylopterus* sheltering below a colony of *I. elongata*; h) Large colony of *I. elongata* with the commensal crustacean *Anamathia rissoana* (white triangle).

Table 1 summary of density data of *Isidella elongata* for each investigated transect, including: max density for sampling unit (SU) and each class of density for SU; total number and proportion of dead colonies and uprooted ones; total area of each transect and the proportion of SU with at least 1 colony m^{-2}

Transect	Mean density (col. m^{-2}) $\pm$ SD	Max density for SU (col. m^{-2})	Number of SU (col. m^{-2}) with:						Tot_ind	Tot. dead colonies	Tot. Uprooted col.	Total_area (m^2)	Area occupied by presences (n SU >0 / total area)
			0 col. m^{-2}	1 col. m^{-2}	2 col. m^{-2}	3 col. m^{-2}	4 col. m^{-2}	5 col. m^{-2}					
CRO_T03	0.015 $\pm$ 0.131	2	1694	22	2	0	0	0	26	7 (21.2%)	0	1718	1.40%
CRO_T04	0.003 $\pm$ 0.057	1	2709	9	0	0	0	0	9	8 (44.4%)	1 (5.6%)	2718	0.33%
CRO_T05	0.011 $\pm$ 0.128	3	2596	18	4	1	0	0	29	8 (21.6%)	0	2619	0.88%
CRO_T06	0.003 $\pm$ 0.061	2	1848	3	1	0	0	0	5	4 (40%)	1 (10%)	1852	0.22%
CRO_T07	0.089 $\pm$ 0.382	4	1042	45	18	4	1	0	97	7 (6,2%)	9 (8%)	1112	6.29%
CRO_T10	0.007 $\pm$ 0.082	1	1335	9	0	0	0	0	9	4 (30.8%)	0	1344	0.67%
CRO_T11	0.128 $\pm$ 0.488	5	1006	72	17	3	4	2	141	3 (2.1%)	1 (0.7%)	1104	8.88%
CRO_T12	0.003 $\pm$ 0.054	1	1038	3	0	0	0	0	3	3 (50%)	0	1041	0.29%
CRO_T16	0.023 $\pm$ 0.177	3	1578	26	4	1	0	0	37	1 (2.6%)	1 (2.6%)	1609	1.93%
CRO_T30	0.015 $\pm$ 0.131	2	791	10	1	0	0	0	12	13 (52%)	0	802	1.37%
CRO_T32	0.021 $\pm$ 0.167	3	2241	36	5	1	0	0	49	6 (10.5%)	2 (3.5%)	2283	1.84%
CRO_T32a	0.022 $\pm$ 0.178	3	2018	35	1	3	0	0	46	3 (6.1%)	0	2057	1.90%

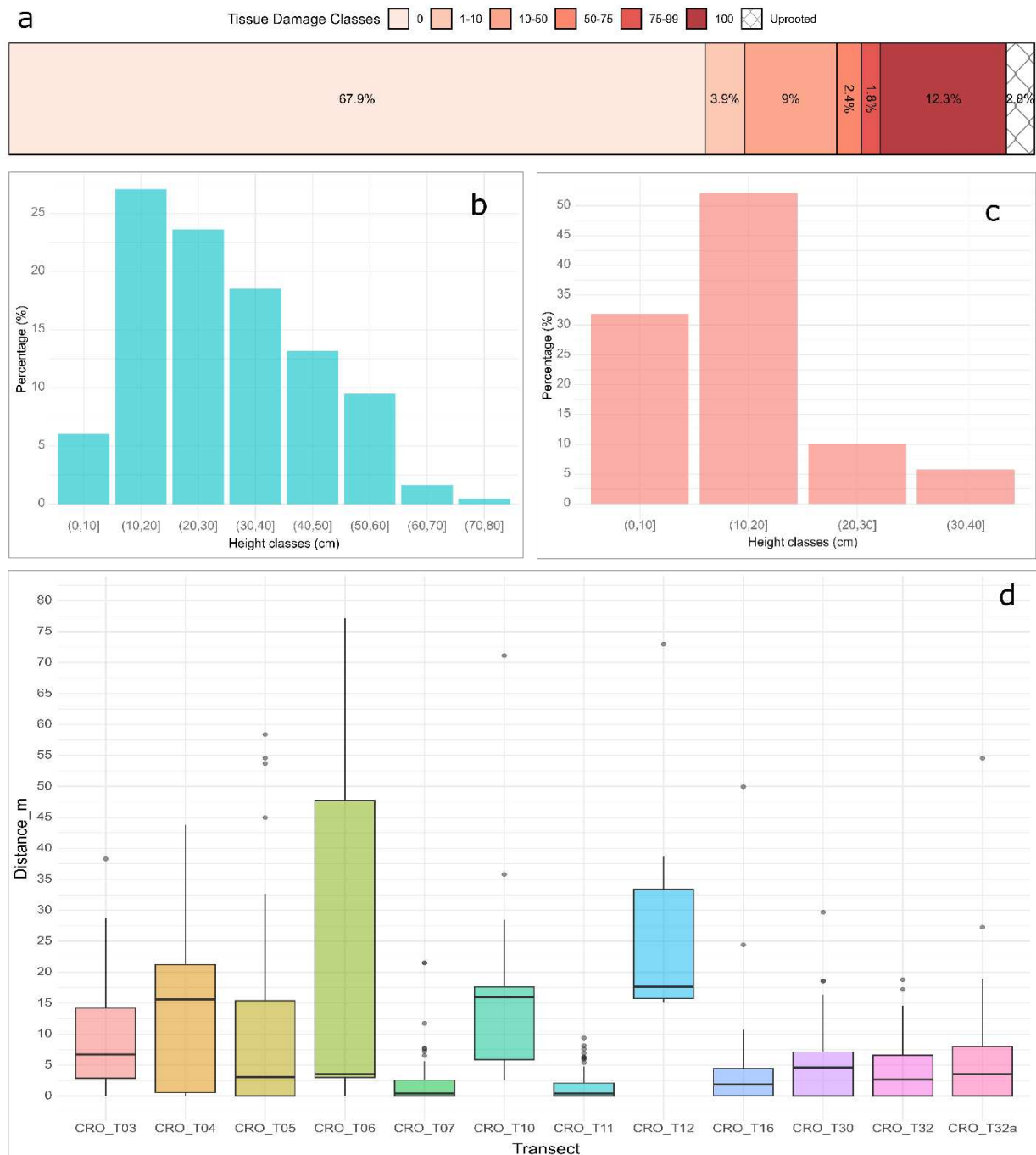


Figure 4: a) class of damage of all encountered *Isidella elongata* colonies; b) Size classes of alive colonies (tissue damage < 100); c) Size classes of dead colonies (Tissue damage = 100); d) Boxplot of Nearest Neighbour Distance analysis: boxes indicate the first and third quartiles; bold lines indicate the median value, lines represent the Whisker (calculated as $1.5 \times IQR$); and dots indicate outliers.

The height distribution of encountered organisms was dominated by small colonies in both live and dead colonies (Fig. 4b,c). Among live specimens, the 10–20 cm class was most abundant (27%), followed by the 20–30 cm (23.5%) and 30–40 cm (18.5%) classes (Fig. 4b). Similarly, the 10–20 cm class was the most abundant in dead colonies, accounting for 54% of all height measurements (Fig. 4c). Most transects exhibited a clustered distribution, with median distances of less than 10 m among colonies and a narrow dispersion of values (Fig. 4d).

Conversely, wide dispersion among colonies was observed only in transects with few observations (e.g., CRO_T06, CRO_T12, CRO_T10, and CRO_T04; Fig. 4d).

Composition of associated fauna

The presence of epibionts was strongly associated with the degree of host tissue damage (Fig. 5a). The actinarian *Amphianthus dohrnii* (Koch, 1878) was the most frequent epibiont, displaying a marked affinity for colonies in the 100% damage class, where it colonized the completely exposed skeletal axis (13 col.; Figs. 3c, 5a). Barnacles were found only on colonies with damaged coenenchyma, but only in two cases and with medium-low tissue damage (Fig. 5a). In contrast, the commensal crustacean decapod *Anamathia rissoana* (Roux, 1828) was more frequently associated with healthy and minimally damaged colonies (Figs. 3g, 5b). Analysis of megafaunal species within the 2-meter proximity buffer of *I. elongata* identified 31 distinct taxa (Fig. 6b). The associated fauna was dominated by sessile benthic organisms (64.1%; Fig. 6b), primarily due to the high abundances of the sea pen *Kophobelemnion stelliferum* (Müller, 1776), followed by *Funiculina quadrangularis* (Pallas, 1766) and the demospongian *Thenea muricata* (Bowerbank, 1858). Nektonic organisms accounted for 21.2% of the total records, comprising 13 distinct fish taxa (Figs. 3d-f, 5b). This group was dominated by *Chlorophthalmus agassizi* Bonaparte 1840 (Figs. 3d, 5b), followed by equal abundances of *Chauliodus sloani* Bloch & Schneider 1801, *Helicolenus dactylopterus* (Delaroche, 1809) (Figs. 3f, 5b), and undetermined lanternfishes (Myctophidae) (Fig. 5b). Vagile benthic specimens constituted the lowest fraction of the assemblage (14.7%; Fig. 5b), mainly represented by the two echinoderms *Hymenodiscus coronata* (Sars, 1871) and *Penilpidia ludwigi* (von Marenzeller, 1893), followed by shrimps belonging to the genus *Plesionika*.

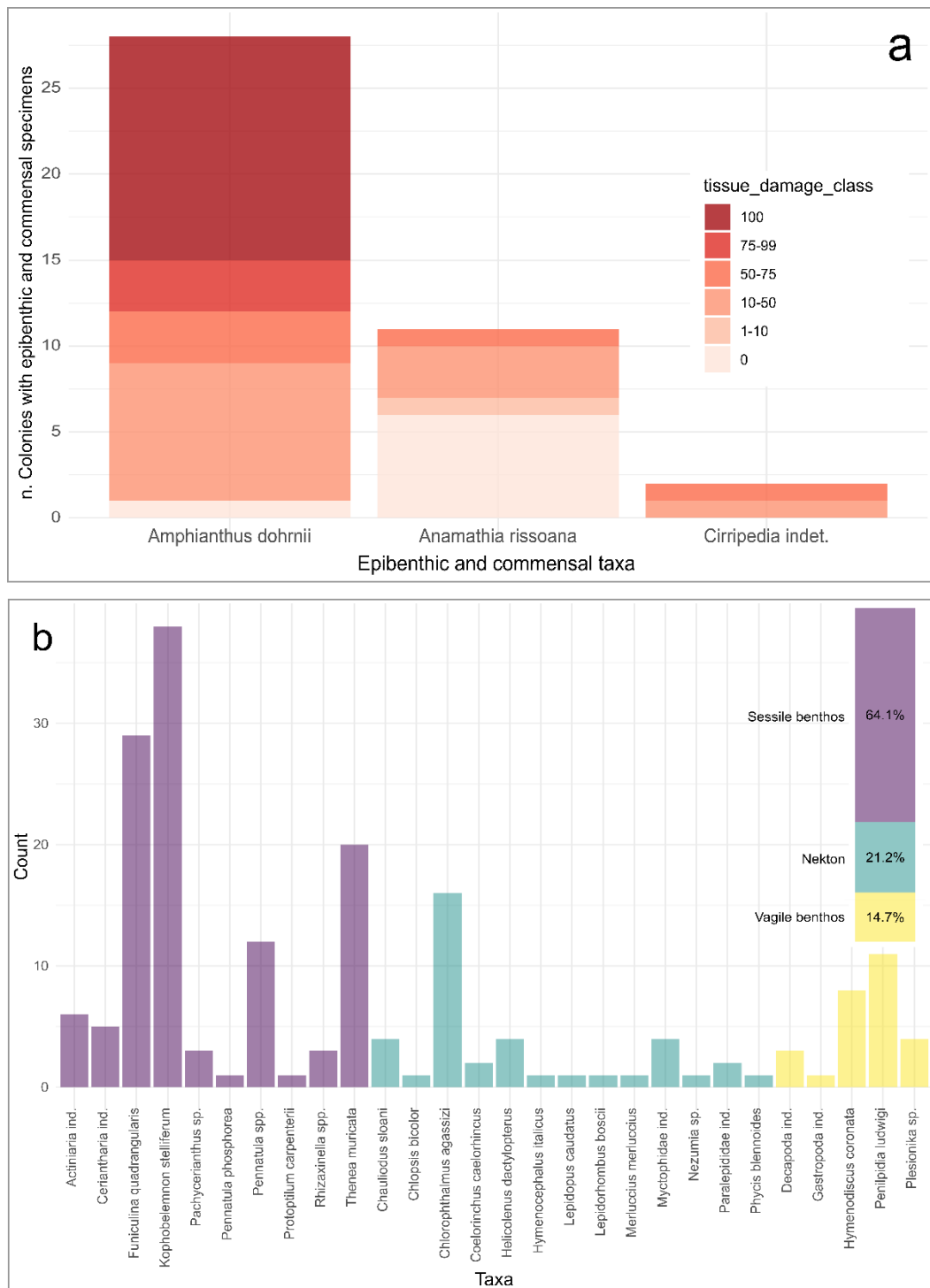


Figure 5: a) number of colonies with corresponding epibenthic specie and commensal ones for each class of damage; b) abundance of taxa identified in the 2m buffer surrounding *I. elongata* colonies. Individual bars show the absolute count for each recorded taxon, categorized into sessile benthos (purple), nekton (teal), and vagile benthos (yellow). The inset stacked bar displays the percentage breakdown of these three main functional ecological groups.

Environmental and anthropogenic drivers of colony presence and health

The ordinal logistic regression model identified a significant relationship between anthropogenic stressors and increased tissue damage of *I. elongata* colonies. Cumulative trawling hours had a significant positive effect ($\beta = 0.038 \pm 0.012$ SE; p -value = 0.001), indicating a higher probability of observing more severe damage with increased trawling hours. The estimated threshold parameters were all statistically significant ($\theta_1 = 1.032 \pm 0.115$ SE, $p < 0.001$; $\theta_2 = 1.796 \pm 0.136$ SE, $p < 0.001$), defining the boundaries between the three cumulative probability regions corresponding to increasing tissue damage categories under baseline conditions (cumulative trawling hours = 0 h). The generalized additive model (GAM) fitted on *I. elongata* presence/absence data explained 34.2% of the null deviance (Tab. 2). Depth, BPI_15, bottom current speed, trawling mark density, and slope all exhibited statistically significant non-linear smooth effects (Tab. 2; Fig 6; p -value < 0.001). Additionally, the log-transformed distance from pockmarks was identified as a significant linear predictor, with increasing distance negatively effecting the probability of coral presence (Tab. 2; p -value < 0.001). Depth showed a slight positive effect from deep waters (1000 m) up to intermediate depths of approximately 500 m, followed by a sharp, significant decline in probability toward the shallowest investigated depths (Fig. 6). The topographic variable BPI_15 exhibited a unimodal, dome-shaped relationship with *I. elongata* probability of occurrence (Fig. 6). Probability of presence was negatively impacted by negative BPI values (localized depressions), peaked at slight elevations ($\sim +2$ m), followed by a mild decline in prominent topographic highs (Fig. 6). Bottom current speed showed a sinusoidal pattern, followed by a marked rise under high hydrodynamic conditions (Fig. 6). The partial effect of seafloor slope remained negligible (near zero) at gentle angles up to approximately 13° – 15° . Beyond this range, the probability of presence steadily declined at steep slopes ($>20^\circ$), though confidence intervals widened due to limited data points (Fig. 6).

Finally, the partial effect of trawling mark density remained stable at low to moderate disturbance levels, but exhibited a steep, threshold-like decline once intensity exceeded approximately 500 marks km^{-2} (Fig. 6).

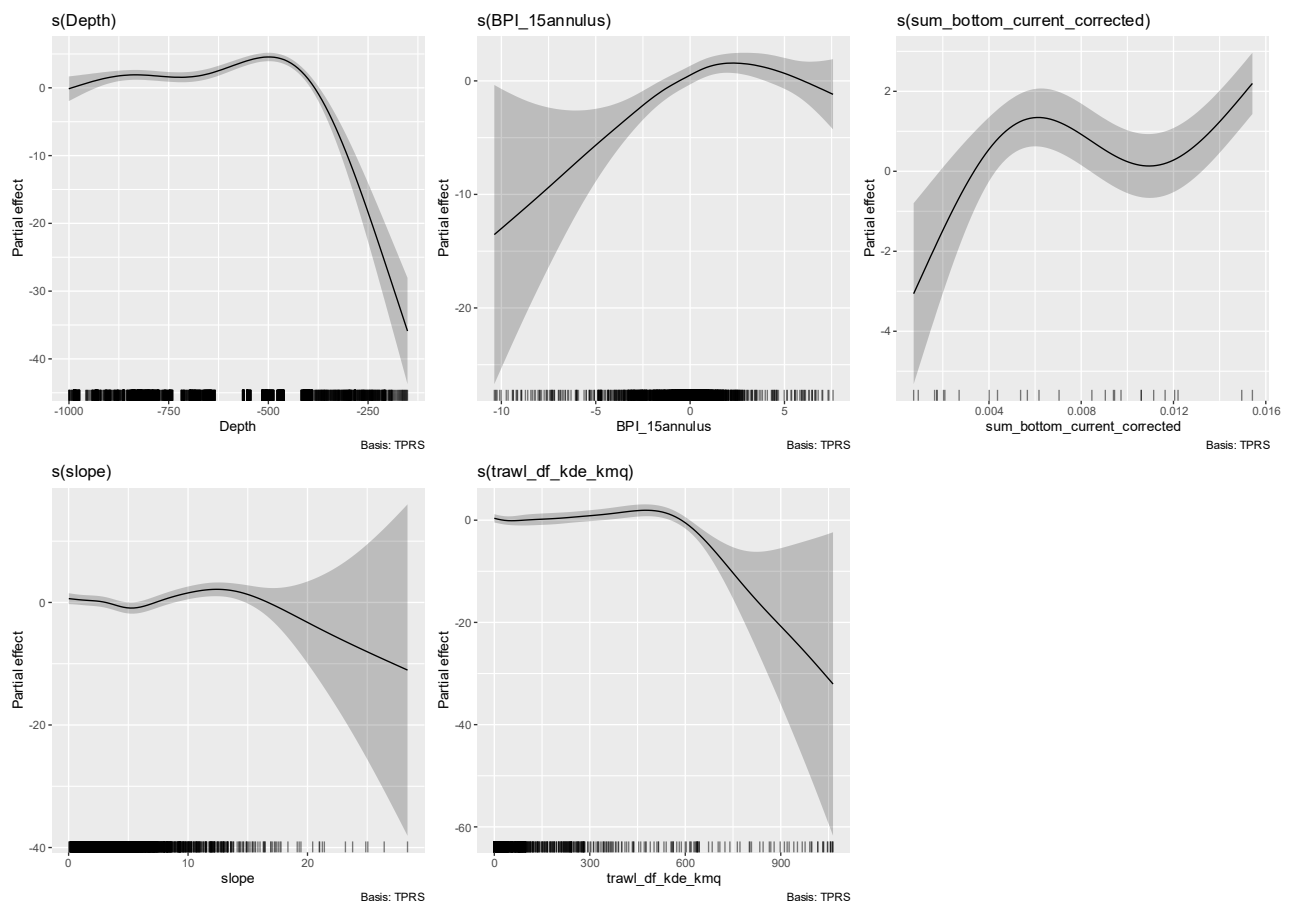


Figure 6. Partial GAM plots for the best binomial and positive models for *l. elongata*. Each plot represents the response variable shape, independent of the other variables, in relation to the probability of the species occurrence in the multivariate model. The ranges of environmental variables are represented on the x-axis and the partial effect is represented on the y-axis (logit scale). Confidence intervals (95%) around the response curve are shaded in grey. The logarithm of the distance from pockmarks is not represented due the linear relationship with the presence of the species.

Table 2 GAM summary for presence-absence model, including the final formula and separated by the parametric coefficients estimation (including only the log distance from pockmarks) and the approximate Significance of the remaining Smooth Terms. The adjusted R and explained deviance are also presented.

GAM function:				
$\text{logit}(P_i) = \beta_0 + \beta_1 \ln(\text{Pockmarks_dist}_i + 1) + s_1(\text{Depth}_i) + s_2(\text{BPI_15annulus}_i) + s_3(\text{Bottom_current}_i) + s_4(\text{Slope}_i) + s_5(\text{Trawl_density}_i)$				
Parametric Coefficients				
Variable	Estimate	Std. Error	z value	p-value
Intercept	-51.175	0.5161	-9.915	< 0.001
Distance from pockmarks	-0.4049	0.0528	-7.665	< 0.001
Approximate Significance of Smooth Terms				
Smooth Term	edf	Ref. df	χ^2 (Chi-sq)	p-value
Depth	3.954	3.998	170.58	< 0.001
Near-bottom current	2.941	2.996	186.42	< 0.001

Slope	5.779	6.738	71.11	< 0.001
Bathymetric Position Index	3.802	4.738	67.72	< 0.001
Trawling effort (KDE)	5.964	6.651	47.89	< 0.001
R-sq.(adj) = 0.193 - Deviance explained = 34.2%				

Discussion

Although the presence of *Isidella elongata* in the western Ionian Sea was previously documented through scientific trawling surveys⁵⁵, this study provides the first video-ROV data for the species in this sector of the Mediterranean Sea. The analysis also enhances our understanding of the habitat requirements and fishing impacts on *I. elongata* within an area subject to a complex regime of bottom trawling disturbance.

The highest mean transect densities observed in this area are consistent with values reported for the central Tyrrhenian Sea³⁰, though relatively higher density values have been documented by ROV surveys in other sectors of the Mediterranean Sea, including the southern Tyrrhenian Sea²² and the Western Mediterranean Sea^{3,8,10,11}. Interestingly, the maximum point density recorded in the present study (5 ind. m⁻²) substantially exceeded values reported for *I. elongata* assemblages in the Tyrrhenian Sea (Pierdomenico et al.²²: 1.6 col. m⁻²; Ingrassia et al.³⁰: 0.32 col. m⁻²) and the Western Mediterranean Sea (Bo et al.⁸: 2.7 col. m⁻²). Nevertheless, comparisons of, mean colony density across different studies require careful interpretation. Even when density is standardized (col. m⁻²), estimated mean values per transect are strongly influenced by spatial extent and sampling design⁵⁶. For benthic megafauna species with highly patchy or aggregated distribution, such as *I. elongata*^{8,25}, large surveys include both colony patches and unoccupied areas, thereby reducing average density, while smaller surveys may overrepresent local hotspots, substantially boosting density values. This pattern is consistent with current estimates of inter-colony distance and colony presence coverage.

In terms of population structure, although small size classes dominated among highly damaged colonies, medium size classes (20–30 cm and 30–40 cm) accounted for a substantial proportion (42 %) of total individuals, and the proportion of large colonies (> 40cm) was higher compared to other studies^{3,10,22}. These findings are consistent with previous observations indicating elevated mortality rates for most measuring less than 20 cm²². Whereas direct gear contact often causes total colonial extirpation, trawl gear can also sever individual skeletal branches, leaving truncated smaller colonies in place. Additionally, smaller individuals are more likely to avoid interception by trawling nets during temporary lift-offs from the seabed⁵⁷. Beyond direct mechanical damage, another critical factor influencing size-dependent mortality is the potential heightened physiological vulnerability of juvenile colonies to sediment resuspension⁵⁸. In fact, if direct exportation is a primary impact of bottom trawling on *I. elongata*, the consequences of polyp clogging and mechanical abrasion from resuspended sediment plumes are also recognized as a significant concern^{23,59}. Under these conditions, a reduced number of polyps increases the probability of simultaneous interception of resuspended particles, and without unaffected sediment-free polyps to maintain baseline respiration and metabolic demands, juveniles may experience complete colonial mortality even under minor turbid plumes⁵⁸. However, the mechanisms of resource allocation and the contribution of individual polyps to colony survival remain poorly understood^{60,61}, though these aspects are crucial for assessing survival thresholds and potential recovery rates following indirect damage. In this study, the percentages of dead polyps varied substantially across colonies, and although estimating recovery probability is not trivial, colony size may play a

fundamental role in this process. Evidence supporting trawling-induced sediment resuspension as a possible cause of these damages was provided by the estimated positive relationship between cumulative trawling hours and increased colonial tissue damage. Repeated sediment resuspension events not only elevate the probability of impacting pristine colonies but also impose additional stress on previously damaged organisms, severely limiting their capacity for tissue regeneration and long-term colonial survival^{18,58}. While colonial tissue damage can be directly quantified, assessing the eradication of colonies by bottom trawlers remains far more challenging. We found that trawl mark density was negatively associated with the probability of *I. elongata* occurrence. Specifically, a threshold density of 500 trawl marks km⁻² corresponded with a sharp decline in the species presence probability. Given the extreme vulnerability of *I. elongata* to mechanical disturbance (e.g.^{4,7,62}), this value should not be interpreted as a biological tolerance threshold. Instead, it serves as a fine-scale indicator of cumulative trawling events, where repeated fishing passes within the same area progressively increases the probability of colony interception, removal, or burial. Trawling events can also lower species presence probability by impairing larval settlement processes⁵⁹. Numerous studies have shown that anthozoan larvae exhibit distinct substrate preferences governed by highly specific conditions, such as the presence of pioneer species, micro-scale environmental variables and physical substrate properties^{63–65}. Trawling-induced sediment resuspension not only risks smothering settling planulae and primary polyps but can also substantially alter sediment grain-size distribution, deplete sedimentary organic matter, and alter biological composition of bathyal muds^{24,66}. Considering the documented bottom trawling activities and associated physical and biological impacts, it is most likely that these bathyal muds historically sustained higher densities of *I. elongata*. Historical declines are more probable in heavily trawled zones, which are generally characterized by low live colony abundance, a high proportion of dead colonies, and the presence of uprooted specimens.

The generalized additive model (GAM) provided critical insights into the complex interplay of environmental factors influencing the presence of *I. elongata*. Depth is a widely recognized predictor of marine species distribution⁶⁷ and often serves as a fundamental covariate for assessing benthic preferences^{9,16,25,68}. Our model identified an optimum around 500 m depth, consistent with findings from various Mediterranean regions (e.g.^{9,22,62}). In addition to depth, near bottom current emerged as an important driver influencing species presence, with a slightly positive partial effect, underscoring the fundamental role of hydrodynamic regimes in shaping the distribution and survival of bathyal cold-water octocorals^{69,70}. Marine currents facilitate the transport of particulate organic matter and zooplankton, ensuring a continuous food supply that sustains the metabolic and reproductive demands of sessile suspension feeders^{71,72}. In addition to bathymetric and oceanographic variables, significant geomorphological descriptors, including bathymetric position index, slope, and proximity to pockmarks, indicated that the occurrence of *I. elongata* is also associated with fine-scale habitat heterogeneity within otherwise uniform bathyal mud habitats. Presence probability increased with BPI values up to an optimum at modest relative elevations (~+2 m), followed by a slight decrease over more pronounced topographic relief. This pattern likely reflects contrasting local conditions: elevated areas experience enhanced currents, while depressions

are characterized by reduced hydrodynamic activity and greater sediment accumulation^{71,72}. By contrast, higher-relief features and high depressions may be associated with reduced sediment stability, potentially limiting the anchoring capacity of *I. elongata* colonies. The GAM model confirmed that *I. elongata* strongly favors low-gradient, muddy bottoms (e.g.^{1,3,8}), with occurrence probability declining markedly beyond a 15° slope. Steeper seabed gradients could increase sediment instability, negatively influencing larval settlement and compromising the mechanical anchorage of colonies. Interestingly, the model also revealed a significant negative linear relationship with log-distance from pockmarks, indicating higher presence probability near these geomorphological features. Pockmarks are crater-like depressions formed by sub-seafloor fluid expulsion (e.g., hydrogen sulfide and hydrocarbons like methane), which create localized topographic complexity in the landscape of soft sediments (Hovland & Judd, 1988). These fluxes can alter local biodiversity, impeding the settlement and survival of unspecialized sessile species while favoring specialized and chemosymbiotic organisms⁷³. This may explain the observed distribution of *I. elongata* colonies along pockmark boundaries, with no occurrences inside large pockmarks. However, increased local biodiversity of methane-resistant bacteria and meiofaunal species⁷³ may alter benthic-pelagic coupling and enhance organic matter availability in the surrounding areas. This process, combined with potentially increased local hydrodynamic conditions, could account for the higher presence probability of *I. elongata* along pockmarks boundaries.

I. elongata plays a fundamental ecosystem engineering role by providing a complex three-dimensional habitat that supports diverse benthic communities^{3,5,6,12}.

The majority of epibiotic species observed consisted of the sea anemone *Amphianthus dohrnii*. There is currently no empirical evidence supporting active exploitation or predation of the host's polyps by *A. dohrnii*. Rather, this species is widely recognized as an opportunistic epibiont, primarily colonizing inter-polyp spaces or denuded skeletal sections where *I. elongata* tissue has already been compromised or removed, indicating a process of secondary colonization⁶. Our visual analysis largely documented these opportunistic colonization events, with dead colonies representing a major biogenic substratum for this epibiotic species. Indeed, even if *A. dohrnii* can colonize alternative biogenic or inorganic substrata, several studies across the Mediterranean Sea documented a strong preference for *I. elongata*^{6,74}. In the present study the crustacean *Anamathia rissoana* was mainly observed on large and healthy colonies of *I. elongata*. The critical role of *I. elongata* in ensuring the survival of this associated commensal species aligns with the baseline trends documented in different studies^{3,4,6}. In fact, even though this crustacean has been found in association with other habitat-forming corals, such as black corals⁸, its secondary loss following the decline of *I. elongata* in heavily trawled areas has been clearly documented⁴. ROV surveys also indicated a relatively low abundance of nektonic species and vagile macrofauna directly associated with *I. elongata* colonies, whereas copresence with other sessile species was more frequent. Evidence of active sheltering or direct interspecific interactions was generally sparse, except for demersal fish such as *Helicolenus dactylopterus* and *Chlorophthalmus agassizii*. This pattern may be related to the low integrity of these aggregations^{3,62}, though assessing nektonic species associations with *I. elongata* using ROV observations alone may introduce a systematic underestimation bias due

to fish avoidance behavior⁷⁵. For example, one observation documented a *H. dactylopterus* specimen seeking immediate refuge at the base of a colony, showing a distinct sheltering response to the vehicle's approach, demonstrating how *I. elongata* serves as essential physical refuge while simultaneously highlighting a ROV avoidance bias. To address these observational artifacts, non-destructive monitoring techniques, such as benthic camera landers, could offer a promising approach to capture unperturbed behavioral dynamics of the macrofauna associated with *I. elongata* aggregations⁷⁶. Regarding the limited copresence of typically associated commercial crustaceans^{1,4}, it is important to note that very few specimens were observed in the entire investigated area (*Nephrops norvegicus*: $n = 1$; *Aristeus antennatus*: $n = 3$; *Aristaeomorpha foliacea*: $n = 1$). Finally, although the spatial coexistence of sessile benthic taxa primarily depends on shared environmental preferences, the copresence of diverse suspension feeders can actively modify near-bottom particle flux and increase organic matter availability for neighboring organisms⁷⁷. This localized particle enhancement may be particularly relevant for the small suspension feeders observed, such as the sponge *Thenea muricata* and the brisingid *Hymenodiscus coronata*, as well as detritivores species, including the holothurian *Penilpidia ludwigi* and various bathyal gastropods. However, to fully understand the role of *I. elongata* as an ecosystem engineer, future research should investigate the traits that contribute to the development of the emergent properties⁷⁷ in these deep-sea structural assemblages. Detailed quantitative data on how morphological and demographic parameters govern ecosystem functionality of octocorals in general are still lacking⁷⁸.

The results of this study enhanced our understanding of the geomorphological and environmental conditions essential for *I. elongata* colonization and survival, contribute to understand its ecological importance and underscores the severe impacts of bottom trawling on a species that is both ecologically pivotal and highly vulnerable. Safeguarding the remaining *Isidella elongata* fields has become a clear conservation imperative, and the urgency has already been widely emphasized^{4,12,16,22}. Fisheries Restricted Areas (FRAs) currently provide the only active protection for *I. elongata* in the Mediterranean Sea, as existing Marine Protected Areas (MPAs) either encompass shallow coastal habitats or lack regulations specifically targeting deep-sea ecosystems^{5,79}. Although the basin-wide ban on bottom-trawling below 1000 m represents the largest FRA, *I. elongata* is primarily distributed at shallower depths^{10,11,16}. Consequently, its protection relies on just 4 of the 11 FRAs, where *I. elongata* facies are present⁷⁹ (FAO, 2025). Resolution GFCM/46/2023/1 recently proposed to lower the basin-wide bottom-trawling ban from 1,000 m to 800 m⁷⁹. If implemented, this management strategy would improve the overall conservation coverage, though introducing new localized and science-informed FRAs is vital to safeguard the remaining spatial extent of *I. elongata*.

Recent basin-scale prioritization frameworks that incorporate depth, vertical connectivity, and climatic stability, the so-called 4D conservation networks, identified deep-sea zones as disproportionately important for maintaining future biodiversity and climatic refugia⁸⁰. Integrating these approaches into regional management would allow FRAs to be placed not only where Vulnerable Marine Ecosystems (VMEs) currently occur, but also where climatic stability and projected species redistribution indicate long-term persistence⁸⁰.

Within modern marine spatial planning frameworks, complementary solutions could involve Floating Offshore Wind Farms (FOWFs). When combined with proactive impact-reduction strategies such as high-resolution benthic mapping, eco-compatible anchoring and low-noise deployment protocols, the physical disturbance associated with FOWFs remains spatially constrained and transient^{81,82}. By strictly minimizing installation and operational impacts, these floating infrastructures can be formally qualified as Other Effective Area-based Conservation Measures (OECMs), offering a dual-purpose strategy that acts as passive benthic sanctuaries excluding destructive bottom trawling while advancing international renewable energy mandates^{81,82} (Lloret et al., 2022; Danovaro et al., 2024). FOWFs could therefore fulfill a critical secondary conservation function in heavily impacted areas where criteria for establishing of FRA are less evident⁷⁹ (FAO, 2025), creating passive benthic sanctuaries that enable the long-term recovery of degraded VMEs. While the short-term socioeconomic friction of excluding trawling activities from productive grounds is understandable, spatial protection remains the keystone strategy to secure the survival of VMEs and safeguard the long-term ecological integrity of deep-sea ecosystems.

Data Availability

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

References

1. Pérès, J. M. & Picard, J. Nouveau manuel de bionomie benthique de la mer Méditerranée. *Recl. Trav. Stn. Mar. Endoume* **31**, 1–137 (1964).
2. Grasshoff, M. Die Meerenge von Gibraltar als Faunen-Barriere: Die Gorgonaria, Pennatularia und Antipatharia der Belgim-Expedition (Cnidaria: Anthozoa). *Senckenberg. Maritima* **20**, 201–223. (1989).
3. Mastrototaro, F. *et al.* *Isidella elongata* (Cnidaria: Alcyonacea) facies in the western Mediterranean Sea: visual surveys and descriptions of its ecological role. *Eur. Zool. J.* **84**, 209–225 (2017).
4. Cartes, J. E., Lolocono, C., Mamouridis, V., López-Pérez, C. & Rodríguez, P. Geomorphological, trophic and human influences on the bamboo coral *Isidella elongata* assemblages in the deep Mediterranean: To what extent does *Isidella* form habitat for fish and invertebrates? *Deep Sea Res. Part Oceanogr. Res. Pap.* **76**, 52–65 (2013).
5. UNEP/MAP – SPA/RAC. *Interpretation Manual of the Reference List of Marine Habitat Types in the Mediterranean of the Barcelona Convention*. (UNEP/MAP-SPA/RAC, Tunis, 2021).
6. Cartes, J. E. *et al.* The macrofauna associated to the bamboo coral *Isidella elongata*: to what extent the impact on isideidae affects diversification of deep-sea fauna. *Coral Reefs* **41**, 1273–1284 (2022).
7. Maynou, F. & Cartes, J. E. Effects of trawling on fish and invertebrates from deep-sea coral facies of *Isidella elongata* in the western Mediterranean. *J. Mar. Biol. Assoc. U. K.* **92**, 1501–1507 (2012).
8. Bo, M. *et al.* Persistence of Pristine Deep-Sea Coral Gardens in the Mediterranean Sea (SW Sardinia). *PLOS ONE* **10**, e0119393 (2015).
9. Lauria, V. *et al.* Species distribution models of two critically endangered deep-sea octocorals reveal fishing impacts on vulnerable marine ecosystems in central Mediterranean Sea. *Sci. Rep.* **7**, 8049 (2017).
10. Angiolillo, M. *et al.* Healthy assemblages of *Isidella elongata* unintentionally protected from trawling offshore of Asinara Island (northwestern Sardinia, NW Mediterranean Sea). *Sci. Rep.* **14**, 12813 (2024).

11. Farriols, M. T. *et al.* New findings of *Isidella elongata* (Esper, 1788) in the Levantine-Balearic demarcation (western Mediterranean Sea). *Mediterr. Mar. Sci.* view (2025) doi:10.12681/mms.40030.
12. Palummo, V. *et al.* Ecological role of benthic Vulnerable Marine Ecosystems (VMEs) indicator taxa on soft bottoms. *Sci. Rep.* **15**, 26654 (2025).
13. FAO. *General Fisheries Commission for the Mediterranean – Report of the Twenty-Fourth Session of the Scientific Advisory Committee on Fisheries (Rome, 20–23 June 2023)*. (2023) doi:10.4060/cc8652en.
14. Maynou, F., Sardà, F., Tudela, S. & Demestre, M. Management strategies for red shrimp (*Aristeus antennatus*) fisheries in the Catalan sea (NW Mediterranean) based on bioeconomic simulation analysis. *Aquat. Living Resour.* **19**, 161–171 (2006).
15. Sardà, F. *et al.* An introduction to Mediterranean deep-sea biology. *Sci. Mar.* **68**, 7–38 (2004).
16. Georges, V. *et al.* Mapping the habitat refugia of *Isidella elongata* under climate change and trawling impacts to preserve Vulnerable Marine Ecosystems in the Mediterranean. *Sci. Rep.* **14**, 6246 (2024).
17. Carbonara, P. *et al.* Age and growth of bamboo coral *Isidella elongata* (Esper, 1788): a Mediterranean Vulnerable Marine Ecosystem indicator taxa. *Coral Reefs* **44**, 1403–1418 (2025).
18. Clark, M. R. *et al.* The impacts of deep-sea fisheries on benthic communities: a review. *ICES J. Mar. Sci.* **73**, i51–i69 (2016).
19. Rogers, A. D. The Biology of *Lophelia pertusa* (Linnaeus 1758) and Other Deep-Water Reef-Forming Corals and Impacts from Human Activities. *Int. Rev. Hydrobiol.* **84**, 315–406 (1999).
20. Topçu, N. E. *et al.* Impact of excessive sedimentation caused by anthropogenic activities on benthic suspension feeders in the Sea of Marmara. *J. Mar. Biol. Assoc. U. K.* **99**, 1075–1086 (2019).
21. Bavestrello, G., Cerrano, C., Zanzi, D. & Cattaneo-Vietti, R. Damage by fishing activities to the Gorgonian coral *Paramuricea clavata* in the Ligurian Sea. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **7**, 253–262 (1997).
22. Pierdomenico, M. *et al.* Effects of trawling activity on the bamboo-coral *Isidella elongata* and the sea pen *Funiculina quadrangularis* along the Gioia Canyon (Western Mediterranean, southern Tyrrhenian Sea). *Prog. Oceanogr.* **169**, 214–226 (2018).
23. Fosså, J. H., Mortensen, P. B. & Furevik, D. M. The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. *Hydrobiologia* **471**, 1–12 (2002).

24. Pusceddu, A. *et al.* Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. *Proc. Natl. Acad. Sci.* **111**, 8861–8866 (2014).
25. González-Irusta, J. M. *et al.* Mapping habitat loss in the deep-sea using current and past presences of *Isidella elongata* (Cnidaria: Alcyonacea). *ICES J. Mar. Sci.* **79**, 1888–1901 (2022).
26. Fabri, M.-C. *et al.* Megafauna of vulnerable marine ecosystems in French mediterranean submarine canyons: Spatial distribution and anthropogenic impacts. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **104**, 184–207 (2014).
27. Carbonara, P. *et al.* Spatio-temporal distribution of *Isidella elongata*, a vulnerable marine ecosystem indicator species, in the southern Adriatic Sea. *Hydrobiologia* **849**, 4837–4855 (2022).
28. Bo, M. *et al.* *Overview of the Conservation Status of Mediterranean Anthozoa*. (IUCN International Union for Conservation of Nature, 2017). doi:10.2305/IUCN.CH.2017.RA.2.en.
29. Georges, V. *et al.* Mapping the habitat refugia of *Isidella elongata* under climate change and trawling impacts to preserve Vulnerable Marine Ecosystems in the Mediterranean. *Sci. Rep.* **14**, 6246 (2024).
30. Ingrassia, M., Martorelli, E., Bosman, A. & Chiocci, F. L. *Isidella elongata* (Cnidaria: Alcyonacea): First report in the Ventotene Basin (Pontine Islands, western Mediterranean Sea). *Reg. Stud. Mar. Sci.* **25**, 100494 (2019).
31. Fabri, M. C. *et al.* Megafauna of vulnerable marine ecosystems in French mediterranean submarine canyons: Spatial distribution and anthropogenic impacts. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **104**, 184–207 (2014).
32. Perez, T. *et al.* Massive mortality of marine invertebrates: an unprecedented event in northwestern Mediterranean. *Comptes Rendus Académie Sci. - Ser. III - Sci. Vie* **323**, 853–865 (2000).
33. Schneider, C. A., Rasband, W. S. & Eliceiri, K. W. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* **9**, 671–675 (2012).
34. ArcGis Pro (version 3.6). Esri in., Redlands, CA, USA (2026).
35. Bo, M. *et al.* Characteristics of a black coral meadow in the twilight zone of the central Mediterranean Sea. *Mar. Ecol. Prog. Ser.* **397**, 53–61 (2009).
36. Deidun, A. *et al.* First characterisation of a *Leiopathes glaberrima* (Cnidaria: Anthozoa: Antipatharia) forest in Maltese exploited fishing grounds. *Ital. J. Zool.* **82**, 271–280 (2015).
37. Hijmans, R. J., Brown, A. & Barbosa, M. *Terra: Spatial Data Analysis*. (2026). doi:10.32614/CRAN.package.terra.

38. R Core Team. *R: A Language and Environment for Statistical Computing*. (R Foundation for Statistical Computing, Vienna, Austria, 2023).
39. Posit Team. *RStudio: Integrated Development Environment for R*. (Posit Software, PBC, Boston, MA, 2023).
40. Horn, B. K. P. Hill shading and the reflectance map. *Proc. IEEE* **69**, 14–47 (1981).
41. Lundblad, E. R. et al. A benthic terrain classification scheme for American Samoa. *Mar. Geod.* **29**, 89–111 (2006).
42. Ilich, A. R., Misiuk, B., Lecours, V. & Murawski, S. A. MultiscaleDTM: An open-source R package for multiscale geomorphometric analysis. *Trans. GIS* **27**, 1175–1198 (2023).
43. European Union-Copernicus Marine Service. Mediterranean Sea Physics Analysis and Forecast. Mercator Ocean international <https://doi.org/10.48670/MDS-00359> (2025).
44. Taviani, M. et al. The Gela Basin pockmark field in the strait of Sicily (Mediterranean Sea): chemosymbiotic faunal and carbonate signatures of postglacial to modern cold seepage. *Biogeosciences* **10**, 4653–4671 (2013).
45. Judd, A. G. & Hovland, M. *Seabed Pockmarks and Seepages: Impact on Geology, Biology and the Marine Environment*. (Graham & Trotman, London, 1988).
46. Nekola, J. C. & White, P. S. The distance decay of similarity in biogeography and ecology. *J. Biogeogr.* **26**, 867–878 (1999).
47. Global Fishing Watch. Global Fishing Watch Map and Data. (2026).
48. Baddeley, A., Rubak, E. & Turner, R. *Spatial Point Patterns: Methodology and Applications with R*. (Chapman and Hall/CRC Press, London, 2015). doi:10.1201/b19708.
49. Bradshaw, C. et al. Bottom trawling resuspends sediment and releases bioavailable contaminants in a polluted fjord. *Environ. Pollut.* **170**, 232–241 (2012).
50. McCullagh, P. Regression models for ordinal data. *J. R. Stat. Soc. Ser. B Methodol.* **42**, 109–127 (1980).
51. Walker, S. H. & Duncan, D. B. Estimation of the probability of an event as a function of several independent variables. *Biometrika* **54**, 167–179 (1967).
52. Agresti, A. *Categorical Data Analysis*. (John Wiley & Sons, 2002). doi:10.1002/0471249688.
53. Wood, S. N. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc. Ser. B Stat. Methodol.* **73**, 3–36 (2011).
54. Burnham, K. P. & Anderson, D. R. Multimodel inference: understanding AIC and BIC in model selection. *Sociol. Methods Res.* **33**, 261–304 (2004).

55. Spedicato, M. T. *et al.* The MEDITS trawl survey specifications in an ecosystem approach to fishery management. *Sci. Mar.* **83**, 9–20 (2019).
56. Gambi, M. C. & Dappiano, M. *Manuale Di Metodologie Di Campionamento e Studio Del Benthos Marino Mediterraneo*. (Società Italiana di Biologia Marina, 2003).
57. Weinberg, K. L. & Kotwicki, S. *Reducing Variability in Bottom Contact and Net Width of a Survey Trawl by Restraining Door Movement and Applying a Constant Ratio of Warp Length to Depth*. (2015).
58. Henry, L.-A. & Hart, M. Regeneration from Injury and Resource Allocation in Sponges and Corals – a Review. *Int. Rev. Hydrobiol.* **90**, 125–158 (2005).
59. Erftemeijer, P. L., Riegl, B., Hoeksema, B. W. & Todd, P. A. Environmental impacts of dredging and other sediment disturbances on corals: a review. *Mar. Pollut. Bull.* **64**, 1737–1765 (2012).
60. Sanchez, J. A. & Lasker, H. R. Patterns of morphological integration in marine modular organisms: supra-module organization in branching octocoral colonies. *Proc. R. Soc. Lond. B Biol. Sci.* **270**, 2039–2044 (2003).
61. Ruiz-Diaz, C. P., Toledo-Hernandez, C., Mercado-Molina, A. E., Pérez, M. E. & Sabat, A. M. The role of coral colony health state in the recovery of lesions. *PeerJ* **4**, e1531 (2016).
62. Carbonara, P. *et al.* Exploring a deep-sea vulnerable marine ecosystem: *Isidella elongata* (Esper, 1788) species assemblages in the Western and Central Mediterranean. *Deep Sea Res. Part Oceanogr. Res. Pap.* **166**, 103406 (2020).
63. Linares, C. *et al.* Early life history of the Mediterranean gorgonian *Paramuricea clavata*: Implications for population dynamics. *Invertebr. Biol.* **127**, 1–11 (2008).
64. Zelli, E. *et al.* Settlement dynamics and recruitment responses of Mediterranean gorgonians larvae to different crustose coralline algae species. *J. Exp. Mar. Biol. Ecol.* **530–531**, 151427 (2020).
65. Manea, E. *et al.* Positive Interactions Under Ocean Warming and Acidification: Crustose Coralline Algae Holobionts Enhance Gorgonian Larval Settlement Under Climate Change. *Environ. Microbiol.* **27**, e70217 (2025).
66. Martín, J., Puig, P., Masqué, P., Palanques, A. & Sánchez-Gómez, A. Impact of Bottom Trawling on Deep-Sea Sediment Properties along the Flanks of a Submarine Canyon. *PLoS ONE* **9**, e104536 (2014).
67. Klaassen, M., Marques, T. A., Alves, F. & Fernandez, M. Trends in marine species distribution models: a review of methodological advances and future challenges. *Ecography* **2026**, e07702 (2026).
68. Palummo, V. *et al.* Effect of environmental and anthropogenic factors on the distribution and co-occurrence of cold-water corals. *Front. Mar. Sci.* **10**, 1272066 (2023).

69. Chimienti, G., Bo, M., Taviani, M. & Mastrototaro, F. Occurrence and Biogeography of Mediterranean Cold-Water Corals. in *Mediterranean Cold-Water Corals: Past, Present and Future* 213–243 (Springer International Publishing, Cham, 2019). doi:10.1007/978-3-319-91608-8_21.
70. Goldberg, W. M. Coral Food, Feeding, Nutrition, and Secretion: A Review. in *Marine Organisms as Model Systems in Biology and Medicine* (eds Kloc, M. & Kubiak, J. Z.) vol. 65 377–421 (Springer International Publishing, Cham, 2018).
71. Thiem, Ø., Ravagnan, E., Fosså, J. H. & Berntsen, J. Food supply mechanisms for cold-water corals along a continental shelf edge. *J. Mar. Syst.* **60**, 207–219 (2006).
72. Roberts, J. M., Wheeler, A. J., Freiwald, A. & Cairns, S. D. *Cold-Water Corals: The Biology and Geology of Deep-Sea Coral Habitats*. (Cambridge University Press, 2009). doi:10.1017/CBO9780511581588.
73. Zeppilli, D., Canals, M. & Danovaro, R. Pockmarks enhance deep-sea benthic biodiversity: a case study in the western Mediterranean Sea. *Divers. Distrib.* **18**, 832–846 (2012).
74. Giova, A., Canese, S., Toma, M., Romeo, T. & Greco, S. Ecological characterization of the sea anemone *Amphianthus dohrnii* in the Northern Sicily Channel. in *3rd Mediterranean Symposium on the Conservation of the Dark Habitats* 107 (2022).
75. Stoner, A. W., Ryer, C. H., Parker, S. J., Auster, P. J. & Wakefield, W. W. Evaluating the role of fish behaviour in surveys conducted with underwater vehicles. *Can. J. Fish. Aquat. Sci.* **65**, 1230–1243 (2008).
76. Bo, M. et al. Diel rhythms of fish frequentation in a temperate mesophotic antipatharian forest and sleeping behaviour of the red swallowtail perch *Anthias anthias* (Linnaeus, 1758). *Mar. Biol.* **171**, 166 (2024).
77. *Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots*. (Springer International Publishing, Cham, 2017). doi:10.1007/978-3-319-21012-4.
78. Lasker, H. R. et al. Caribbean octocoral communities: finding the forest for the trees? *Coral Reefs* **45**, 111–120 (2026).
79. FAO. *The State of Mediterranean and Black Sea Fisheries 2025*. (2025) doi:10.4060/cd7701en.
80. Doxa, A. et al. 4D marine conservation networks: Combining 3D prioritization of present and future biodiversity with climatic refugia. *Glob. Change Biol.* **28**, 4577–4588 (2022).
81. Lloret, J. et al. Unravelling the ecological impacts of large-scale offshore wind farms in the Mediterranean Sea. *Sci. Total Environ.* **824**, 153803 (2022).
82. Danovaro, R. et al. Making eco-sustainable floating offshore wind farms: Siting, mitigations, and compensations. *Renew. Sustain. Energy Rev.* **197**, 114386 (2024).

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F.P.: Data curation, Analysis, Validation, Writing – original draft. L.C.: Data curation, Analysis, Writing – review & editing. L.V.: Investigation, Writing – review & editing. D.D.B.: Data curation, Writing – review & editing. S.M.: Analysis, Validation, Writing – review & editing. B.Z.D.: Data curation, Writing – review & editing. F.S.: Investigation, Data curation, Writing – review & editing. L.D.V.: Analysis, Writing – review & editing. P.B.: Analysis, Writing – review & editing. E.S.: Data curation, Writing – review & editing; T.R.: Funding acquisition, Project administration, Writing – review & editing. S.G.: Funding acquisition, Project administration, Writing – review & editing. S.C.: Project administration, Writing – review & editing.

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Competing interests

The authors declare no competing interests.

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