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## Chapter

# The Mauritanian Slope (NE Atlantic) Has No Desert: *Swiftia phaeton* (Holaxonia: Plexauridae) Shaping Coral Gardens

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## Abstract

*Swiftia* Duchassaing & Michelotti, 1864, is often found sparse in the NE Atlantic Ocean and Mediterranean Sea. When the cruise MSM 16/3 “PHAETON” filmed the upper bathyal off Mauritania in 2010, the first dense populations dominated by *Swiftia* were discovered in the NE Atlantic Ocean, co-occurring with the framework-forming scleractinians *Desmophyllum pertusum* (Linnaeus, 1758) and *Madrepora oculata* Linnaeus, 1758. Remotely operated vehicle (ROV) video annotation from two canyons and two coral mounds considered *Swiftia phaeton* Sampaio, Beuck & Freiwald, 2022 presence, size class and abundance as well as substrate and geomorphology of the seafloor. Coral gardens definition included abundance and size of the species. Dense and very dense mono- and multispecific coral gardens dominated by *S. phaeton* were mapped between 20°24'N and 17°54'N in 470–640 m depth. The resilience of these coral gardens off Mauritania is mainly linked to the presence of hard substrate available to settle and to the exposition of currents rich in food. Still, these ecosystems are located inside a hydrocarbon exploration area off Mauritania and where fisheries occur since the 1960s. Sedimentation plumes caused by both activities can travel and impact on settlement, development, and survival of these populations. Hence, these vulnerable “oases” should be protected.

**Keywords:** canyons, conservation, coral mounds, deep sea, NW Africa, Octocorallia, vulnerable marine ecosystem (VME)

## 1. Introduction

The contemporary era of deep-sea exploration is related to the exponential development of the technology able to map, to visualize, and to sample extreme environments. In consequence, coral ecosystems are being discovered at a higher rate than ever with remotely operated vehicles (ROVs) in unexplored deep-sea areas [1–4]. Octocorals are the most dominant subclass of corals in cold waters of deep-sea

environments, forming high-density assemblages with the dominance of a single species or multispecific coral gardens in the NE Atlantic Ocean [5–7]. As key elements of coral gardens, octocorals are ecosystem engineers that create three-dimensionality for feeding and spawning, and to serve as nursery grounds for a great range of invertebrate taxa and fish species [5, 8, 9]. Though representing a prodigious amount of biodiversity, octocorals are characterized by life traits such as long life span, slow growth, low fecundity, late maturity, and reproduction, which translate in low resilience and slow recovery from the human activities. Major anthropogenic impacts on octocorals include bottom trawling, seabed mining, and hydrocarbon drilling, but natural geological processes such as landslides can also be threats to octocorals [10–13].

Academia awareness and call for urgent action on the unregulated exploitation of cold-water coral and sponge ecosystems have led the United Nations to act [14]. The United Nations General Assembly [15] firstly created a moratorium on bottom trawling at High Seas (Resolution 61/105) [16]. Then, it called the attention of governments and regional organizations for research, mapping, and conservation ecosystems from bathyal cold waters [16, 17]. The Food and Agriculture Organization (FAO) followed, defining the management standards and criteria for the definition of Vulnerable Marine Ecosystems (VMEs) [18]. Henceforward, the Convention for the Protection of the Marine Environment of the North-East Atlantic has considered coral gardens, including octocorals as the key components of VMEs [19, 20]. Now, Europe is leader on deep-sea habitat classification schemes of the NE Atlantic Ocean, which have their southern threshold at the Strait of Gibraltar. Hence, both European Nature Information System (EUNIS) and the CoraFISH cold-water coral biotope classification scheme do not consider African NE Atlantic VMEs, which are excluded from further management actions [21, 22].

The North Atlantic Ocean is the most explored oceanic area in the world. Yet, the NW of Africa's remains understudied. The deep sea of NW Africa has been explored only since the late nineteenth century. Here exploration occurred sporadically, for example, during the *Talisman* and *Michael Sars* North Atlantic Deep-Sea expedition (1883 and 1910, respectively) and regularly by later Dutch and Spanish expeditions [23–27]. Nowadays, exploration targets also nearby Areas Beyond National Jurisdiction (ABNJ) [28].

Few scientific expeditions have specifically focused at the Mauritanian coast (*Tydemann* Madeira-Mauritania—CANCAP III in 1978, *Tyro* Mauritania II in 1988 and Spanish MAURIT surveys (2007–2010)) [24, 25, 27]. Yet, at Mauritania is located the world's largest coral mound barrier, parallel to the coast [11, 29]. While deep-sea benthonic fauna from Mauritania is mostly unknown, live scleractinians were already found sparsely distributed through coral mounds, and widespread scleractinian framework was discovered in canyons off Mauritania [30–32]. Few octocorals, including *Swiftia dubia* (Thomson, 1929) [104], were already reported to the deep sea of the region by the Maurit-Expeditions [27].

Octocoral gardens seem to be widespread throughout the NE Atlantic Ocean from the Hardangerfjord in Norway to the Mid-Atlantic Ridge (MAR) and island slopes and seamounts of the Azores; and in the Mediterranean Sea [5, 7, 33–35]. In this area, colonies of three species of the genus *Swiftia* Duchassaing and Michelotti, 1864 [91] were mostly found to be sparsely distributed and associated with hard substrates, between 20 and 2400 m depth [36, 37]. Nonetheless, *Swiftia dubia* (as *S. pallida* Madsen, 1970 [101]) is considered a dominant species of the “cold-water gorgonians on hard/mixed substrate or compact mud” category of the CoralFISH cold-water coral biotope classification scheme, indicating the presence of *Swiftia* coral gardens in the area [22].

In 2010, RV *Maria S. Merian* cruise MSM 16/3 “PHAETON”—Paleoceanographic and paleoclimatic record on the Mauritanian shelf off Mauritania was targeting the coral-mound barrier off Mauritania with an ROV and an exploratory mindset that led to the discovery of octocoral gardens throughout its slope [30]. As a result of this expedition, a new species of the genus *Swiftia* was discovered and recently submitted on a distinct publication including its distribution [38]. With this study, we aim to characterize the first African biotope of the genus *Swiftia* in the NE Atlantic Ocean, to discuss its distribution, considering biotic factors and anthropogenic influences, using it as a case study to discuss the definition of the concept “coral garden” and its implications for deep-sea conservation.

## 2. Materials and methods

### 2.1 Study area

The NW Africa, offshore Mauritania, is where a coral mound province was mapped from the Tanoûdêrt Canyon at 20°15'N until close to the Senegalese border at 16°03'N (**Figure 1**) [39]. Through at least 580 km, the coral mounds represent one of the largest known complexes positioned in two-slope parallel chains and named Mauritanian Coral Province [29, 32]. The coral mounds are on the bathymetrical range between 400 and 550 m depth and can achieve a height up to 100 m, supporting abundant associated species and live corals [30]. New species associated with this coral mound complex have been described recently: Bryozoa [40], Hydrozoa [41], Porifera [42], Crustacea [43], and Mollusca [44]. The live reef-forming corals associated with the coral mound complex of Mauritania are the abundant *Desmophyllum pertusum* (Linnaeus, 1758) [100] and *Madrepora oculata* (Linnaeus, 1758) [100] also associated with other scleractinians such as *Dendrophyllia cornigera* (Lamarck, 1816) [99], *Solenosmilia variabilis* Duncan, 1873 [92], and *Desmophyllum dianthus* (Esper, 1794) [45, 94].

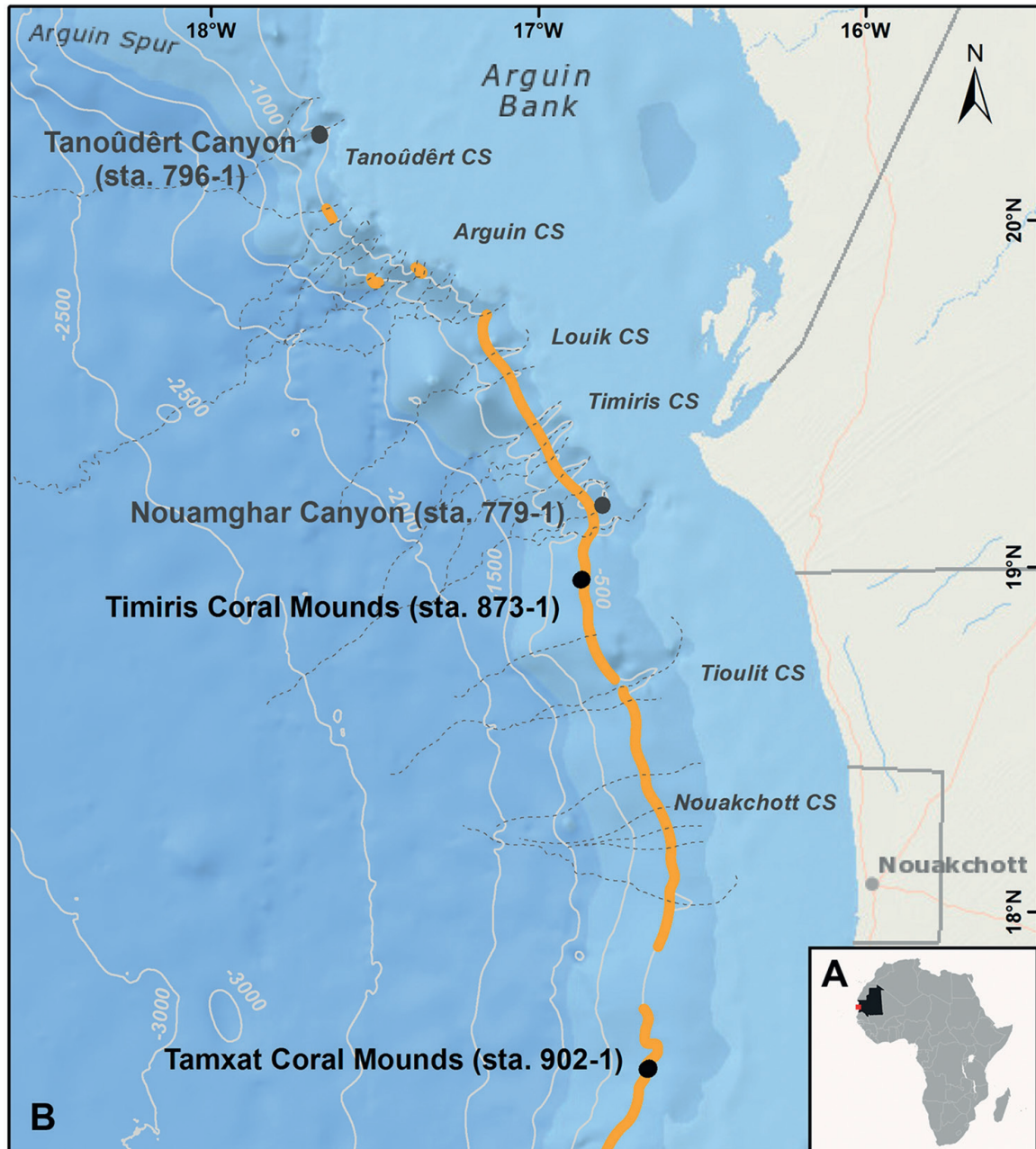
At the same time, several gullies divide the slope and merge into submarine canyon systems that may extend over several hundreds of kilometers deep off Mauritania [39]. While corals are scarce on Mauritanian mounds, canyons have abundant corals and may act as refuges that permit recolonization of the mounds [32].

Mauritania is an example of the existence of eutrophic large-scale tropical ecosystems with a major coastal upwelling system that leads to high-productivity waters [46]. There, oceanography is influenced by intermediate water masses: the North and South Atlantic Central Waters (NACW and SACW) from 150 to 600 m depth, the Antarctic Intermediate Water (AAIW) from 600 to 1000 m depth, and the North Atlantic Deep Water (NADW) from 1000 to 1600 m depth [47, 48]. Besides, the Poleward undercurrent (PUC) that runs along the slope between 100 and 300 m depth carries the SACW to the north [49]. Both the SACW and the NACW met off Cape Blanc and are forced seaward to form the Cape-Verde Frontal Zone with permanent upwelling conditions north of the oceanic front and seasonal upwelling, south of the oceanic front.

From the latitude of 5°N–20°N, there is an Oxygen Minimum Zone (OMZ) (~300–700 m depth) at the SACW lower core, above the AAIW [50]. The upwelling of nutrient-rich waters occurring in this area generates high productivity on the surface, which by export of high organic matter and its degradation leads to higher consumption of oxygen [32].

In 2010, the cruise MSM 16/3 “PHAETON”—Paleoceanographic and paleoclimatic record on the Mauritanian shelf off Mauritania onboard RV *Maria S. Merian* targeted





**Figure 1.** Location of (A) Mauritania and (B) the four ROV dives of MSM 16/3—Phaeton on the continental slope off Mauritania analyzed herein. Highlighted stations with site name and GeoB station (sta.): grey = canyons; black = coral mounds; orange = scleractinian distribution. Basemap from ESRI [85], contours from GEBCO compilation group [86], scleractinian distribution, canyon position and names from [39].

the upper canyon flanks and coral mound complexes along the Mauritanian margin, where footage of octocorals was collected (**Figure 1**) [30].

## 2.2 ROV survey

Twelve dives were performed by an ROV along an N-S stretch of about 353 km. The spatial coverage of the dives went from off Cape Blanc (20°14'N) to the south (17°08'N) and the longitude 16°39'W to 17°40'W, between 417 m and 642 m depth on the continental slope off Mauritania (**Figure 1**; **Table 1**). Vessel-based Posidonia system was used as positioning system, and *via* time code, the video footage was linked to the navigation track. Footage was collected by the ROV Sperre AS

Dive No.	Area	Station	Latitude	Longitude	Depth (m)		DO (m/l)	S (PSU)	T (°C)
					Shallower	Deeper			
1	Arguin south canyon	14.759-1	19°44'03" to 19°44'16"	-17°08'44" to -17°08'50"	488	546			
2	Nouamghar canyon	14.779-1	19°10'47" to 19°10'36"	-16°48'21" to -16°48'17"	449	619	1.54	35.21	9.95
3	Tanoûdêrt canyon	14.796-1	20°14'50" to 20°14'35"	-17°40'12" to -17°40'04"	487	642	1.63	35.20	9.95
4A	Inchiri canyon	14.871-1	19°08'21" to 19°08'22"	-16°45'53" to -16°45'49"	519	589			
4B	Inchiri canyon	14.871-2	19°08'21" to 19°08'14"	-16°45'51" to -16°45'40"	427	564			
5	Deep Timiris mound complex	14.873-1	18°57'41" to 18°57'53"	-16°52'17" to -16°52'01"	480	603	1.39	35.27	10.63
6	Shallow Timiris mound complex	14.874-1	18°58'00" to 18°57'36"	-16°51'15" to -16°51'04"	429	525			
7	Tioulit canyon (S)	14.886-1	18°39'01" to 18°38'29"	-16°43'35" to -16°43'45"	475	641			
8	Tioulit canyon (N)	14.891-1	18°39'51" to 18°39'57"	-16°43'26" to -16°43'29"	502	592			
9	Tamxat mound complex (c)	14.902-1	17°32'28" to 17°32'51"	-16°40'06" to -16°39'41"	396	588	1.20	35.27	10.80
10	Banda mound complex	14.908	17°40'13" to 17°40'12"	-16°40'50" to -16°40'17"	455	574			
11	Tamxat mound complex (S)	14.909-1	17°28'57" to 17°28'57"	-16°41'57" to -16°41'28"	423	560			
12	Tiguent mound complex	14.914	17°08'12" to 17°07'54"	-16°49'29" to -16°48'53"	409	515			

**Table 1.**

ROV dives performed during MSM 16/3—Phaeton on the shelf and continental slope off Mauritania. Details: Dive number, area where the dive took place, station number, latitude, longitude, depth range, and mean oceanographic variables at coral garden locations (mean oxygen concentration, mean salinity, and mean temperature).

Sub-fighter 7500 DC (Sven Lovén Centre for Marine Infrastructure, University of Gothenburg) on board the R/V Maria S. Merian. The ROV equipment encompassed a Sperre HD video camera (1080 I and 720 p), two standard video cameras and a still camera (Canon Powershot G9, 12 Mpixel), two Deep Sea Systems red lasers (50 mm distance), and a HYDRI-LEK-5-function hydraulic manipulator-type EH and sampler box [30]. A total video record of 47 h 83 m totalized ~3000 still images with 12-Mp resolution. During the dive, the video signal from the front-looking camera was stored in digital Quick Time MPEG-4 format (\*.mov) with a resolution of 1280x720 pixels, a bit rate of 100 MB/s, and in sequences of about 5 minutes each. Oxygen concentration (ml/l), salinity (PSU), and temperature (°C) were measured with ROV-mounted sensors. Cleaning of the ROV navigation track was done with the ArcGIS extension Adelie of IFREMER by manual cleaning and Gaussian smoothing.

### 2.3 Video annotation of *Swiftia phaeton*

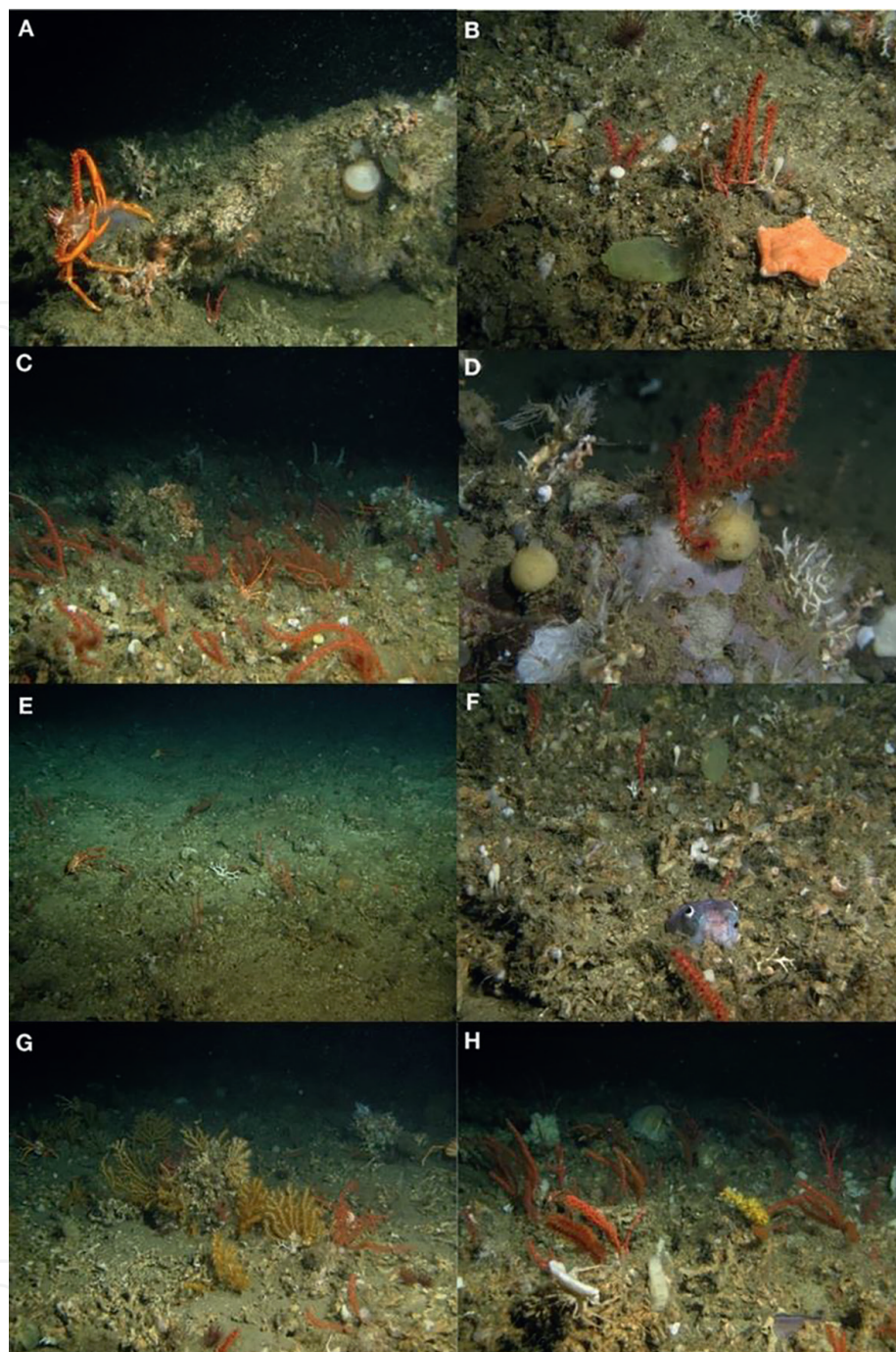
The presence of *Swiftia phaeton* Sampaio, Beuck & Freiwald 2022 [42] was scrutinized through four ROV dives, where it occurred in higher abundance, in particular two dives in canyons (Nouamghar and Tanoûdêrt canyons) and two dives in coral mound complexes (deep Timiris Mound Complex and Tamxat Mound Complex). High-resolution videos of the four dives were annotated every 10 seconds considering the following aspects: *S. phaeton* presence, size class, and relative abundance. ROV footage lacked fundamental variables to calculate size of the colonies and area of the footage. Therefore, three size classes of colonies of *S. phaeton* were considered: 1) small (<5 cm in length), 2) medium (5–15 cm in length), and 3) large (15–30 cm in length) (**Figure 2A–C**). The relative abundance of *S. phaeton* was estimated through the establishment of a length/distance ratio between individuals of the same species, divided into five classes: 1) isolated (> 15 m = >50 lengths of distance); 2) scattered (150 cm–15 m = 5–50 lengths of distance); 3) frequent (90–150 m = 3–5 lengths of distance); 4) dense (30–90 cm = 1–3 lengths of distance); and 5) very dense (<30 cm = <1 length of distance) (**Figure 2D–H**).

Coral gardens were defined and identified based on the two classes of abundance, dense and very dense, and their horizontal and vertical distributions were mapped. In order to understand which factors could be influencing the distribution of the species and the coral gardens it forms, we annotated the type of substrate and the geomorphology of the seafloor. A dataset with the complete video annotation was deposited at the World Data Center PANGAEA (<https://doi.pangaea.de/10.1594/PANGAEA.910893>). Finally, the main components of the megabenthic community and *S. phaeton* associated fauna were identified to the lowest possible taxonomic level.

Maps were based on the most accurate bathymetrical data, collected by the ROV.

Analyses of the data, done using the Excel plug-in XLStat 2019.1 (Addinsoft, Boston, USA), excluded annotations in which the ROV was not in movement to avoid repetition. Three datasets were then considered for comparison: (1) absence and presence of *S. phaeton*, (2) presence of *S. phaeton*, and (3) presence of coral gardens formed by *S. phaeton*. Multiple correspondence analyses (MCA) were performed to understand how factors were linked to the distribution of the species and to the distribution of the coral gardens this species forms. Chi-squared tests were made to verify the link between pairs of two factors: (1) substrate and size, (2) type of location and size, (3) geomorphology and size, and (4) depth and type of location, on the presence of the species and the coral gardens it forms.





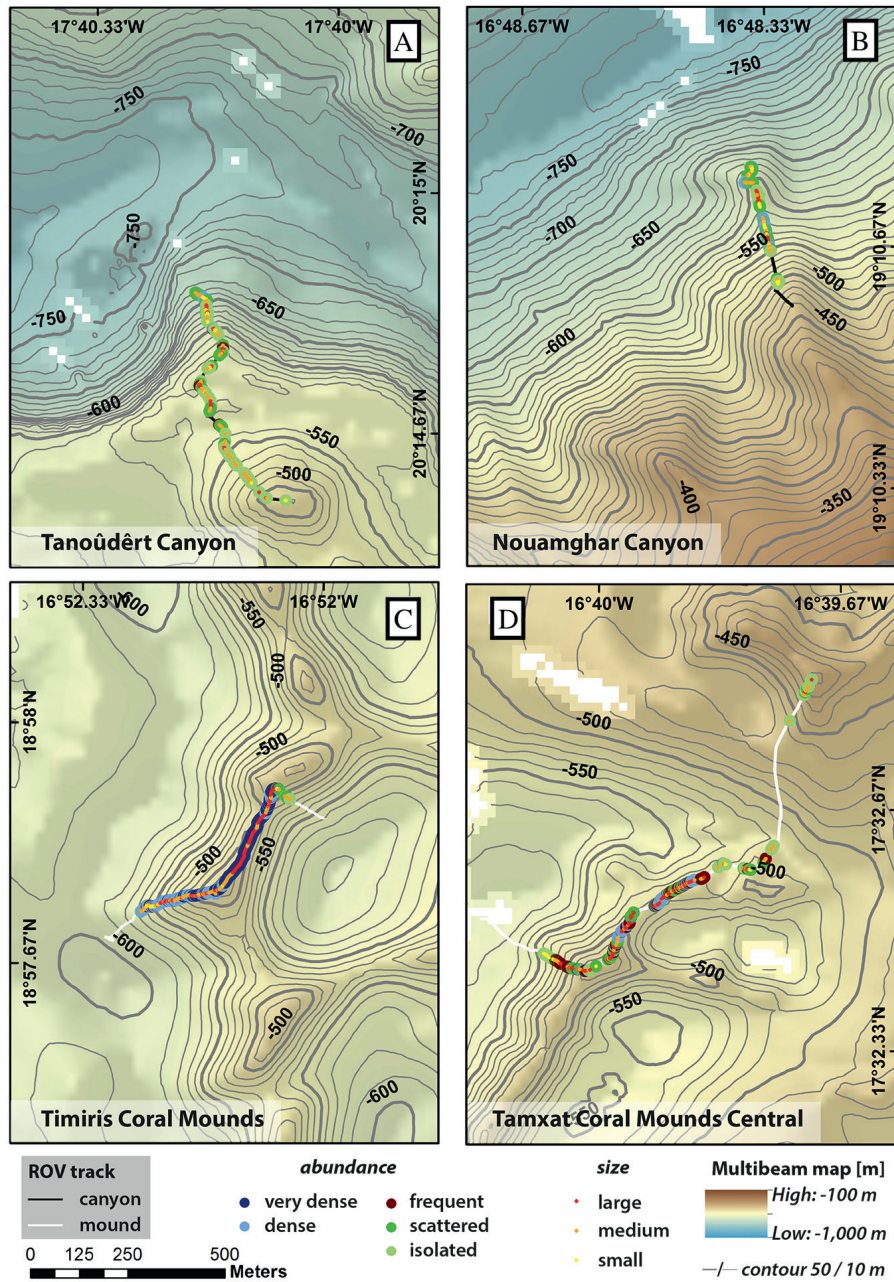
**Figure 2.** Size and relative abundance classes of *Swiftia phaeton* considered in the video annotation of four ROV dives performed during MSM 16/3—*Phaeton* off Mauritania: (A) small, (B) medium, and (C) large colonies and (D) isolated, (E) scattered, (F) frequent, (G) dense, and (H) very dense colonies and communities. Types of coral gardens formed by *Swiftia phaeton* are also represented in (C) monospecific coral garden and (G) multispecific coral garden with undescribed *Plexauridae* species.

### 3. Results

#### 3.1 Distribution of *Swiftia phaeton*

Detailed maps of *S. phaeton* distribution were made based on video annotation of Nouamghar and Tanoûdêrt Canyons and deep Timiris and Tamxat Mound Complexes (Figure 3; Table 1). The species is widespread at Nouamghar Canyon and deep





**Figure 3.** Distribution of *Swiftia phaeton* and the coral gardens it forms along four locations off Mauritania where it is more common. Video annotation of ROV dive tracks has considered the species size and relative abundance. Dense and very dense abundances characterize coral gardens. Bathymetry from [51].

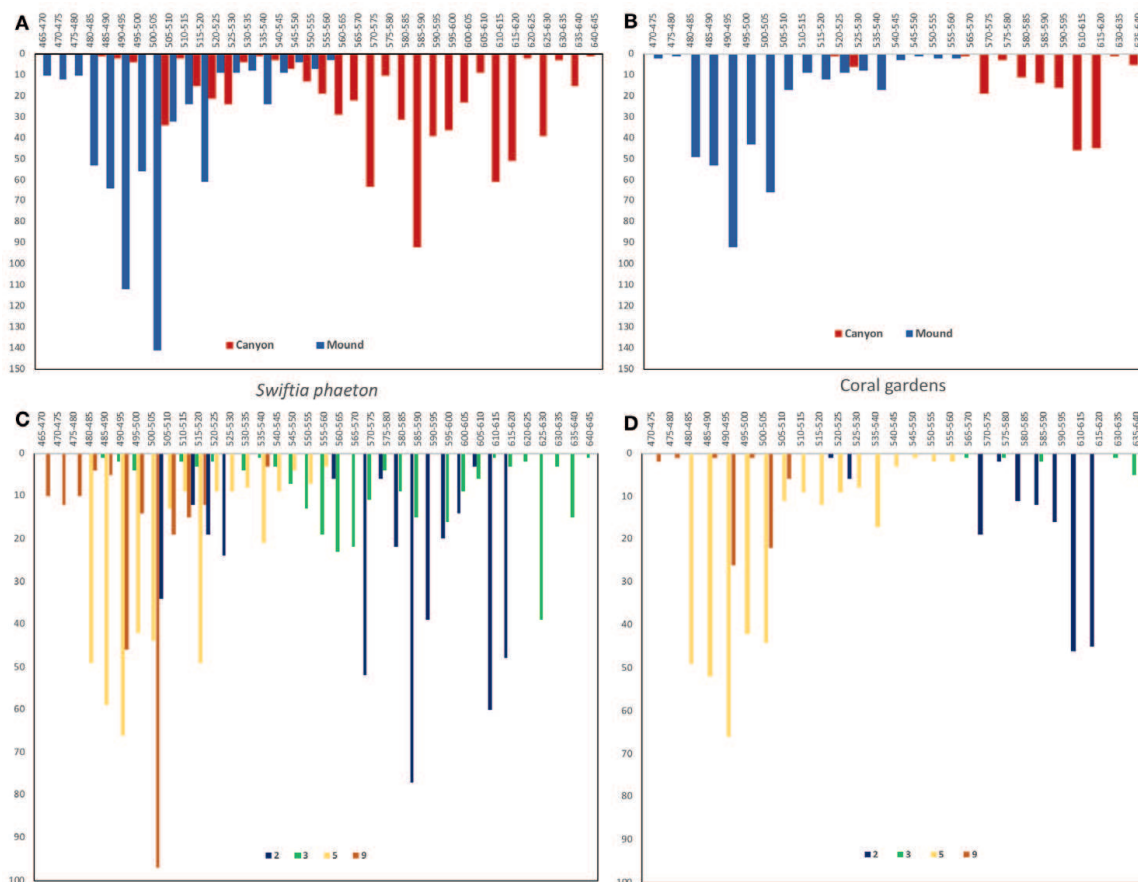
Timiris Mound Complex, yet it is absent at specific depths. At Tanoûdêrt Canyon, *S. phaeton* is also widespread but mainly sparsely distributed. Its deepest record is localized at 550 m depth, on the deeper coral mound of the central Tamxat Mound Complex.

Presence of *S. phaeton* at Mauritania varies from isolated colonies to very dense coral gardens, dominating the monospecific biotope or in association with other Plexauridae species forming multispecific biotopes (Figure 3). Herein, we report the first coral gardens dominated by a species of the genus *Swiftia* on the NE Atlantic Ocean (Figure 3). The extensive habitats dominated by *S. phaeton* were recorded between 20°24'N and 17°54'N in 470–640 m depth, co-occurring with the

framework-forming scleractinians *Desmophyllum pertusum* (Linnaeus, 1758) [100] and *Madrepora oculata* Linnaeus, 1758 [100] (**Figure 3**). Coral gardens of *S. phaeton* are predominant at the Nouamghar Canyon and at the Timiris Mound Complex, though also occurring at the Tanoûdêrt Canyon and the Tamxat Mound Complex (**Figure 3**). These coral gardens are mostly formed by dense aggregations of branched, large (15–30 cm in length), or medium (5–15 cm in length) colonies of *S. phaeton* and some very dense assemblages (**Figures 2B, C, H and 3**).

Dense coral gardens were observed scattered at the flank of Nouamghar Canyon: from 520 to 530 m and from 610 to 620 m depth between 19°10'47"N and 19°10'37"N and between 16°48'21"W and 16°48'19"W, respectively (**Figures 3 and 4**). There, the *S. phaeton* garden has the largest extension of ~523 m along the ROV track, and it is located between 570 and 595 m depth with medium-sized colonies and from 570 to 580 m depth with larger colonies (**Figures 3 and 4**). The dense coral gardens of the Tanoûdêrt Canyon were found between 20°14'47"N and 20°14'51"N and between 17°40'10"W and 17°40'11"W. There, the coral garden with the longest lateral extension along the ROV track is formed by larger colonies between 565 and 590 m depth but the canyon flank also has two coral gardens formed by small (5 cm in height) colonies between 630 and 640 m depth (**Figures 3 and 4**).

The most extended coral garden of all the study sites was recorded at the eastern mound top and the ridge, between two mounds of the deep Timiris Mound Complex, from 18°57'44"N to 18°57'54"N and from 16°52'15"W to 16°52'04"W and between



**Figure 4.** Bathymetric distribution of *Swiftia phaeton* and the coral gardens it forms off Mauritania, at distinct types of locations (A, B) and at different locations (ROV dives) (C, D).

480 and 560 m depth (**Figures 3 and 4**). Here, very dense aggregations of *S. phaeton* were recorded dominated by large colonies. Besides, there are two coral mounds with a widespread coral garden starting at 560 m depth on the western flank of one and ending on the second mound top. At the central Tamxat Mound Complex, dense coral gardens with large colonies were located sparse at the western flank of the deeper coral mound and at the ridge between coral mounds, from 17°32'27"N to 17°32'35"N and from 16°40'03"W to 16°39'48"W between 470 and 510 m depth (**Figures 3 and 4**).

The bathymetric distribution of the coral gardens formed by *S. phaeton* is mostly focused on the range of 490–495 m depth. Yet, coral gardens are also frequent between 480 and 505 m depth and between 610 and 620 m depth (**Figure 4**). These ecosystems are significantly deeper when found in canyons (520–640 m depth), when compared with mound locations (470–510 m depth) (chi-square and Fisher's exact test <0.0001) (**Figure 4A, B**).

### 3.2 Factors influencing *Swiftia phaeton*'s distribution

The distributions of the species and the coral gardens it forms are influenced by several factors, such as substrate and geomorphology. At Mauritania, distinct variables of each factor seem to be related to specific locations, as revealed by the results of two MCAs on the presence of the species and of the coral gardens (**Figure 5**).

The Tanoûdêrt Canyon has isolated and scattered colonies that grow on framework located at the canyon shoulder/plateau (**Figures 3 and 5A**). Its coral gardens have dense assemblages living on framework (**Figures 3 and 5B**). At Nouamghar Canyon, the species is small or medium in size, it prefers rocky substrate, and it lives on the coral mound or at the canyon flank, while the coral gardens only exist at the canyon flank (**Figures 3 and 5**). Very dense communities, which settle on coral rubble at the mound flank or at the mound top, characterize the Timiris Mound Complex, whereas large colonies inhabit the ridge, either in frequent aggregations or forming coral gardens at the Tamxat Mound Complex (**Figure 5**).

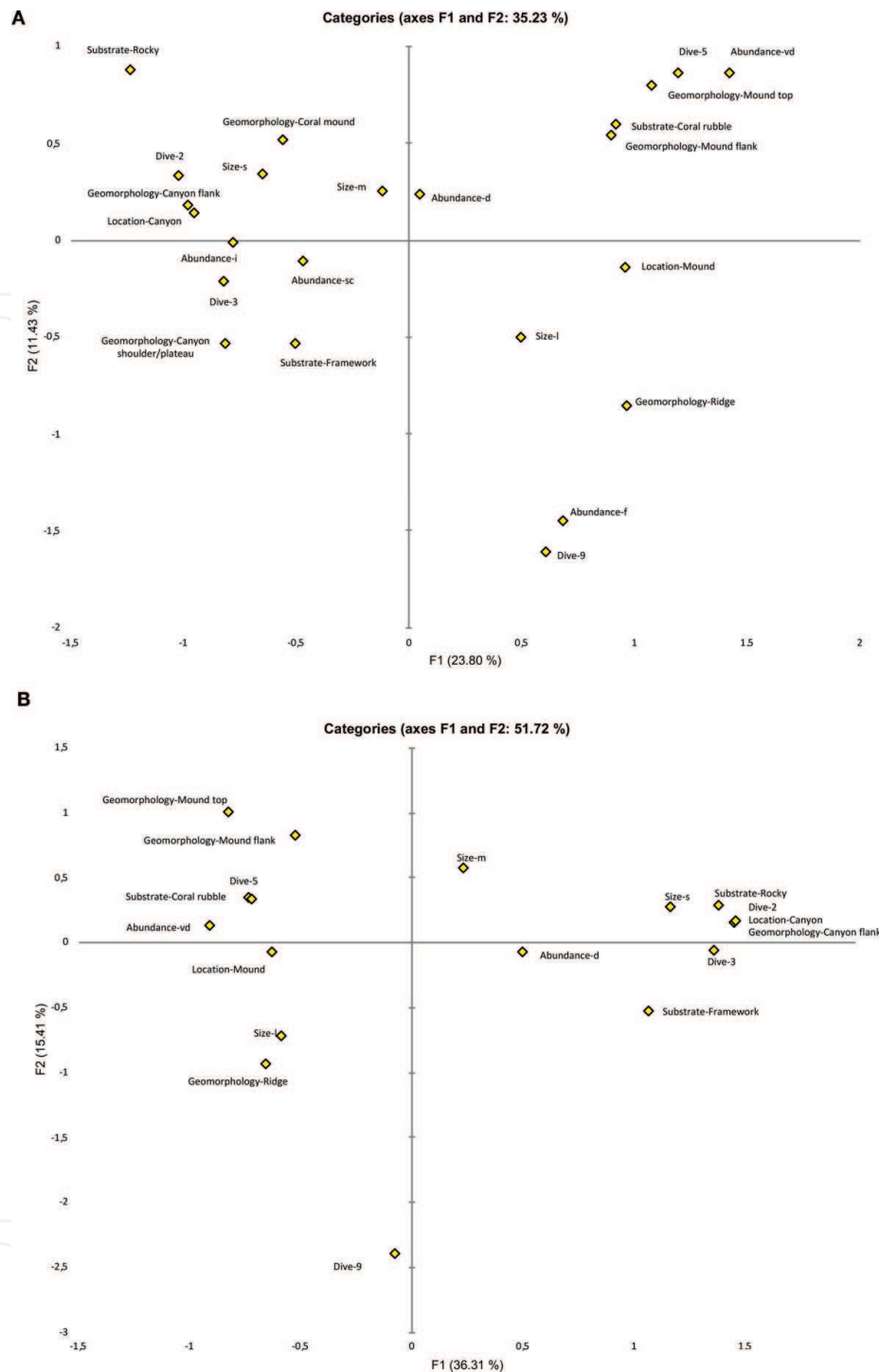
#### 3.2.1 Type of location

The species is present in both canyons and on coral mounds, but the coral gardens are mostly found on mounds. Thus, the type of location was significantly related to the size of the species, even when it forms coral gardens (chi-square and Fisher's exact test <0.0001). While larger colonies predominantly inhabit coral mounds, medium or small ones dominate in canyons (**Figure 6A**). Though, when forming coral gardens, a lower proportion of smaller colonies exist on canyons. Likewise, a higher proportion of larger and medium colonies exist in coral mounds (**Figure 6B**).

#### 3.2.2 Substrate

Higher abundance of *S. phaeton* was exclusively found when hard substrate (coral framework, coral rubble, and rocky substrate) was present, while the absence of the species dominated with soft sediment. Type of substrate was found to be significantly related to the size of the colonies, even when forming coral gardens (chi-square and Fisher's exact test <0.0001). While the colonies settling on coral rubble were medium or large, when forming a coral garden, the colonies were mostly large sized (**Figure 6C and D**). On the other hand, when the colonies live



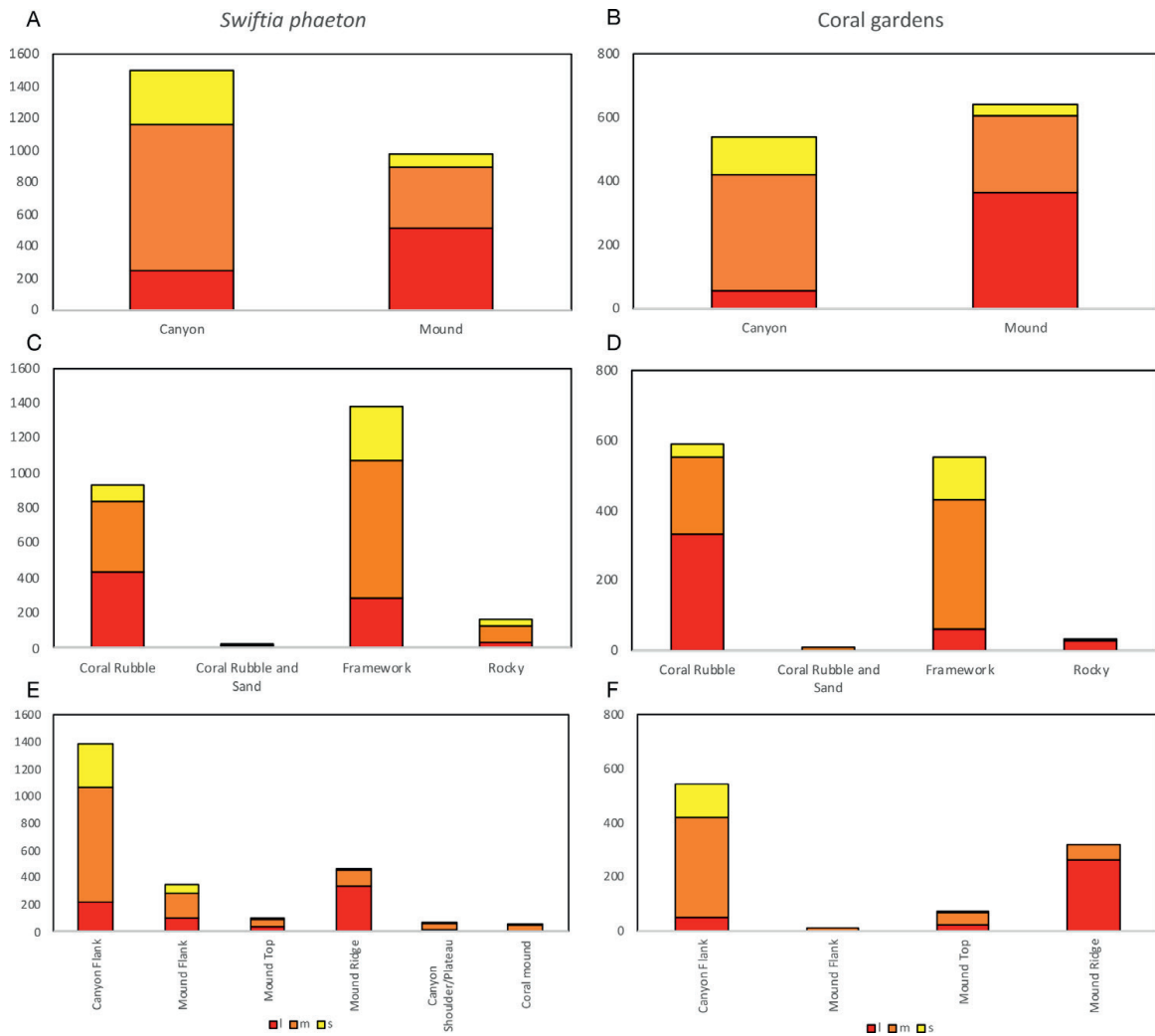


**Figure 5.** Multiple correspondence analysis (MCA) on the distribution of *Swiftia phaeton* (A) and on the distribution of coral gardens formed by *Swiftia phaeton* off Mauritania (B).

on scleractinian framework, they have medium size, especially where coral gardens exist. Rocky substrate supports medium colonies of the species or large colonies, when it forms coral gardens (Figure 6C and D).

### 3.2.3 Geomorphology

Annotations revealed that *S. phaeton* prevails at canyon flanks and ridges, while it is absent on a slope (Tamxat coral mounds), a coral mound, and at mound bases.



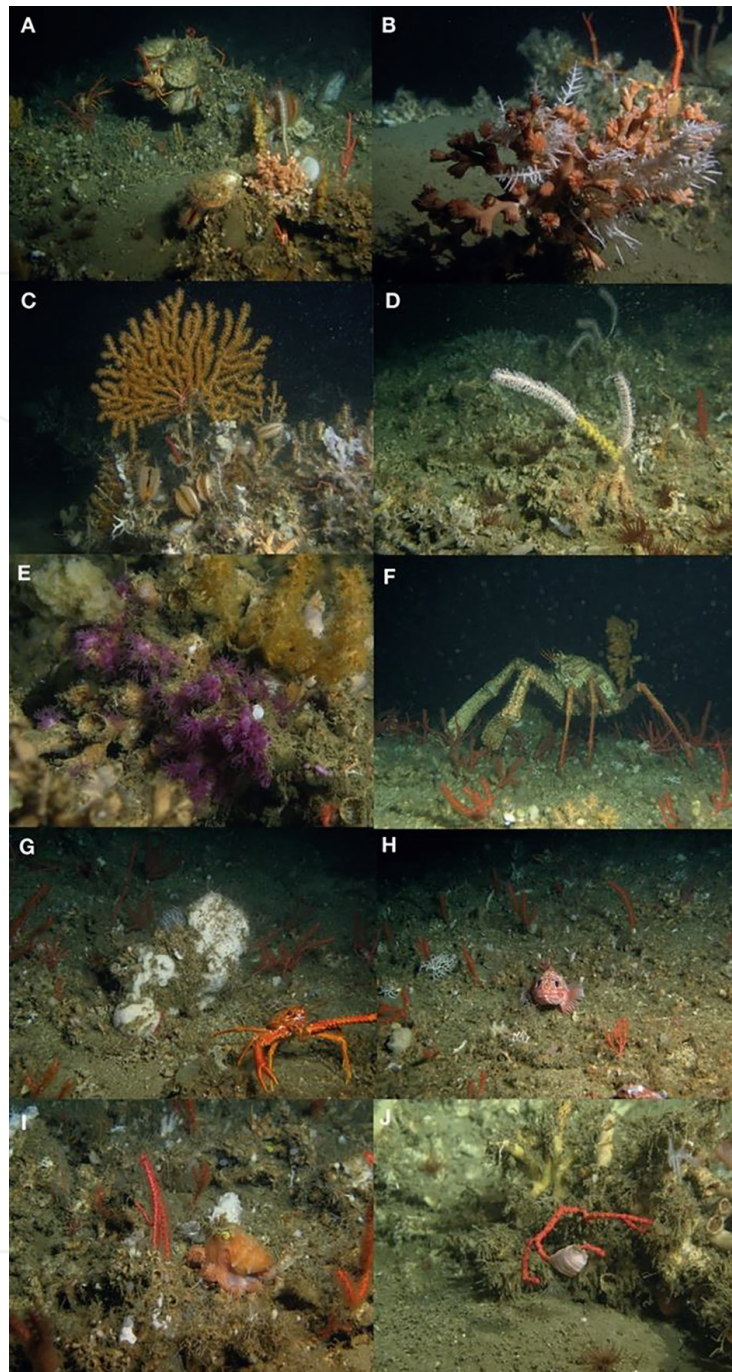
**Figure 6.** Distribution of the size of colonies of *Swiftia phaeton* (l: large, m: medium, s: small), in general and when forming coral gardens at four selected locations off Mauritania according to the influence of distinct factors: type of location (A, B), type of substrate (C, D), and geomorphology (E, F).

Geomorphological features of the deep sea off Mauritania were discovered to be significantly related to the size of the colonies of *S. phaeton*, and with the size of the colonies when this species forms coral gardens (chi-square and Fisher's exact test  $<0.0001$ ).

Larger colonies of *S. phaeton* were found associated with ridges between coral mounds, while smaller colonies were mainly found at flanks of canyons and mounds (**Figure 6E**). The same occurred with larger colonies forming coral gardens, but the smaller colonies of coral gardens were found at flanks of canyons. Nonetheless, most colonies forming coral gardens, when associated with canyon flanks, had medium size (**Figure 6F**).

### 3.3 Fauna associated with *Swiftia phaeton*'s coral gardens

Monospecific coral gardens formed by *Swiftia phaeton* are able to agglomerate diverse associated fauna. The fauna associated with *S. phaeton*'s coral gardens is mainly constituted by crabs such as *Eumunida bella* de Saint-Laurent and Macpherson, 1990 [88] (**Figure 7F**) and *Paromola cuvieri* (Risso, 1816) [102] but also



**Figure 7.** *Swiftia phaeton* coral gardens community and associated fauna: (A) *Swiftia phaeton* and *Thesea talismani* Grasshoff, 1986 [95] on *Desmophyllum pertusum* (Linnaeus, 1758) [100] and *Acesta sp. frameworks*, (B) *Desmophyllum pertusum* with associated *Cladorhiza corallophila* Göcke, Hestetun, Uhlir, Freiwald, Beuck & Janussen, 2016 [42], (C) undescribed *Plexauridae*, (D) *Thesea talismani* with associated zoantharian, (E) cf. *Clavularia borealis* Koren and Danielssen, 1883 [98] on coral rubble, (F) *Paromola cuvieri* (Risso, 1816) [102] with *Plexauridae*, (G) “*Lithistidae*”, (H) *Helicolenus dactylopterus* (Delaroche, 1809) [89], (I) *Pteroctopus tetracirrhus* (Delle Chiaje, 1830) [90], and (J) *S. phaeton* associated eggcase.

by a diverse variety of animals such as sponges, fish, octopus, mollusks, and grazing echinoderms such as seastars (Figures 2 and 7). Grazing behavior of mollusks was also observed in some colonies of this species (see also [52]).

When *S. phaeton*'s coral gardens are part of multispecific biotopes, the upper bathyal of Mauritania's megabenthic community has a patchy distribution of other species of octocorals from the families *Plexauridae* Gray, 1859 [96], *Anthoethelidae*



Broch, 1916 [87], and Acanthogorgiidae Gray, 1859 [96], but also from the suborder Stolonifera Thomson and Simpson, 1909 [103] (**Figure 7**).

#### 4. Discussion

*Swiftia phaeton* Sampaio, Beuck & Freiwald, 2022 [42] is the first species of its genus to be recorded as a fundamental habitat builder of coral gardens. Coral gardens formed by *S. phaeton* were discovered predominantly in mounds of the Mauritanian slope. The most extensive coral garden was found at the deep Timiris Mound Complex, the preferable location of this species off Mauritania, where it achieves a larger size at the ridge, forming the unique very dense assemblages known for the region (**Figures 3 and 6**). Timiris Mound Complex is part of the world longest coral mound barrier, located parallel to the slope at ~500 m depth. Small abundant outcrops of the barrier, which used to be a deep-water coral reef, are present at Timiris. This barrier is providing potential settlement ground for the proliferation of this species at the upper bathyal [11, 29]. Local favorable factors to the growth of this octocoral may promote the monospecific coral garden predominance, despite the dormant state of the coral mounds [32]. Coral mounds have higher framework composed of *Desmophyllum pertusum* (Linnaeus, 1758) [100], increasing the surface for settling of *S. phaeton* larvae, and its access to food in the water column. Suspension feeders on mounds are favored by their location on the limit of water masses, where their food accumulates after transport by tidal currents and downwelling internal waves [53, 54]. High quantity of food at coral mound depths might compensate the presence of an oxygen minimum zone (OMZ) at the same depth. Moreover, the thermocline and the halocline located at ~450 m depth [11] are the upper limit to coral gardens of *S. phaeton* found at coral mounds.

Other extensive coral gardens of *S. phaeton* were discovered at the Nouamghar Canyon, where advantages for the settlement and development of corals, such as hard substrate and current-exposed conditions, are present (**Figures 3 and 4**) [30]. Deep submarine canyons are affected by dense shelf water cascading, which transport organic matter and oxygen-rich waters from the surface to deeper waters, supplying deep-sea filter and suspension feeders with higher quantities of nutritive and fresh plankton, favoring their development [32, 55]. Mauritanian canyons harbor scleractinians at least since the Late Holocene and might be acting as guardians of colonies that will be the source of larvae for the recolonization of neighbor coral mounds and also refuge from unfavorable conditions at the Mauritanian slope.

Geomorphological distribution patterns found herein might be dependent on location with canyon and canyon flank meaning instead Nouamghar, and coral mound and ridge between mounds meaning Timiris (**Figure 4D**). Despite the diverse geomorphology found at the Mauritanian slope, small and medium *S. phaeton* colonies occur preferably at canyon flanks and larger colonies on ridges between coral mounds (**Figure 6**). Exposed flanks and ridges are topographic elevations, essential for settlement of corals, with high food supply by local accelerated hydrography [56, 57]. Still, distinct sizes of *S. phaeton* might be related to 1) long-lasting lack of new recruits of *S. phaeton* on coral mounds or 2) local coral communities and their competition with *S. phaeton*. No data on the growth rate of *Swiftia* species are available, but plexaurid gorgonians have slow growth rates [58], meaning that larger colonies of *S. phaeton* present on mounds can be much older than the younger small/medium colonies on canyons. Probably, for a long time there has been no recruitment or settlement of *S. phaeton* on mounds. On the other side, Nouamghar Canyon has abundant live colonies

of reef-forming scleractinians [30] and other predominant undescribed Plexauridae species, which form multispecific coral gardens with *S. phaeton*. However, the Timiris mounds, by being related to a younger aggradation period of coral mound [32], have less scleractinian occurrence. Therefore, there might be less competition with *S. phaeton*, less sediment and consequent impact on the gorgonian survival. Both factors could contribute to the presence of larger colonies at Timiris Mound Complex. Other factors might also be influencing distinct distribution of sizes of this species such as unfavorable conditions for larvae, grazing pressure, and spawning events after fishing impact or even environmental changes.

Coral gardens of *S. phaeton* are also associated with framework formed by *Desmophyllum pertusum* (Linnaeus, 1758) [100] and *Madrepora oculata* Linnaeus, 1758 [100]. Considering that most of the video annotations were made on hard substrate, the results found are potentially biasing (**Figure 6**). Anyway, hard substrate (coral framework, coral rubble, and rocky substrate) is essential for gorgonians settlement and for development of coral gardens, as it is for anemones and sponges [11, 59]. The high species richness of the tropics is also associated with hard substrate on coral reefs [60]. However, *S. phaeton* does not seem to be able to grow to larger sizes if framework is its substrate (**Figure 6**). This might reveal 1) lack of stability of high framework, an irregularly shaped substrate, which is needed for growth 2) competition in dominance between coral reef and coral garden-forming species. If *D. pertusum* forms live dense assemblages, *S. phaeton* is not able to settle its larvae, grow to larger sizes, and has the same access to food. Yet, if coral rubble and rock are the substrate, they are the base for settlement of the gorgonian larvae and are stable for the development of its holdfast and the growth of larger colonies.

In summary, coral gardens of *S. phaeton* are preferably formed on mound ridges and canyon flanks as well as on coral rubble and framework (**Figure 6**). Large colonies forming coral gardens were found mostly on ridges and coral rubble, which are favorable and undisturbed locations with food availability during their life time. Future expeditions looking for coral gardens can now consider these types of locations and geomorphologies as targets of exploration.

During MSM 16/3—Phaeton, the oceanographic data collected were not sufficient to analyze its influence on the distribution of coral gardens formed by *S. phaeton* at a local level [30]. Nevertheless, oceanography explains biogeographical patterns on the distribution of corals. Scleractinians in the NE Atlantic Ocean are influenced by the Equatorial Countercurrent [61], and the structure of primnoid octocorals of Antarctica is related to a natural “soft” biogeographic barrier, the Antarctic Circumpolar Current [62]. In Mauritania, the upper bathyal (400–600 m depth) is influenced by the water masses NACW, north of the Cape Verde Frontal Zone, and SACW, south of the Cape Verde Frontal Zone [48]. Below 300 m depth is the lower SACW characterized by more nutrients and less oxygen, forming the OMZ until 700 m depth [32, 49]. However, at 450 m depth, saline water sits on top of the AAIW forming a layer with a thermocline and a halocline that limits the coral gardens of *S. phaeton* on coral mounds of Mauritania. There, these assemblages thrive at lower temperatures and salinities and are found shallower (480–560 m depth) than in canyons (520–640 m depth). In conjunction with a pronounced seasonal nepheloid layer, both thermocline and halocline promote the development of suspension feeders with high quantity of particulate organic matter [32, 49, 63].

Mauritania is a major upwelling region with a post-glacial oceanography less appropriate for reef-forming scleractinian development, in comparison with the oceanography during glacial times, or at the current northern latitudes [29, 64].

Hydroclimatic condition complexity and paleogeography off Mauritania explain the absence of more diversity and abundance of corals in the deep sea [60], since corals need not only high productivity at the ocean surface, but also lower temperature and higher oxygen concentration for a persistent growth [54]. Climate seems to be related to the distribution of Plexauridae species in the NE Atlantic Ocean, as indicated by distinct species found at temperate (most Macaronesian archipelagos) and tropical waters (Cape Verde) [36]. This is a zoogeographical pattern revealed by several other marine taxa of this area [65]. At the subtropical Mauritania, the Plexauridae are the dominant family of octocorals, but it has distinct diversity than the deep sea of the central NE Atlantic and the Cape Verde Archipelago [36, 37]. Moreover, a non-exhaustive taxonomic assessment of few samples of Plexauridae from Cape Verde and Mauritania revealed different fauna between regions (Sampaio personal observation). The North West African Upwelling acts as a biogeographic barrier for species dispersal between the mainland of Africa and Cape Verde [65]. Also, below the Cape Verde Frontal Zone (CVFZ), where the SACW is located [32], faunistic changes occur and the coral gardens of *S. phaeton* stand in Mauritania at the northern alternance region of the tropical zone, which is characterized by strong seasonal contrasts [60]. In any case, before drawing a portrayal of biogeographical patterns for these regions, higher sampling at unexplored areas and taxonomic revisions are of crucial need to understand the Octocorallia of the deep NW African region and help to predict spatial range changes of deep-sea species under future climate change scenarios.

#### 4.1 Natural and anthropogenic impacts on coral gardens

The oldest collection of *S. phaeton* off Mauritania dates back to 1988. After filming *S. phaeton* abundance during *Phaeton* expedition in 2010, specimens deposited at Naturalis, caught during Tyro Mauritania II expedition, were discovered during a visit to the museum [36]. The lack of knowledge on past abundance of this species hampers conclusions on the real natural and anthropogenic impacts on the ecosystems it forms. Hence, we might still infer few impacts affecting these coral gardens. Despite depleted oxygen supply, which can prompt local extinction of benthic fauna, *S. phaeton* is thriving in Mauritania. Yet, ongoing climate change can threaten this ecosystem with further increased oceanic deoxygenation [66]. Sedimentation caused by natural landslides and mechanic anthropogenic events, as the local oil exploration and demersal fisheries, can interfere with the survival of corals, which are suspension feeders. Eolian sediments are deposited off Mauritania by numerous landslides associated with the canyons, especially offshore the Sahara Desert [32, 67]. Known effects caused by sedimentation and oil exposure on corals are the death of the colonies, the shift of its feeding behavior, growth and reproduction, or the disruption on the movement of the polyps and on the calcification of the coral [68, 69]. Sedimentation plumes formed by hydrocarbons-related explorations and bottom trawling are not stagnant and may travel downward, thus affecting deeper communities [70]. *Swiftia exserta* (Ellis & Solander, 1786) [93] forms coral gardens at the Caribbean Sea [71], and it was impacted by the Deepwater Horizon oil spill of the Gulf of Mexico [72–74]. Almost half of the large colonies were injured: broken, with bare branches, overgrowth by hydroids, or covered by sediments below the oil spill [76–78]. Feeding on oil-derived marine snow that sank to the bottom with the pelagic food was also disruptive of the octocoral survival [75]. Gulf of Mexico and Mauritania have hydrocarbon fields [11, 76]. Off Mauritania, the most extensive area of coral gardens of *S. phaeton* (Nouamghar canyon and Timiris Mound Complex) is located on the Block 6 at the area designed for hydrocarbon exploration [11]. The



Chinguetti oil field is situated further to the south (Block 4) and deeper at 800 m depth; however, sediment plumes of the extraction might have traveled toward the coral gardens. Recurrent trawling might increase sedimentation over coral mounds too, reducing settlement, development, and survival of sessile epifauna [29]. When recurrent, trawling reduces the time for continuous growth of colonies and hinders recolonization by new colonies at trawled areas [77]. Longline and trawling fisheries of fish and crustaceans occur in the area since the 1960s, exploring the upper bathyal, where *S. phaeton* lives. Moreover, trawling occurs near the Chinguetti oil field around 600 m depth. On fisheries targeting the Pink spiny lobster *Palinurus mauritanicus* Gruvel, 1911 [97], by-catch of scleractinians was recorded [11]. Yet, fishermen avoid reefs to protect their fishing gears, and while fisheries might have modified the seabed in the past, track marks are far from mound structures [29].

#### 4.2 Definition of octocoral garden for conservation

The current definition of coral garden used by the Oslo-Paris Convention (OSPAR) in alignment with the 61/105 [16] aiming to protect deep-sea VMEs from anthropogenic pressures includes all the coral taxa, except the reef-building scleractinians [78]. Nevertheless, the term “coral garden” was initially applied specifically to dense assemblages of octocorals in cold waters [9]. Increasing the number of taxa within this definition led to a higher complexity of assemblages, biotopes, and substrates caught within the coral garden concept. When the density of these assemblages is not considered to establish boundaries on their distribution, it is difficult to clearly isolate the idea of what is a coral garden and apply conservation measures [79]. A density criterion of  $>0.1$  colonies  $m^{-2}$  across an area of at least  $25 m^2$  was added to the coral garden definition: areas where the coral garden-forming species forms dense aggregations [19, 79, 80]. ICES [81] had previously tried to include the density of corals to remove arbitrary decisions on this term, but it was difficult to quantify densities of corals *in situ*. This is commonly the case with deep-sea exploratory cruises, not aiming to quantify assemblages, but to understand what taxonomic groups inhabit the area. On the other hand, it is hard to calculate the area observed, without considering several measurements while annotating ROV images [82]. In the absence of a calculated area on the ROV images from Mauritania, we used a proxy of the species density: classes of relative abundance related to its size. Coral gardens were then defined when dense and very dense assemblages were annotated. Herein, we added the size to the density on the concept of coral garden, because the size of a species is important to define the scale of the ecosystem it forms. If a gorgonian has a smaller maximum size, as it is the case of *S. phaeton*, it will consequently form coral gardens on a smaller scale and area, than a species with a higher maximum size. Therefore, instead of stipulating  $25 m^2$  for all the species, the definition of coral garden should indeed consider areas, which take into account the maximum size a species can achieve. The long-lasting discussion on the definition of terrestrial forests should be applied to biotope concepts in marine sciences. Current concepts of forest vary, but already include the size of the species and the size of the forests it forms [83, 84].

#### 5. Conclusions

The ongoing effort to define marine-protected areas (MPAs) off Mauritania should now consider the locations where *Swiftia phaeton* forms coral gardens in

higher density and longer areas. The Timiris Mound Complex, where the species thrives, is particularly important, and it is located nearby an oil exploration field. Therefore, Timiris should be protected from hydrocarbon exploration and trawling fisheries. Future cruises and studies should visit it along with other locations where the species is less abundant, in order to collect local oceanographic data and infer the influence of currents and climate, on the distribution of this species and its coral gardens.

Coral gardens of *S. phaeton* harbor several kinds of taxa that may depend on this species to feed, hide, or reproduce. This flag species of gorgonian, commonly associated with *D. pertusum*, should be a priority for conservation in Mauritania, where it forms the most abundant assemblages of the genus *Swiftia*, unique at the NE Atlantic and Mediterranean scale.

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