



What do glass sponges do when no one is looking? *Vazella pourtalesii*: Responses to sediment deposition, passive locomotion, and contracting behavior

Jordi Grinyó^{a,*}, Jacopo Aguzzi^{b,c}, Luciano Ortenzi^d, Ellen Kenchington^e, Simona Violino^f, Ulrike Hanz^g, Andreu Santín^{b,h}, Tim W. Nattkemperⁱ, Furu Mienis^a

^a Department of Ocean Systems, Royal Netherlands Institute for Sea Research (NIOZ), Den Burg, the Netherlands

^b Department of Renewable Marine Resources, Institut de Ciències Del Mar (ICM-CSIC), Passeig Marítim de La Barceloneta, Barcelona, Spain

^c Department of Research Infrastructures for Marine Biological Resources, Anton Dohrn Zoological Station, Naples, Italy

^d Department of Agriculture and Forest Sciences (DAFNE), Via S. Camillo De Lellis, s.n.c., 01100 Viterbo & Via Angelo Maria Ricci 35a 02100, Rieti, Italy

^e Department of Fisheries and Oceans, Ocean Ecology Section, Bedford Institute of Oceanography, Dartmouth, NS, Canada

^f Consiglio per la ricerca in agricoltura e l'analisi dell'economia agraria (CREA) - Centro di ricerca Ingegneria e Trasformazioni agroalimentari, Via della Pascolare 16, 00015 Monterotondo (Rome), Italy

^g Benthic-Pelagische Prozesse (BPP), Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research (AWI), Bremerhaven, Germany

^h CIIMAR-Interdisciplinary Centre of Marine and Environmental Research, University of Porto, Porto, Portugal

ⁱ Biodata Mining Group, Faculty of Technology, Bielefeld University, 33615 Bielefeld, Germany

ARTICLE INFO

Keywords:

Hexactinellida
Deep sea
Sponge grounds
Northwest Atlantic
Behavior ecology

ABSTRACT

Behavioral response of deep-sea sponges can provide crucial insights into the mechanisms shaping energy fluxes and ecosystem functioning. Although some advances have been made, the behavior of deep-sea Hexactinellid still remain widely unknown. In the present study we address the glass sponge *Vazella pourtalesii* behavior. High-temporal resolution imaging and environmental data were acquired with an autonomous lander deployed in the Sambro Bank Sponge Conservation Area (Scotian Shelf) at a depth of 150 m, representing the upper limit of this deep-sea species' distribution and what is commonly regarded as the deep sea.

For 94 days, a *V. pourtalesii* individual was monitored, providing quantitative information on its response to sediment deposition triggered by a storm, as well as on its passive locomotion and contractive behavior. Sediment was cleared from its surface within 72 h, which is highly relevant for its filtering capacity, indicating that this sponge species can cope with high suspended sediment concentrations. This enables it to occur on sedimentary environments like the Scotian Shelf. As observed in other deep-sea hexactinellids, the monitored individual engaged in rhythmic contractions, which appear to be driven by physiological process/es rather than environmental factors. During the study period, strong bottom currents (>37 cm/s) toppled and displaced the monitored individual several times. Despite changes in position and orientation that can negatively impact the filtering capacity of sponges, no signs of deterioration were observed. *V. pourtalesii*'s vase-like body morphology and attachment to cobbles, as a gravitational center, may allow it to have a more homogeneous interaction with currents which may permit them to better cope with positional changes. Overall, this study highlights that deep-sea Porifera display a wide array of phenological changes in response to both biotic and abiotic factors.

1. Introduction

Benthic ecosystems, like cold-water coral reefs and sponge grounds in deep-sea environments often rely on food sources originating in the photic zone, and are influenced by hydrodynamic and meteorological processes that originate on the surface and develop at depth (Duineveld

et al., 2007; Hanz et al., 2021a, 2021b). The way organisms interact with their environment is a fundamental question in ecology, since environmental variations may have a large impact on species functioning from individual to community levels (Schlosser et al., 1990; De Araujo Lira et al., 2018; Gómez Gras et al., 2021; Sigwart et al., 2023).

Elucidating the behavioral response of deep-sea megabenthic species

* Corresponding author.

E-mail address: jordigrinyo85@gmail.com (J. Grinyó).

<https://doi.org/10.1016/j.dsr.2024.104388>

Received 13 September 2023; Received in revised form 21 August 2024; Accepted 24 August 2024

Available online 29 August 2024

0967-0637/© 2024 Published by Elsevier Ltd.

to changing environmental conditions may therefore provide crucial insights into the mechanisms shaping energy fluxes and ecosystem functioning (Milligan et al., 2020). However, knowledge on the behavior of deep-sea species is difficult to assess since high-resolution and prolonged time series of observations are scarce. Recently, time-lapse image-based studies have allowed for an assessment of the response of deep-sea megabenthic organisms to environmental conditions (Aguzzi et al., 2009, 2011), such as particulate organic carbon (POC) supply, hydrodynamic processes (e.g. internal tides, resuspension events) (e.g. Hanz et al. 2021; 2022) or the intrusion of different water masses (e.g., Dunlop et al., 2016; Kuhnz et al., 2020; Chatzievangelou et al., 2021). Yet, most of this research has been focused on motile megabenthic species (e.g., Aguzzi et al., 2018; Chatzievangelou et al., 2021). Despite the intrinsic ecological relevance of sessile structuring organisms, temporal studies addressing their behavior and response to environmental processes in deep-sea environments are still limited and have mostly focused on cold-water corals (Purser, 2015; Johanson et al., 2017; Girard et al., 2022; Osterloff et al., 2019; Zuazo et al., 2020), with only a few studies having been dedicated to sponges (Möller et al., 2018; Kahn et al., 2020; Harrison et al., 2021).

Sponges are ubiquitous to all benthic environments, and in the deep sea they can form sponge-dominated communities and sponge grounds (Cathalot et al., 2015; Maldonado et al., 2015). These biogenic habitats provide refuge, feeding, spawning and nursery grounds to a wide range of associated species (Ryer et al., 2004; Goren et al., 2021; Grinyó et al., 2023), enhancing local abundances and biodiversity (Beazley et al., 2015; Hawkes et al., 2019), and having a major role in biogeochemical cycles (e.g., Cathalot et al., 2015; Pham et al., 2019; Hanz et al., 2022).

Sponge-dominated assemblages in deep-sea environments worldwide are facing significant threats from various anthropogenic activities (Hogg et al., 2010). Among these, fishing practices, particularly bottom trawling, have been reported to have profound and extensive effects on sponge communities (Klitgaard and Tendal, 2004). This destructive method involves nets and doors equipment that indiscriminately scrape and disturb the seabed, breaking and removing sessile structuring fauna (Wassenberg et al., 2002). Such activities lead to long-term habitat simplification, biodiversity loss, and impaired ecosystem functioning diminishing sponge habitat ecosystem services (Francis et al., 2024). In addition to bottom trawling, emerging activities like deep-sea mining and the offshore green energy installation are anticipated to have extensive and detrimental impacts on these fragile ecosystems (Dunham et al., 2015; Wurz et al., 2021). Like bottom trawling, these activities not only cause immediate physical destruction but also result in indirect effects such as sediment resuspension (Dunham et al., 2015). Disturbed sediments can smother sponges another filter feeders, disrupt their feeding mechanisms, and alter the chemical environment, further endangering these vital marine organisms (Bell et al., 2015; Haffert et al., 2020; Wurz et al., 2021). The cumulative impact of these threats underscores the urgent need for protective measures to preserve the biodiversity and functionality of deep-sea sponge assemblages.

Vazella pourtalesii (Schmidt, 1870) is a glass sponge and the sole representative of the genus *Vazella*, which is exclusively found to inhabit deep-sea environments in the northwest Atlantic Ocean (Reiswig, 1996; Tabachnick, 2002). On the Scotian Shelf off Nova Scotia, Canada (NW Atlantic), *V. pourtalesii* can occur at high densities, developing large monospecific sponge grounds that provide habitat to numerous other species, locally enhancing associated species abundance (Hawkes et al., 2019). Like all glass sponges, *V. pourtalesii*'s skeletal structure is made of a delicate, glass-like silica mesh, which can accumulate in great quantities in surrounding sediments, playing a crucial role in the biogenic silica cycle (Maldonado et al., 2021, 2022) and being considered as community structuring agents (Barthel, 1992; Barthel and Tendal, 1993). Thus, its habitat-forming abilities and functionality make this sponge assemblage important contributors to the health and diversity of these remote and often poorly understood underwater environments.

Over the past years, *V. pourtalesii* has been the subject of numerous

studies addressing its ecology, associated microbiome, potential response to anthropogenic impacts and implications in geochemical cycles (Beazley et al., 2018, 2021; Bayer et al., 2020; Busch et al., 2020; Maldonado et al., 2021; Wang et al., 2021; Wurz et al., 2021; Grinyó et al., 2023). However, knowledge on *V. pourtalesii* behavior is still very limited.

The present study aims at broadening the current knowledge on *V. pourtalesii* behavior by means of a long and high-frequency time series of imaging and environmental data, acquired *in situ* with an Autonomous Lander for Biological Experiments (ALBEX). During 94 days a *V. pourtalesii* individual attached to a cobble was monitored to characterize a) its response to sediment deposition; b) passive locomotion and its c) contracting behavior.

2. Material and methods

2.1. Study area

The Sambro Bank Sponge Conservation Area is located on the Scotian Shelf (Fig. 1) covering an area of 62 km² between 150 and 175 m water depth. In 2013, Fisheries and Oceans Canada (DFO) closed this area to bottom trawling as it hosts one of the highest *V. pourtalesii* aggregations in the northwest Atlantic (Hawkes et al., 2019). Substrates are composed of a mosaic of soft sediments with a scatter of cobbles and boulders (Beazley et al., 2018; Hawkes et al., 2019; Grinyó et al., 2023). The waters of the Conservation Area are typical of the stratified system of the central Scotian Shelf, with surface and Cold Intermediate layers, derived from the Gulf of St. Lawrence outflow, overlying a warmer, saltier layer from the continental slope which floods the sponge grounds. In recent decades, the latter has usually been composed of Warm Slope Water but that is intermittently replaced by colder Labrador Sea Water (Hannah et al., 2001; Loder et al., 2001; Drinkwater et al., 2003). In general, the Scotian Shelf is dominated by a semidiurnal tidal cycle that enhances hydrodynamic processes like vertical mixing and enhanced current speed (Chen et al., 2011; Hanz et al., 2021a). Meteorological events can influence hydrodynamic processes resulting in "benthic storms", producing extreme sediment resuspension events and sponge displacements (Hanz et al., 2021a).

2.2. Image and oceanographic data collection

An ALBEX multiparametric video-lander (Duineveld et al., 2004) was deployed at 154 m water depth, at the center of the Sambro Bank closure zone (43.898 N, 63.052 E) (Fig. 1). The lander was deployed from the September 8, 2017 until June 19, 2018. During this period strong hydrodynamic processes turned the lander shifting the video camera's field of view. For this study we considered data acquired between the 5th of January to the April 9, 2018 during which a *V. pourtalesii* individual was fully in the field of view (Fig. 2). This individual was attached to a cobble, providing a low center of mass (Fig. 2A). The lander was equipped with a NIOZ made HD video camera equipped with two white LED lights. The camera acquired 20 s videos every 4 h resulting in 6 daily sampling events (00:00, 04:00, 08:00, 12:00, 16:00, 20:00). The lander was also equipped with a CTD sensor (Sea-Bird SBE37SM-RS232), an ARO-USB oxygen sensor (JFE Advantech™) attached (at 1 m above bottom) and an Aquadopp 2 MHz (Nortek™) Acoustic Doppler Current Profiler (ADCP) attached to the lander (at 2 m above the bottom). The lander environmental sensors registered salinity, temperature (T°C), oxygen (mg/L), and current speed (m s⁻¹), all sensors sampled at a frequency of 15 min. More detailed information regarding lander deployment and environmental sensor specifications can be found in Hanz et al. (2021a). Fluctuations in oxygen concentrations were statistically tested using a two factor unnested PERMANOVA (Permutational Multivariate Analysis of Variance) using the free software PAST 2.17c (Hammer-Muntz et al., 2001).

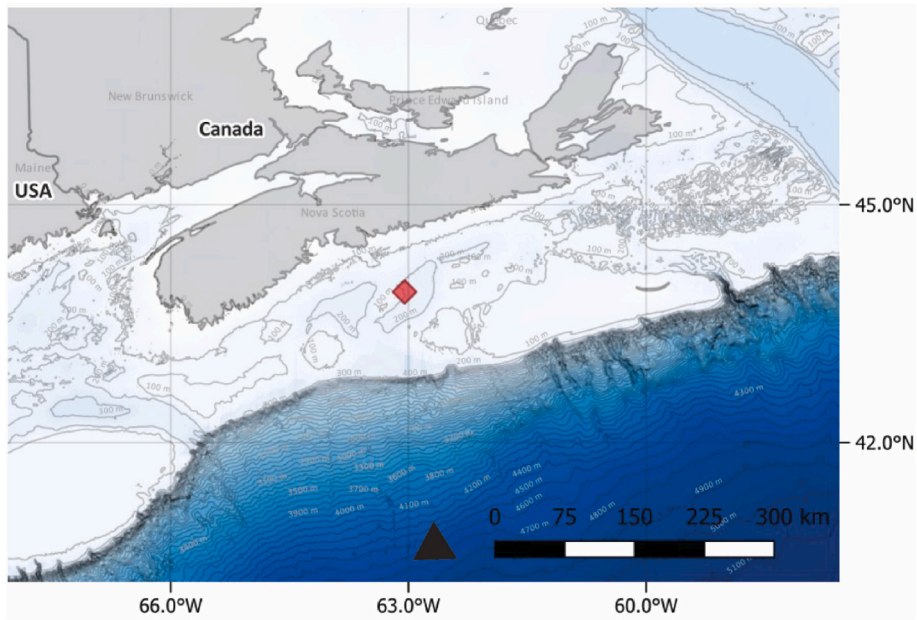


Fig. 1. Location of the Sambro Bank sponge conservation area on the Scotian Shelf (indicated by the red rhombus). Arrow head points North. Bathymetric data was obtained from the European Marine Observation and Data Network (EMODnet-Bathymetry via harmonized Digital Terrain Model (DTM). “EMODnet Digital Bathymetry (DTM)”, 2018, http://data.europa.eu/88u/dataset/EMODnet_bathymetry.

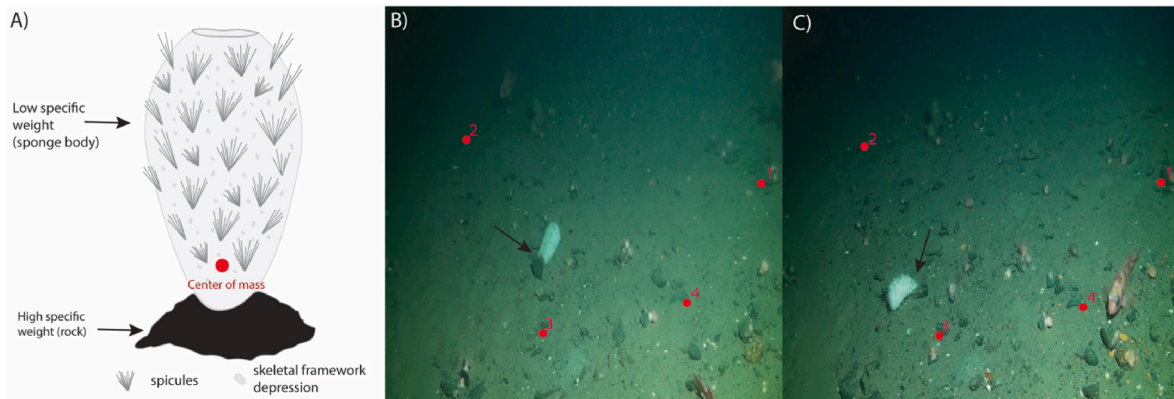


Fig. 2. A) Schematic view of the sponge’s weight distribution. Landmarks positioned in the still images during B) January 15, 2018 at 16:00 and C) February 9, 2018 at 16:00. Arrows in images B) and C) show the presence of the sponge.

2.3. Meteorological data

Wind velocity data was acquired by means of a 6-m NOMAD buoy of the Environment and Climate Change Canada (Data provided by the Department of Fisheries and Oceans Canada, ID44150- La Have Bank).

2.4. Image analyses

A total of 515 videos were recorded covering a time period of 94 days, for each video a still image was extracted using Google Colab. Posteriorly, these images were used to assess *V. pourtalesii* response to sediment deposition, passive locomotion, and contraction.

2.4.1. Sediment deposition response

Sediment deposition on a *V. pourtalesii* individual and adjacent cobbles was visually monitored during 72 h after a major resuspension event that began on the January 5, 2018.

2.4.2. Passive locomotion

V. pourtalesii passive locomotion was assessed recording its position

in time through an object detection algorithm named You Only Look Once (YOLO) in its version 8 (Jocher, 2023). The algorithm takes in input an image or a video frame and outputs the position and the dimension of a rectangular bounding box centered around the sponge. The algorithm was trained on 513 still images, while 2 images were discarded as the sponge was covered by fragments of a detached *V. pourtalesii* individual. Images were annotated with YOLO v8 (Jocher, 2023) format, adapted to the 640 × 640 px size.

The dataset was divided into training, validation, and test set with a ratio of 70 (350): 20 (50):10(113) respectively. To allow for a better generalization of the model, the images used for training and test the model were not superimposed. Once trained, the model was applied on superimposed images to track the sponge movement.

Indeed, to allow the spatial quantitative comparison among images, four landmarks (e.g. stone apex) whose position remained constant, were superimposed in each image to allow a spatial quantitative comparison among images (Fig. 2). Landmarks were positioned with the software TPSdig2 (Rohlf, 2005). A consensus configuration (i.e., average shape) was calculated (Cadrin, 2020) to align all images through the superimposition of their landmarks. The software TPSsuper (Rohlf,

2013) allowed us to unwarped the images to the consensus shape (target shape). The images, in this way, were aligned to landmark locations and superimposed.

Due to the high level of accuracy and elaboration velocity needed, the YOLO v8 model was chosen. The algorithm converged after 200 iterations with a batch size of 16, and a learning rate of 0.01.

To test model performance, Precision (P) and Recall (R), defined respectively as (Jocher, 2023) were also calculated:

$$P = TD / (TD + FD) \text{ and } R = TD / (TD + FU)$$

In the formula TD and FD respectively stand for “true detection” and “false detection” based on the intersection over union $IoU \geq 0.7$. IoU is the area of intersection between the ground truth bounding box and the detected one. FU (False Un-detection) and indicates the number of undetected objects.

In multiclass object detection, not only the detection of the bounding box, but also the classification of the detected object, is important. For this reason, the Average Precision for detection confidence equal to 0.5 (mAP@0.5) and detection confidence between 0.5 and 0.95 (mAP@0.5:0.95) were also calculated. The Average Precision was calculated as the weighted mean of precisions at each confidence threshold; the weight is the increase in recall from the prior threshold.

2.4.3. Contracting and expanding behavior

The software ImageJ2 (Schneider et al., 2012) was used to measure the proportion of pixels taken up by the monitored individual of *V. pourtalesii*. Images were calibrated using landmarks (see Fig. 2). Sponge surface variations were expressed as percentage value normalized by the largest surface value in each position. Images in which a fish obstructed the full view of the sponge (2.7% of all images) were discarded.

To explore potential occurrence of contraction rhythms, a wave form analysis was performed by averaging surface percentages for each sampling event (00:00, 04:00, 08:00, 12:00, 16:00, 20:00). Average values were then plotted along with the Standard Error (SE) and the Midline Estimated Statistic of Rhythm (MESOR), as represented as a horizontal threshold line (Francescangeli et al., 2022). The MESOR were calculated by averaging all sampling events average values. Values above the MESOR are considered peaks of maximum surface expansion.

Additionally, rhythmicity was also explored by means of the contraction kinetics approach (Elliott and Leys, 2007; Nickel, 2004; Kahn et al., 2020). This approach establishes that organisms move through four stages: contraction (reduction in size over time) (phase 1), to a fully contracted state (stage of maximum contraction) (phase 2), followed by expansion (increase in size over time) (phase 3) leading to the fully expanded state (stage of maximum expansion) (phase 4). The first three phases, cover the interval in which organism is in a state of reduction from full expansion, and define the contraction cycle. The full interval from one contraction cycle to the next, including the expanded state, was called the contraction period.

To explore the relationship with sponge contraction with respect to environmental variables (current velocity, temperature, oxygen concentration and salinity) a Principal Component Analysis (PCA) was performed. The PCA was represented graphically using biplots, where the percentage of explained variance (eigenvalues) for each axis, the plotted coordinates in the PC space (scores), and the vectors representing the importance of the variables (loading) were reported. The PCA was performed using the free software PAST 2.17c (Hammer-Muntz et al., 2001).

3. Results

3.1. Environmental variables

During the study period, water temperature at the seafloor ranged between 9.3 and 11.9 °C (10.7 ± 0.4 °C; Average±SD), salinity between

34.2 and 35.3 (35 ± 0.13 Average±SD) and oxygen concentration between 5.8 and 8.9 mg/L (6.2 ± 0.5 mg/L Average±SD). Currents at 3 mab were on average 0.13 m s^{-1} with peak velocities of 0.38 m s^{-1} ($12 \pm 6 \text{ m s}^{-1}$ Average±SD) in March (Fig. 3).

One major turbidity event was registered on early January 5th, 2018 (Fig. 4). This event, was triggered by storms, which caused large fluctuations in water temperature and salinity (Fig. 3) and were associated to peaks in wave height (15.5 m, 4:20 on the 5th of January; 10.6 m, 21:20 on the 3rd of May; $3.1 \pm 1.8 \text{ m}$ Average ± SD, during the study period) and wind (24.2 m s^{-1} 5th of January; 21.1 m s^{-1} 3rd of March ($9.3 \pm 4 \text{ m s}^{-1}$ Average ± SD, during the study period).

3.2. Sediment resuspension events

On January 5th, 2018, at 20:00 a major turbidity event began. During the first 44 h since the beginning of the event, visualization of the seafloor was lost due to high particle concentrations in the water column. Once suspended sediment cleared from the water column it was observed that the monitored *V. pourtalesii* individual was covered by a sediment veneer (Fig. 5). Sediment was progressively cleared from the monitored *V. pourtalesii* individual during the hours that followed the turbidity event:

0 h–12 h: *V. pourtalesii* was covered with a sediment veneer that prevented visualization of the skeletal framework depressions from all visible sites.

24 h–36 h: Sediment was cleared from the side making skeletal framework depressions visible, sediment still covered the top surface (maybe due to continuing settlement of sediment).

48 h–60 h: Sediment on the top surface of the *V. pourtalesii* was progressively cleared, yet small sediment patches remained. Skeletal framework depressions were evident on most areas of the top surface.

72 h: Sediment on the top surface of *V. pourtalesii* was cleared of sediment. Skeletal framework depressions were visible from all sites.

3.3. Passive locomotion

The accuracy of YOLOv8 in detecting, training, and validating *V. pourtalesii* was high (Table 1). Average detection frequency for this model was 28.7 ms per frame on a laptop mounting the NVIDIA GPU RTX 3070Ti with 8 Gb VRAM.

During the 94-day period the sponge changed its position 21 times (Fig. 6A), moving 3156 pixels from its original position (Fig. 6B).

3.4. Contracting and expanding behavior

Twelve days after monitoring started, *V. pourtalesii* began to rhythmically contract. A total of 20 contractions were observed during a 28-day period after which they suddenly stopped (Fig. 7A, Supplementary material 1). During contractions a reduction on its lateral surface was observed, causing the sponge to become thinner but not shorter. The contraction cycle lasted on average $18.4 \pm 8.4 \text{ h}$ (SD), during which contraction stages (contraction and fully contracted) lasted between 4 and 48 h ($14.3 \pm 5.2 \text{ h}$ (SD)), representing 68.7% of the time, while expansion stages (expansion and fully expanded) lasted 4–16 h ($7.8 \pm 4.7 \text{ h}$ (SD)), representing 31.3% of the time. Waveform analyses showed that the *V. pourtalesii* averaged surface presented two large peaks (i.e., values above the MESOR defining the phase of the count rhythm) at 00:00 and 20:00 and a small one on 08:00 (Fig. 6B).

The PCA biplot on 131×4 matrix of the first two axes showed how *V. pourtalesii* surface variation percentage (% increase) is positioned on the negative side of the first PC (44.3%) together with oxygen concentration. High values of surface variation % is directly related with oxygen concentration values and inversely related with temperature and salinity, positioned on the positive side of the same axis. Current velocity was positioned on the positive side of the second PC (20.8%) which does not seem to have a strong relationship with *V. pourtalesii*'s surface

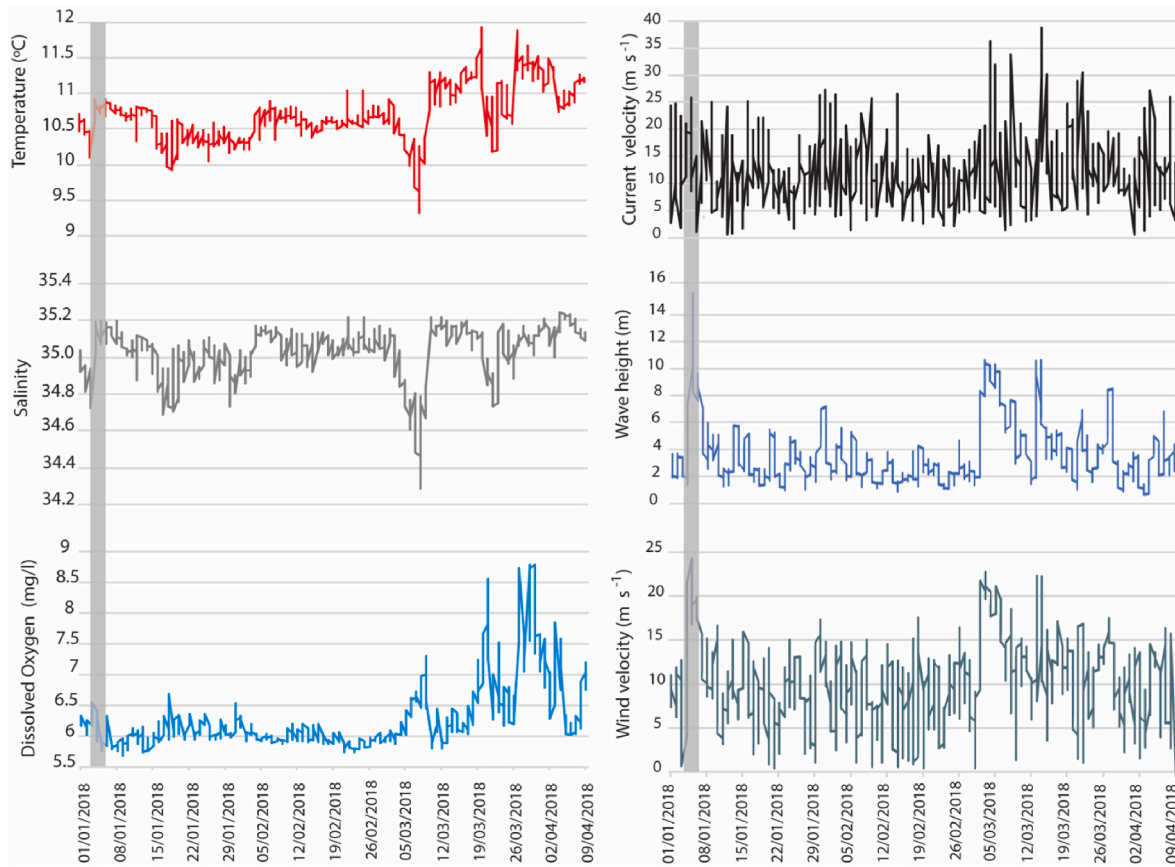


Fig. 3. Near-seabed environmental conditions and meteorological data recorded from January 01, 2018 to April 19, 2018. The storm events are marked with grey boxes.

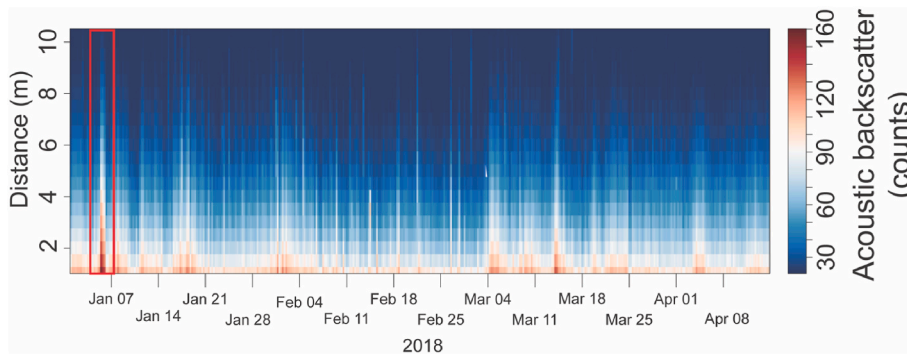


Fig. 4. Acoustic backscatter (counts) for turbidity concentration in 0–10 m above the sea floor. Red box identifies a resuspension event triggered by a storm which caused sediment deposition on the monitored *V. pourtalesii* individual.

variation (Fig. 8).

4. Discussion

The present study assessed the hexactinellid sponge phenology, linking it to both surface and near bed environmental processes by means of a temporally high-resolution and relatively long-term (94 days) time series of images. Different behavioral responses were quantified with a combined manual and CNN automated approach (i.e. YOLOv8).

4.1. Sediment deposition response

Although little is known on how deep-sea sponges respond to both

increased suspended sediment concentrations and deposition, it is generally assumed that its effects are adverse (Bell et al., 2015). Increased suspended sediment concentrations and subsequent deposition can result in alterations on feeding behavior (e.g. clogging of feeding structures), physiological stress (e.g. altered respiration rates, increase in mucus secretion, reallocation of reserves) or smothering of sessile organisms (Brooke et al., 2009; Grant et al., 2018; Topçu et al., 2018; Kutti et al., 2022). During turbidity events sponges are exposed to elevated suspended matter concentrations, which accumulate in their aquiferous system and coanocyte chambers, causing clogging and a diminished filtration capacity. This leads to reduced feeding, and oxygenation resulting in physiological stress (Tompkins-MacDonald and Leys, 2008; Tjensvoll et al., 2013; Wurz et al., 2021). Additionally, sediment deposition can cause sponge smothering resulting in at least



Fig. 5. Response of *Vazella pourtalesii* to resuspension event and subsequent sediment deposition. 0 h (0 h) indicates the moment when visibility was restored 44 h after the beginning of a turbidity event in 5th of January. Black arrow points at a cobble which remained covered in sediment, white arrows point at the *V. pourtalesii* individual.

Table 1

Detection preferences of YOLOv8 on the validation set in detecting Sponges. **maP@0.5** and **map@0.5:95** are average precision for detection confidence equal to 0.5 and detection confidence between 0.5 and 0.95 respectively.

Class	Images	Instances	Box (P)	Recall (R)	mAP50	mAP50-95
All	50	50	1.00	0.995	0.995	0.887

partial mortality after 14 days (Pineda et al., 2016). However, this is not the case in the present study as the monitored *V. pourtalesii* individual was able to clear sediment from its surface within a 72-h period (Fig. 4) and in the following month it did not show any signs of necrosis. This agrees with Wurz et al. (2021) which observed no structural necrosis or other signs of decreased health on ten *V. pourtalesii* individuals

repeatedly exposed in the laboratory to elevated suspended sediment concentrations during 21-days.

Bottom currents likely have contributed to this process since water flow can benefit the filtering capacity of sponges (Leys et al., 2011). This is a biotic process within the sponge individual, since adjacent cobbles with similar orientation remained covered by sediment (Fig. 3). Laboratory and field studies have shown that certain sponge species can cope with sedimentation through different mechanisms such as producing mucus to clear sponge surfaces, temporally stopping pumping activity to avoid clogging, or by inducing a complete flow reversal as a measure to remove sediment from its surface (Leys, 1999; Kornder et al., 2022). Although it is unclear if *V. pourtalesii* engages in any of these behaviors, it has recently been observed, under laboratory conditions, how *V. pourtalesii* is capable of rapidly expelling large sediment particles from the osculum, completely clearing its surface of sediment 38 days after

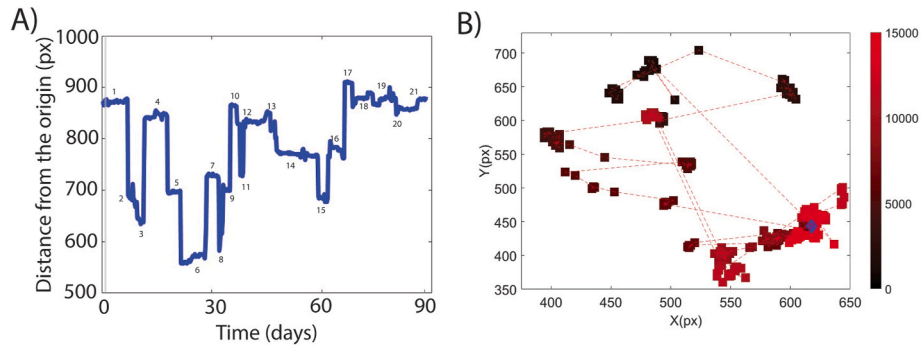


Fig. 6. A) Distance of the bounding boxes from the origin as a function of time. The greyline indicates the moment when the storm event occurs. Numbers represent the number of times the sponge moved. B) *Vazella pourtalesii* moved from black to dark red to light red points. Sponge movement starts from the blue polygon. The colored scale indicates the time lapse in minutes from the sponge’s original position. Black and dark red correspond to the closest moment in time from the original position, while light red represents the furthest in time.

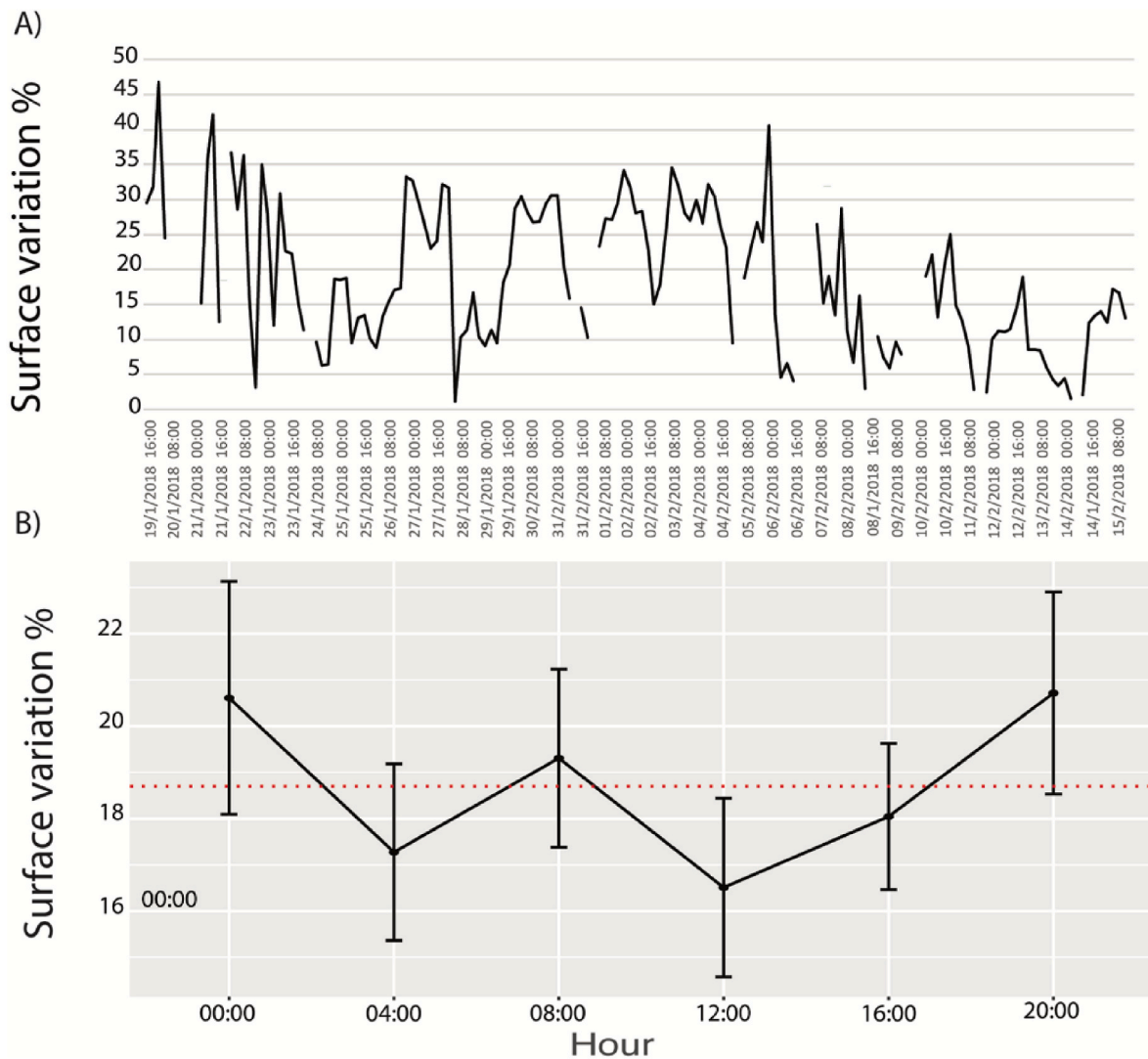


Fig. 7. A) Analysis of contraction of the monitored *Vazella pourtalesii* individual. B) Waveform analysis of hourly means (\pm SE) of *V. pourtalesii* surface variation percentage. Red horizontal dashed red lines represent the MESOR.

sediment exposure had stopped (Wurz et al., 2021). Therefore, it could be inferred that *V. pourtalesii* is well adapted to sedimentary environments being able to cope with resuspension events. The capacity of *V. pourtalesii* to actively remove deposited sediment may pose an adaptative advantage over other sessile passive suspension feeding taxa,

contributing to its high abundance over vast extensions of the Scotian Shelf, an area regularly exposed to extreme natural turbidity events related to surface storms or hurricanes (Hanz et al., 2021a) and anthropogenic activities such as fisheries (e.g. Koen-Alonso et al., 2018).

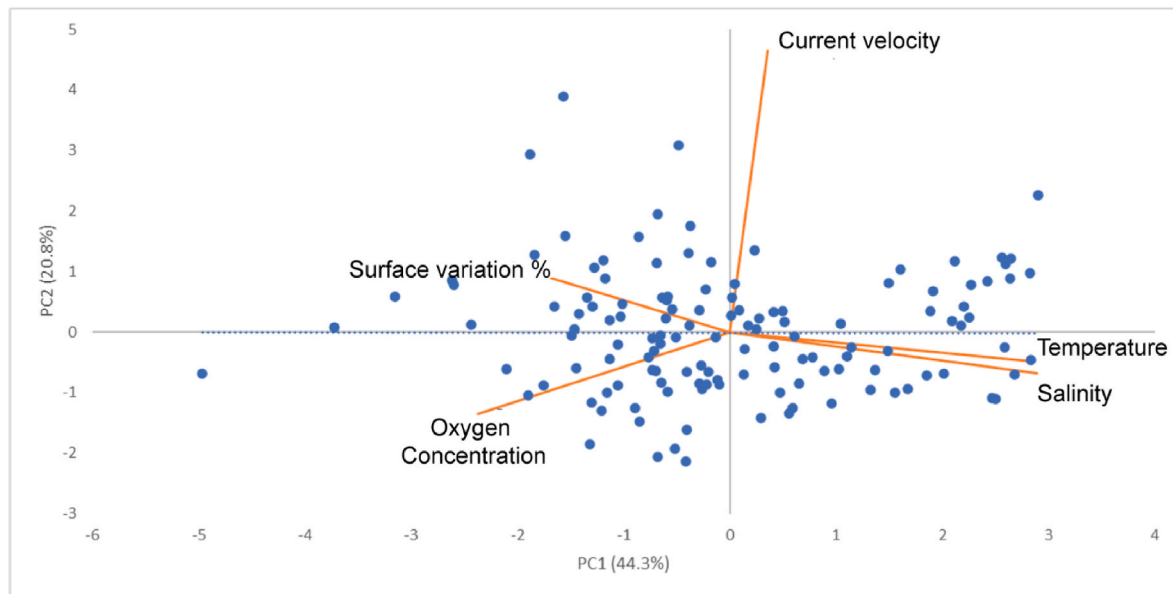


Fig. 8. Principal component analyses showing the surface variation % and the role of the significant environmental variables (orange vectors), whose length is proportional to their significance in explaining the distribution of biological data as response variables.

4.2. Passive locomotion

Sponges are generally understood to be non-motile sessile organisms, however mobility related to spatial movement has been reported in both laboratory conditions and in the field (Bond and Harris, 1988). As observed in the present study, large epibenthic sponges have generally been described to passively move, becoming toppled or unattached by bottom currents, substrate instability or storm events (Bell and Barnes, 2002; Mercurio et al., 2006; Kahn et al., 2020; Hanz et al., 2021b). For passive suspension feeders, toppling or detachment is considered one of the main causes of mortality (Grigg, 1977; Weinbauer and Velimirov, 1996; Coma et al., 2004). A stable position is highly relevant as most sponge species grow in a favourable orientation that maximises their feeding success and prevents sediment accumulation (Bell and Barnes, 2002).

Sponges that have detached from the substrates will have limited control on their orientation and filtering capacity could be compromised. In this regard, detached branching sponges occurring on littoral environments have been reported to reduce their growth rates and eventually decay after several months (Bell and Barnes, 2002). Contrarily, vase-shaped sponges in abyssal plains that were monitored for several months (1.5–4 months) did not show any signs of deterioration or decay despite frequently changing their position (Kahn et al., 2020). Sponges with rounded or vase-like morphologies (vase-shaped or barrel-shaped), like *V. pourtalesii*, have a wider filtering surface which ensures a more homogeneous interaction with currents, which may allow them to better cope with position changes than other erect (George et al., 2018; Schönberg, 2021) or fan shaped morphologies (Santín et al., 2019; Grinyó et al., 2022). Hanz et al. (2021a) described how a detached *V. pourtalesii* individual with a flattened morphology, rapidly decayed in the span of several days (Supplementary material 2). Contrary, in Grinyó et al. (2023) several toppled and detached barrel shaped *V. pourtalesii* individuals, which were visible for several months, did not show any signs of decay (Supplementary material 2).

Furthermore, despite being a basiphytose species (Beazley et al., 2018), which requires attachment to hard substrates and thus might seem more susceptible to displacement from its original position, the monitored individual overcame this vulnerability by attaching itself to cobblestones. This adaptation allowed it to maintain a low center of mass (Fig. 2A), enabling it to alternate between laying and

upright positions in response to changing bottom currents, effectively attaining a “free-living” status.

4.3. Contracting behavior

Contraction temporal patterns were observed during a 28-day period and were associated with low oxygen concentrations (Fig. 7). Oxygen concentrations ranged between 5.8 and 6.5 mg/l (6.05 ± 0.12 (SD)) being significantly lower than other periods in which *V. pourtalesii* did not contract (PERMANOVA, p -value >0.001). Although low oxygen depletion can cause sponges to contract (Leys and Kahn, 2018), it seems unlikely that low oxygen concentrations triggered *V. pourtalesii*'s contractions as other individuals in the field of view did not display this behavior. Therefore, we consider that the observed contracting behavior is triggered by physiological processes rather than environmental mechanisms.

Many sponge species have been reported to contract or alter their filtering behavior as a response to changing environmental conditions (e.g. water turbidity) or physiological processes (e.g. waste removal) (Kornder et al., 2022). Numerous studies have addressed contracting behavior in sponges (Demospongiae and Calcarea) (e.g. Nickel, 2004, 2011 Elliott and Leys, 2007; Leys et al., 2019; Harrison et al., 2021; Kornder et al., 2022; Flensburg et al., 2022), however, hexactinellid contracting behavior still remains poorly studied, having only been addressed in one study (Kahn et al., 2020). Recently, Kahn et al. (2020) observed how several hexactinellid sponge species in abyssal plain environments contracted. As observed in this study, contractions were rhythmic (Fig. 6A) and consisted of a lateral compression without affecting the sponge total length (Kahn et al., 2020). Contracting rhythmicity in shallow demosponges has been associated with light intensity (Strehlow et al., 2016), however, in most cases the lack of long-term data sets prevents identification of the environmental triggers modelling rhythmicity. Wave form analyses displayed two major peaks (Fig. 7B), which could suggest that the contraction rhythms are governed by the semi-diurnal tide cycle in the Scotian Shelf (Hanz et al., 2021a). Yet, 68% of contraction periods exceeded the tidal cycle, which lasts 12.75 h. Therefore, further research is needed to confirm this potential trend between tides and *V. pourtalesii*'s contracting rhythmicity. Furthermore, contraction cycles were longer than other hexactinellid sponges (Kahn et al., 2020) but the reasons for these prolonged

durations remain unknown.

5. Conclusions

The monitored *Vazella pourtalesii* cleared sediment from its surface within 72 h, and, although the exact mechanism it uses remains unclear, it indicates the species can cope with sediment deposition indicating its adaptation to sedimentary environments exposed to resuspension events especially in this environment. Over the span of 94 days the monitored individual changed positions 21 times. Although toppling and change in position is known to cause deterioration in sessile suspension feeders, the monitored individual showed no signs of deterioration over the said time course. In this sense, it is likely that *V. pourtalesii*'s vase-like morphology allowed it to have a more homogeneous interaction with currents which may allow them to better cope with positional changes. As observed in other deep-sea hexactinellids, the monitored *V. pourtalesii* individual engaged in rhythmic contractions, the trigger/s of which is still not properly understood, although it appears to be driven by physiological processes rather than environmental factors. Overall, this article sheds light on the poorly understood behavior of deep-sea hexactinellids, and highlights that sessile benthic fauna, and Porifera, are not just static organisms, but display a wide array of physiological changes in response to both biotic and abiotic factors. Yet, replicability would be advisable to confirm and better comprehend the observed behavioral patterns.

Furthermore, these findings highlight the pressing significance of this research in the context of deep-sea habitat conservation. It's crucial to recognize that deep-sea mining and prolonged bottom fishing activities can lead to the disruption of these fragile ecosystems by raising sediment plumes, potentially causing enduring harm to these hexactinellids and their fellow inhabitants. While these organisms may exhibit the ability to recover from disturbances, it's essential to acknowledge that long-term, sustained disruption can inflict irreparable damage on both the species and the habitat as a whole. Therefore, the insights gained from this study underscore the urgency of preserving these unique and vulnerable ecosystems, shedding light on the intricate mechanisms underlying their resilience, and emphasizing the importance of responsible environmental stewardship in the face of evolving industrial activities. These findings challenge our preconceived notions of deep-sea ecosystems, demonstrating the complexity and adaptability of life in these extreme environments. The research underscores the importance of studying and preserving these often-overlooked animals, as they play a crucial role in the ocean's delicate balance. By gaining a deeper understanding of the intricacies of hexactinellid behavior, researchers can better contribute to the conservation of these unique ecosystems.

Ethics statement

Ethical review and approval was not required for the animal study because this study is based on images recorded in the deep-sea benthic environments. No organisms were captured nor manipulated in any way.

CRediT authorship contribution statement

Jordi Grinyó: Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jacopo Aguzzi:** Writing – original draft, Conceptualization. **Luciano Ortenzi:** Writing – original draft, Methodology, Data curation. **Ellen Kenchington:** Writing – original draft, Supervision, Conceptualization. **Simona Violino:** Writing – original draft, Formal analysis. **Ulrike Hanz:** Writing – review & editing, Writing – original draft, Conceptualization. **Andreu Santín:** Writing – review & editing, Writing – original draft, Conceptualization. **Tim W. Nattkemper:** Writing –

original draft, Conceptualization. **Furu Mienis:** Writing – original draft, Supervision, Resources, Project administration, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

This study is part of the SponGES project, which received funding from the European Union's Horizon 2020 Research and Innovation Program under grant agreement no. 679849. Cruises were funded by Fisheries and Ocean's Canada's (DFO) International Governance Strategy awarded to EK, Bedford Institute of Oceanography, and supported by Hans Tore Rapp (University of Bergen, Norway). Dr. Jordi Grinyó has received funding from the European Union's Horizon 2020 research and Innovation program. Action MSCA-IF-EF-ST fellowship, CWCC-Dynamics project under the grant agreement no. 101028621. Dr. Luciano Ortenzi acknowledges the Ministry of University and Research (MUR) initiative "Departments of Excellence" (Law 232/2016) DAFNE Project 2023-27 "Digital, Intelligent, Green and Sustainable (acronym: D.I.Ver. So). Dr. Jacopo Aguzzi acknowledges that the research has been carried out within the framework of the project "Severo Ochoa Center of Excellence" financially supported by ICM-CSIC (CEX2019-000928-S) and the Research Unit Tecnoterra (ICM-CSIC/UPC) of the Spanish Government. The authors would like to thank Dr. Amanda S. Kahn for her valuable advice on addressing *V. pourtalesii* contraction behavior. We also extend our sincere gratitude to Dr. Trevor Kenchington for his contributions to the study's conceptualization, the insights he provided in interpreting the Scotian Shelf environmental data and its potential effects on *V. pourtalesii*, and his support in improving the manuscript's writing.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr.2024.104388>.

References

- Aguzzi, J., Bahamon, N., Marotta, L., 2009. The influence of light availability and predatory behavior of the decapod crustacean *Nephrops norvegicus* on the activity rhythms of continental margin prey decapods. *Mar. Ecol.* 30 (3), 366–375. <https://doi.org/10.1111/j.1439-0485.2008.00276.x>.
- Aguzzi, J., Costa, C., Menesatti, P., Garcia, J.M., Bahamon, N., Puig, P., Sardà, F., 2011. Activity rhythms in the deep-sea: a chronobiological approach. *Front. Biosci.* 16 (1), 131. <https://doi.org/10.2741/3680>.
- Aguzzi, J., Fanelli, E., Ciuffardi, T., Schirone, A., De Leo, F., Doya, C., Kawato, M., Miyazaki, M., Furushima, Y., Costa, C.A., Fujiwara, Y., 2018. Faunal activity rhythms influencing early community succession of an implanted whale carcass offshore Sagami Bay, Japan. *Sci. Rep.* 8 (1) <https://doi.org/10.1038/s41598-018-29431-5>.
- Barthel, D., 1992. Do hexactinellids structure Antarctic sponge associations? *Ophelia* 36 (2), 111–118.
- Barthel, D., Tandal, O., 1993. Sponge spicules in abyssal and bathyal sediments of the NE Atlantic. *Deep Sea News.* 20, 15–18.
- Bayer, K., Busch, K., Kenchington, E., Beazley, L., Franzenburg, S., Michels, J., Hentschel, U., Slaby, B.M., 2020. Microbial strategies for survival in the glass sponge *Vazella pourtalesii*. *mSystems* 5 (4). <https://doi.org/10.1128/msystems.00473-20>.
- Beazley, L., Kenchington, E., Yashayaev, I., Murillo, F.J., 2015. Drivers of epibenthic megafaunal composition in the sponge grounds of the Sackville Spur, northwest Atlantic. *Deep-sea Research Part I-oceanographic Research Papers* 98, 102–114. <https://doi.org/10.1016/j.dsr.2014.11.016>.
- Beazley, L., Wang, Z., Kenchington, E., Yashayaev, I., Rapp, H.T., Xavier, J.R., Murillo, F.J., Fenton, D., Fuller, S.D., 2018. Predicted distribution of the glass sponge *Vazella*

- pourtalesii* on the Scotian Shelf and its persistence in the face of climatic variability. *PLoS One* 13 (10), e0205505. <https://doi.org/10.1371/journal.pone.0205505>.
- Beazley, L., Kenchington, E., Murillo, F.J., Brickman, D., Wang, Z., Davies, A., Roberts, E. M., Rapp, H.T., 2021. Climate change winner in the deep sea? Predicting the impacts of climate change on the distribution of the glass sponge *Vazella pourtalesii*. *Mar. Ecol. Prog. Ser.* 657, 1–23. <https://doi.org/10.3354/meps13566>.
- Bell, J.F., Barnes, D., 2002. Density, distribution and decline of two species of unattached demosponge. *Sarsia*. <https://doi.org/10.1080/003648202320205184>.
- Bell, J.F., McGrath, E., Biggerstaff, A., Bates, T., Bennett, H., Marlow, J., Shaffer, M.R., 2015. Sediment impacts on marine sponges. *Mar. Pollut. Bull.* 94 (1–2), 5–13. <https://doi.org/10.1016/j.marpolbul.2015.03.030>.
- Bond, C., Harris, A.L., 1988. Locomotion of sponges and its physical mechanism. *J. Exp. Zool.* 246 (3), 271–284. <https://doi.org/10.1002/jez.1402460307>.
- Brooke, S.D., Holmes, M.W., Young, C.M., 2009. Sediment tolerance of two different morphotypes of the deep-sea coral *Lophelia pertusa* from the Gulf of Mexico. *Mar. Ecol. Prog. Ser.* 390, 137–144. <https://doi.org/10.3354/meps08191>.
- Busch, K., Beazley, L., Kenchington, E., Whoriskey, F.G., Slaby, B.M., Hentschel, U., 2020. Microbial diversity of the glass sponge *Vazella pourtalesii* in response to anthropogenic activities. *Conserv. Genet.* 21 (6), 1001–1010. <https://doi.org/10.1007/s10592-020-01305-2>.
- Cadrin, S.X., 2020. Advances in morphometric identification of fishery stock. *Rev. Fish Biol. Fish.* 10, 91–112.
- Cathalot, C., Van Oevelen, D., Cox, T., Kutti, T., Lavaleye, M.S.S., Duineveld, G., Meysman, F.J.R., 2015. Cold-water coral reefs and adjacent sponge grounds: hotspots of benthic respiration and organic carbon cycling in the deep sea. *Front. Mar. Sci.* 2, 37. <https://doi.org/10.3389/fmars.2015.00037>.
- Chatzievanghelou, D., Bahamon, N., Martini, S., Del Río Fernandez, J., Riccobene, G., Tangherlini, M., Danovaro, R., De Leo, F.C., Pirenne, B., Aguzzi, J., 2021. Integrating diel vertical migrations of bioluminescent deep scattering layers into monitoring programs. *Front. Mar. Sci.* 8 <https://doi.org/10.3389/fmars.2021.661809>.
- Chen, C., Huang, H., Beardsley, R.C., Xu, Q., Limeburner, R., Cowles, G.W., Sun, Y., Qi, J., Lin, H., 2011. Tidal dynamics in the Gulf of Maine and new england shelf: an application of FVCOM. *J. Geophys. Res.* 116 (C12) <https://doi.org/10.1029/2011jc007054>.
- Coma, R., Pola, E., Ribes, M., Zabala, M., 2004. Long-term assessment of temperate octocoral mortality patterns, protected vs. unprotected areas. *Ecol. Appl.* 14 (5), 1466–1478. <https://doi.org/10.1890/03-5176>.
- De Araujo Lira, A.F., DeSouza, A.M., De Albuquerque, C.M.R., 2018. Environmental variation and seasonal changes as determinants of the spatial distribution of scorpions (Arachnida: scorpiones) in Neotropical forests. *Can. J. Zool.* 96 (9), 963–972. <https://doi.org/10.1139/cjz-2017-0251>.
- Drinkwater, K.F., Petrie, B., Smith, P.C., 2003. Climate variability on the scotian shelf during the 1990s. *ICES Marine Science Symposium* 219, 40–49.
- Duineveld, G.C., Lavaleye, M.S.S., Berghuis, E., 2004. Particle flux and food supply to a seamount cold-water coral community (Galicia Bank, NW Spain). *Mar. Ecol. Prog. Ser.* 277, 13–23. <https://doi.org/10.3354/meps277013>.
- Duineveld, G.C., Lavaleye, M.S.S., Bergman, M.J., De Stigter, H., Mienis, F., 2007. Trophic structure of a cold-water coral mound community (Rockall Bank, NE Atlantic) in relation to the near-bottom particle supply and current regime. *Bull. Mar. Sci.* 81 (3), 449–467. <https://dialnet.unirioja.es/servlet/articulo?codigo=4908505>.
- Dunham, A., Regg, J.R., Carolsfeld, W., Davies, S., Murfitt, I., Boutillier, J., 2015. Effects of submarine power transmission cables on glass sponge reef and associated megafaunal community. *Mar. Environ. Res.* 107, 50–60.
- Dunlop, K., Van Oevelen, D., Ruhl, H.A., Huffard, C.L., Kuhn, L.A., Smith, K.J., 2016. Carbon cycling in the deep eastern North Pacific benthic food web: investigating the effect of organic carbon input. *Limnol. Oceanogr.* 61 (6), 1956–1968. <https://doi.org/10.1002/lno.10345>.
- Elliott, G.R., Leys, S.P., 2007. Coordinated contractions effectively expel water from the aquiferous system of a freshwater sponge. *J. Exp. Biol.* 210 (21), 3736–3748. <https://doi.org/10.1242/jeb.003392>.
- Flensburg, S.B., Garm, A., Funch, P., 2022. The contraction–expansion behaviour in the demosponge *Tethya wilhelma* is light controlled and follows a diurnal rhythm. *bioRxiv* 225 (24). <https://doi.org/10.1242/jeb.244751>.
- Francescangeli, M., Sbragaglia, V., Del Río Fernandez, J., Trullols, E., Antonijuan, J., Massana, I., Prat, J., Cervera, M.N., Toma, D.M., Aguzzi, J., 2022. Long-term monitoring of diel and seasonal rhythm of dentex dentex at an artificial reef. *Front. Mar. Sci.* 9 <https://doi.org/10.3389/fmars.2022.837216>.
- Francis, F.T., Burke, L., Marliave, J., Schultz, J., Borden, L., Weltman, A., Duham, A., 2024. Fishing damage to cloud sponges may lead to losses in associated fish communities in Pacific Canada. *Mar. Environ. Res.* 197, 106448.
- George, A.M., Brodie, J., Daniell, J., Capper, A., Jonker, M., 2018. Can sponge morphologies act as environmental proxies to biophysical factors in the Great Barrier Reef, Australia? *Ecol. Indic.* 93, 1152–1162. <https://doi.org/10.1016/j.ecolind.2018.06.016>.
- Girard, F., Litvin, S.Y., Sherman, A., McGill, P., Gannon, A., Lovera, C., DeVogelaere, A., Burton, E.J., Graves, D., Schnittger, A., Barry, J., 2022. Phenology in the deep sea: seasonal and tidal feeding rhythms in a keystone octocoral. *Proc. Biol. Sci.* 289. <https://doi.org/10.1098/rspb.2022.1033>, 1985.
- Gómez-Gras, D., Linares, C., Dornelas, M., Madin, J.S., Brambilla, V., Ledoux, J., López-Sendino, P., Bensoussan, N., Garrabou, J., 2021. Climate change transforms the functional identity of Mediterranean coralligenous assemblages. *Ecol. Lett.* 24 (5), 1038–1051. <https://doi.org/10.1111/ele.13718>.
- Goren, L., Idan, T., Shefer, S., Ilan, M., 2021. Macrofauna inhabiting massive demospores from shallow and mesophotic habitats along the Israeli Mediterranean coast. *Front. Mar. Sci.* 7, 612779.
- Grant, N., Matveev, E., Kahn, A.S., Leys, S.P., 2018. Suspended sediment causes feeding current arrests in situ in the glass sponge *Aphrocallistes vastus*. *Mar. Environ. Res.* 137, 111–120.
- Grigg, R.W., 1977. Population dynamics of two gorgonian corals. *Ecology* 58 (2), 278–290. <https://doi.org/10.2307/1935603>.
- Grinyó, J., Francescangeli, M., Santín, A., Ercilla, G., Estrada, F., Mecho, A., Fanelli, E., Costa, C., Danovaro, R., Company, J.B., Sobrino, I., Valencia, J., Aguzzi, J., 2022. Megafaunal assemblages in deep-sea ecosystems of the Gulf of Cadiz, northeast Atlantic ocean. *Deep Sea Res. Oceanogr. Res. Pap.* 183, 103738.
- Grinyó, J., Aguzzi, J., Kenchington, E., Costa, C., Hanz, U., Mienis, F., 2023. Occurrence and behavioral rhythms of the endangered acadian redfish (*Sebastes fasciatus*) in the Sambre Bank (scotian shelf). *Front. Mar. Sci.* 10 <https://doi.org/10.3389/fmars.2023.1158283>.
- Haffert, L., Haeckel, M., de Stigter, H., Janssen, F., 2020. Assessing the temporal scale fo deep-sea mining impacts on sediment biogeochemistry. *Biogeosciences* 17, 2767–2789.
- Hammer-Muntz, O., Harper, D., Ryan, P., 2001. PAST: paleontological statistics software package for education and data analysis version 2.09. *Palaeontol. Electron.* 4. <http://scienceopen.com/document?vid=f7c81409-9131-4ded-a3d6-e1509342d3df>.
- Hannah, C.G., Shore, J., Loder, J.W., Naimie, C.E., 2001. Seasonal circulation on the western and central scotian shelf. *J. Phys. Oceanogr.* 31 (2), 591–615. [https://doi.org/10.1175/1520-0485\(2001\)031](https://doi.org/10.1175/1520-0485(2001)031).
- Hanz, U., Beazley, L., Kenchington, E., Duineveld, G.C., Rapp, H.T., Mienis, F., 2021a. Seasonal variability in near-bed environmental conditions in the *Vazella pourtalesii* glass sponge grounds of the scotian shelf. *Front. Mar. Sci.* 7 <https://doi.org/10.3389/fmars.2020.597682>.
- Hanz, U., Roberts, E.M., Duineveld, G.C., Davies, A., Van Haren, H., Rapp, H.T., Reichart, G., Mienis, F., 2021b. Long-term observations reveal environmental conditions and food supply mechanisms at an arctic deep-sea sponge ground. *J. Geophys. Res.* 126 (3). <https://doi.org/10.1029/2020je016776>.
- Hanz, U., Riekenberg, P.M., De Kluijver, A., Van Der Meer, M.T.J., Middelburg, J.J., De Goeij, J.M., Bart, M.C., Wur, E., Colaco, A., Duineveld, G.C., Reichart, G., Rapp, H. T., Mienis, F., 2022. The important role of sponges in carbon and nitrogen cycling in a deep-sea biological hotspot. *Funct. Ecol.* 36 (9), 2188–2199. <https://doi.org/10.1111/1365-2435.14117>.
- Harrison, D., De Leo, F.C., Gallin, W.J., Mir, F., Marini, S., Leys, S.P., 2021. Machine learning applications of convolutional neural networks and unet architecture to predict and classify demosponge behavior. *Water* 13 (18), 2512. <https://doi.org/10.3390/w13182512>.
- Hawkes, N.J., Korabik, M., Beazley, L., Rapp, H.T., Xavier, J.R., Kenchington, E., 2019. Glass sponge grounds on the Scotian Shelf and their associated biodiversity. *Mar. Ecol. Prog. Ser.* 614, 91–109. <https://doi.org/10.3354/meps12903>.
- Hogg, M.M., Tendal, O.S., Conway, K.W., Pomponi, S.A., Van Soest, R.W.M., Gutt, J., Krautter, M., Roberts, J.M., 2010. Deep-sea sponge grounds: reservoirs of biodiversity. *UNEP-WCMC biodiversity series* 32, 1–86.
- Jocher, G., 2023. Ultralytics YOLOv8. <https://github.com/ultralytics/ultralytics>.
- Johanson, A.N., Flögel, S., Dullo, W., Linke, P., Hasselbring, W., 2017. Modeling polyp activity of *Paragorgia arborea* using supervised learning. *Ecol. Inf.* 39, 109–118. <https://doi.org/10.1016/j.ecoinf.2017.02.007>.
- Kahn, A.S., Pennelly, C., McGill, P.R., Leys, S.P., 2020. Behaviors of sessile benthic animals in the abyssal northeast Pacific Ocean. *Deep-Sea Research Part I-topical Studies in Oceanography* 173, 104729. <https://doi.org/10.1016/j.dsr2.2019.104729>.
- Klitgaard, A.B., Tendal, O.S., 2004. Distribution and species composition of mass occurrences of large-sized sponges in the northeast Atlantic. *Prog. Oceanogr.* 61, 57–98.
- Koen-Alonso, M., Favaro, C., Ollerhead, N., Benoit, H., Bourdages, H., Sainte-Marie, B., Treble, M., Hedges, K., Kenchington, E., Lirette, C., King, M., Coffen-Smout, S., Murillo, J., 2018. Analysis of the overlap between fishing effort and significant benthic areas in Canada's atlantic and eastern arctic marine waters. *DFO Can. Sci. Advis. Sec. Res. Doc.* 270, 2018/015.
- Kornder, N.A., Esser, Y., Stoupin, D., Leys, S.P., Mueller, B., Vermeij, M.J.A., Huisman, J., De Goeij, J.M., 2022. Sponges sneeze music to shed particulate waste from their seawater inlet pores. *Curr. Biol.* 32 (17), 3855–3861.e3. <https://doi.org/10.1016/j.cub.2022.07.017>.
- Kuhn, L.A., Ruhl, H.A., Huffard, C.L., Smith, K.J., 2020. Benthic megafauna assemblage change over three decades in the abyss: variations from species to functional groups. *Deep-Sea Research Part I-topical Studies in Oceanography* 173, 104761. <https://doi.org/10.1016/j.dsr2.2020.104761>.
- Kutti, T., Legrand, E., Husa, V., Olsen, S.A., Gjelsvik, Ø., Carvajalino-Fernandez, M., Johnsen, I.A., 2022. Fish farm effluents cause metabolic depression, reducing energy stores and growth in the reef-forming coral *Lophelia pertusa*. *Aquaculture Environment Interactions* 14, 279–293. <https://doi.org/10.3354/aei00442%0a>.
- Leys, S.P., 1999. The choanosome of hexactinellid sponges. *Invertebr. Biol.* 118 (3), 221. <https://doi.org/10.2307/3226994>.
- Leys, S.P., Kahn, A.S., 2018. Oxygen and the energetic requirements of the first multicellular animals. *Integr. Comp. Biol.* 58 (4), 666–676. <https://doi.org/10.1093/icb/icy051>.
- Leys, S.P., Yahel, G., Reidenbach, M.A., Tunnicliffe, V., Shavit, U., Reisinger, H.M., 2011. The sponge pump: the role of current induced flow in the design of the sponge body plan. *PLoS One* 6 (12), e27787.
- Leys, S.P., Mah, J., McGill, P.R., Hamonic, L., De Leo, F.C., Kahn, A.S., 2019. Sponge behavior and the chemical basis of responses: a post-genomic view. *Integr. Comp. Biol.* 59 (4), 751–764. <https://doi.org/10.1093/icb/icz122>.

- Loder, J.W., Shore, J.A., Hannah, C.G., Petrie, B.D., 2001. Decadal-scale hydrographic and circulation variability in the Scotia–Maine region. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 48 (1–3), 3–35. [https://doi.org/10.1016/S0967-0645\(00\)00080-1](https://doi.org/10.1016/S0967-0645(00)00080-1).
- Maldonado, M., Aguilar, R.G., Bannister, R., Bell, J.F., Conway, K.W., Dayton, P.A., Díaz, C., Gutt, J., Kelly, M., Kenchington, E., Leys, S.P., Pomponi, S.A., Rapp, H.T., Rützler, K., Tendal, O.S., Vacelet, J., Young, C.M., 2015. *Sponge Grounds as Key Marine Habitats: A Synthetic Review of Types, Structure, Functional Roles, and Conservation Concerns*. Springer eBooks, pp. 1–39. https://doi.org/10.1007/978-3-319-17001-5_24-1.
- Maldonado, M., López-Acosta, M., Busch, K., Slaby, B.M., Bayer, K., Beazley, L., Hentschel, U., Kenchington, E., Rapp, H.T., 2021. A microbial nitrogen engine modulated by bacteriosyncytia in hexactinellid sponges: ecological implications for deep-sea communities. *Front. Mar. Sci.* 8 <https://doi.org/10.3389/fmars.2021.638505>.
- Maldonado, M., López-Acosta, M., Abalde, S., Martos, I., Ehrlich, H., Leynaert, A., 2022. On the dissolution of sponge silica: assessing variability and biogeochemical implications. *Front. Mar. Sci.* 9, 1005068.
- Mercurio, M., Corriero, G., Gaino, E., 2006. Sessile and non-sessile morphs of *Geodia cydonium* (Jameson) (Porifera, Demospongiae) in two semi-enclosed Mediterranean bays. *Marine Biology* 148 (3), 489–501. <https://doi.org/10.1007/s00227-005-0092-4>.
- Milligan, R., Scott, E., Jones, D.B., Bett, B.J., Jamieson, A.J., O'Brien, R.L., Costa, S.S., Rowe, G.T., Ruhl, H.A., Smith, K.R., De Susanne, P., Vardaro, M.F., Bailey, D.H., 2020. Evidence for seasonal cycles in deep-sea fish abundances: a great migration in the deep SE Atlantic? *J. Anim. Ecol.* 89 (7), 1593–1603. <https://doi.org/10.1111/1365-2656.13215>.
- Möller, T., Nilssen, L., Nattkemper, T.W., 2018. Tracking sponge size and behaviour with fixed underwater observatories. In: *Lecture Notes in Computer Science*. Springer Science+Business Media, pp. 45–54. https://doi.org/10.1007/978-3-030-05792-3_5.
- Nickel, M., 2004. Kinetics and rhythm of body contractions in the sponge *Tethya wilhelma* (Porifera: Demospongiae). *J. Exp. Biol.* 207 (26), 4515–4524. <https://doi.org/10.1242/jeb.01289>.
- Nickel, M., Scheer, C., Hammel, J.U., Herzen, J., Beckmann, F., 2011. The contractile sponge epithelium *sensu lato* – body contraction of the demosponge *Tethya wilhelma* is mediated by the pinacoderm. *J. Exp. Biol.* 214 (10), 1692–1698. <https://doi.org/10.1242/jeb.049148>.
- Osterloff, J., Nilssen, L., Järnegen, J., Van Engeland, T., Buhl-Mortensen, P., Nattkemper, T.W., 2019. Computer vision enables short- and long-term analysis of *Lophelia pertusa* polyp behaviour and colour from an underwater observatory. *Sci. Rep.* 9 (1) <https://doi.org/10.1038/s41598-019-41275-1>.
- Pham, C.K., Murillo, F.J., Lirette, C., Maldonado, M., Colaço, A., Ottaviani, D., Kenchington, E., 2019. Removal of deep-sea sponges by bottom trawling in the Flemish Cap area: conservation, ecology and economic assessment. *Sci. Rep.* 9 (1) <https://doi.org/10.1038/s41598-019-52250-1>.
- Pineda, M.C., Duckworth, A., Webster, N.S., 2016. Appearance matters: sedimentation effects on different sponge morphologies. *J. Mar. Biol. Assoc. U. K.* 96 (2), 481–492. <https://doi.org/10.1017/s0025315414001787>.
- Purser, A., 2015. A time series study of *Lophelia pertusa* and reef megafauna responses to drill cuttings exposure on the Norwegian margin. *PLoS One* 10 (7), e0134076. <https://doi.org/10.1371/journal.pone.0134076>.
- Reiswig, H.M., 1996. Redescription and placement of the rossellid genus *Vazella* gray (hexactinellida : lyssacinosida). *Bulletin de l'Institut royal des Sciences naturelles de Belgique* 135–141, 66 Suppl. 1.
- Rohlf, F.J., 2005. *tpsDig, Digitize Landmarks and Outlines, Version 2.05*. Department of Ecology and Evolution, State University of New York at Stony Brook.
- Rohlf, F.J., 2013. *TpsSuper, Superimposition and Image Averaging*. Stony Brook University, Stony Brook, NY, USA. Department of Anthropology, version 1.15.
- Ryer, C.H., Stoner, A.W., Titgen, R.H., 2004. Behavioral mechanisms underlying the refuge value of benthic habitat structure for two flatfishes with differing anti-predator strategies. *Mar. Ecol. Prog. Ser.* 268, 231–243.
- Santín, A., Grinyó, J., Ambroso, S., Uriz, M.J., Dominguez-Carrió, C., Gili, J.M., 2019. Distribution patterns and demographic trends of demosponges at the menorca channel (northwestern mediterranean sea). *Prog. Oceanogr.* 173, 9–25. <https://doi.org/10.1016/j.pocean.2019.02.002>.
- Schlosser, I.J., 1990. Environmental variation, life history attributes, and community structure in stream fishes: implications for environmental management and assessment. *Environ. Manag.* 14 (5), 621–628. <https://doi.org/10.1007/bf02394713>.
- Schneider, C.C., Rasband, W., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* 9 (7), 671–675. <https://doi.org/10.1038/nmeth.2089>.
- Schönberg, C.H.L., 2021. No taxonomy needed: sponge functional morphologies inform about environmental conditions. *Ecol. Indicat.* 129, 107806 <https://doi.org/10.1016/j.ecolind.2021.107806>.
- Sigwart, J.D., Brandt, A., Di Franco, D., Briones Escobar, E., Gerken, S., Gooday, A.J., Grimes, C.J., Głuchowska, K., Hoffmann, S., Jazdzewska, A.M., Kamyab, E., Kelch, A., Knauber, H., Kohlenbach, K., Olmo, M.S., Moreau, C., Ogawa, A., Polisenio, A., Santín, A., Tandberg, A.H.S., Theising, F.L., Walter, T., Wölfl, A.-C., Chen, C., 2023. Heterogeneity on the abyssal plains: a case study in the Bering Sea. *Front. Mar. Sci.* 9 <https://doi.org/10.3389/fmars.2022.1037482>.
- Strehlow, B.W., Jorgensen, D., Webster, N.S., Pineda, M.-C., Duckworth, A., 2016. Integrating a thermistor flowmeter and time lapse imagery to monitor sponge (Porifera) behaviour. *PeerJ* 4, e2137v1.
- Tabachnick, K.R., 2002. Family rossellidae schulze, 1885. In: Hooper, J.N.A., Van Soest, R.W.M. (Eds.), (2002) *Systema Porifera - A Guide to the Classification of Sponges*, vol. 2. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 1441–1505, 1708 + xvliii. ISBN 0-306-47260-0.
- Tjensvoll, I., Kutti, T., Fosså, J.H., Bannister, R., 2013. Rapid respiratory responses of the deep-water sponge *Geodia barretti* exposed to suspended sediments. *Aquat. Biol.* 19 (1), 65–73. <https://doi.org/10.3354/ab00522>.
- Tompkins-MacDonald, G.J., Leys, S.P., 2008. Glass sponges arrest pumping in response to sediment: implications for the physiology of the hexactinellid conduction system. *Marine Biology* 154 (6), 973–984. <https://doi.org/10.1007/s00227-008-0987-y>.
- Topçu, N.E., Turgay, E., Yardımcı, R.E., Topaloğlu, B., Yükek, A., Steinum, T., Karataş, S., Öztürk, B., 2018. Impact of excessive sedimentation caused by anthropogenic activities on benthic suspension feeders in the Sea of Marmara. *J. Mar. Biol. Assoc. U. K.* 99 (5), 1075–1086. <https://doi.org/10.1017/s0025315418001066>.
- Wang, S., Kenchington, E., Wang, Z., Davies, A., 2021. Life in the fast lane: modeling the fate of glass sponge larvae in the Gulf stream. *Front. Mar. Sci.* 8 <https://doi.org/10.3389/fmars.2021.701218>.
- Wassenberg, T.J., Dews, G., Cook, S.D., 2002. The impact on megabenthos (sponges) on the north-west shelf of Australia. *Fish. Res.* 58, 141–151.
- Weinbauer, M.G., Velimirov, B., 1996. Population dynamics and overgrowth of the sea fan *Eunicella cavolini* (coelenterata: octocorallia). *Estuar. Coast Shelf Sci.* 42 (5), 583–595. <https://doi.org/10.1006/ecss.1996.0038>.
- Wurz, E., Beazley, L., Macdonald, B., Kenchington, E., Rapp, H.T., Osinga, R., 2021. The hexactinellid deep-water sponge *Vazella pourtalesii* (schmidt, 1870) (rossellidae) coex with temporarily elevated concentrations of suspended natural sediment. *Front. Mar. Sci.* 8 <https://doi.org/10.3389/fmars.2021.611539>.
- Zuazo, A., Grinyó, J., López-Vázquez, V., Rodríguez, E., Costa, C., Ortenzi, L., Flögel, S., Valencia, J., Marini, S., Zhang, G., Wehde, H., Aguzzi, J., 2020. An automated pipeline for image processing and data treatment to track activity rhythms of *Paragorgia arborea* in relation to hydrographic conditions. *Sensors* 20 (21), 6281. <https://doi.org/10.3390/s20216281>.