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Article

First Macro-Colonizers and Survivors Around Tagoro Submarine Volcano, Canary Islands, Spain

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Abstract: Tagoro, the youngest submarine volcano of the Canary Islands, erupted in 2011 South of El Hierro Island. Pre-existing sea floor and inhabiting biological communities were buried by the newly erupted material, promoting the appearance of new habitats. The present study pursues to describe the first metazoans colonizing different new habitats formed during the eruption and to create precedent on this field. Through dredge and remote operated vehicle samplings, five main habitat types have been detected based on the substrate type and burial status after the eruption. Inside the Tagoro volcanic complex (TVC), two new habitats are located in and around the summit and main craters—hydrothermal vents with bacterial mats and sulfurous-like fields mainly colonized by small hydrozoan colonies. Two other habitats are located downslope the TVC; new hard substrate and new mixed substrate, holding the highest biodiversity of the TVC, especially at the mixed bottoms with annelids (*Chloeia* cf. *venusta*), arthropods (*Monodaeus couchii* and *Alpheus* sp.), cnidarians (*Sertularella* cf. *tenella*), and molluscs (*Neopycnodonte cochlear*) as the first colonizers. An impact evaluation was done comparing the communities of those habitats with the complex and well-established community described at the stable hard substrate outside the TVC, which is constituted of highly abundant hydrozoans (*Aglaophenia* sp.), antipatharians (*Stichopates setacea* and *Antipathes furcata*), and colonizing epibionts (e.g., *Neopycnodonte cochlear*). Three years after the eruption, species numbers at Tagoro were still low compared to those occurring at similar depths outside the TVC. The first dominant species at the TVC included a large proportion of common suspension feeders of the circalittoral and bathyal hard bottoms of the area, which could have exploited the uncolonized hard bottoms and the post eruptive fertilization of water masses.

Keywords: hydrothermal vents; submarine volcano; first colonizers; benthos; Tagoro; El Hierro; Canary Islands

1. Introduction

The majority of Earth's volcanic activity occurs beneath the sea, and oceanic intraplate volcanism represents an important fraction of this phenomenon [1]. There are thousands of seamounts throughout the deep ocean that are by majority extinct volcanoes [2]. The Canary Islands are a volcanic alignment of eight islands, composing an East–West trending archipelago located to the Northwest of the African continent [3,4] (Figure 1A). In October 2011, a submarine eruption took place south of El Hierro Island on the border of the Natural Reserve "Punta de la Restinga—Mar de las Calmas" (27°37′07″ N–017°59′28″ W, Figure 1B). The eruption covered a pre-existing underwater gully with basaltic lava (Figure 1C), creating the youngest shallowest submarine volcano of the Canary Archipelago, Tagoro (Figure 1D). This led to numerous multi-faceted novel studies—geological, physical, chemical, and biological [5–9]—that are producing exciting results to date. Significant anomalies in temperature (>+18.8 °C), pH_T (ΔpH up to -2.9 units), and concentration of the reduced species were observed South of El Hierro Island during the first weeks, resulting in a decrease in the oxidation potential (ORP, from 0.2 V to -0.03 V) as well as an enrichment of Fe(II) (>50 µmol kg^{-1}) and inorganic nutrients. As a consequence, the eruption generated an episode of natural ocean acidification and fertilization [10]. Unlike the detailed study on physical–chemical parameters of the water column after the eruptive process [6,10–12], no study has yet focused on the survival and colonization by marine benthic and demersal species at the newly formed submarine volcano.

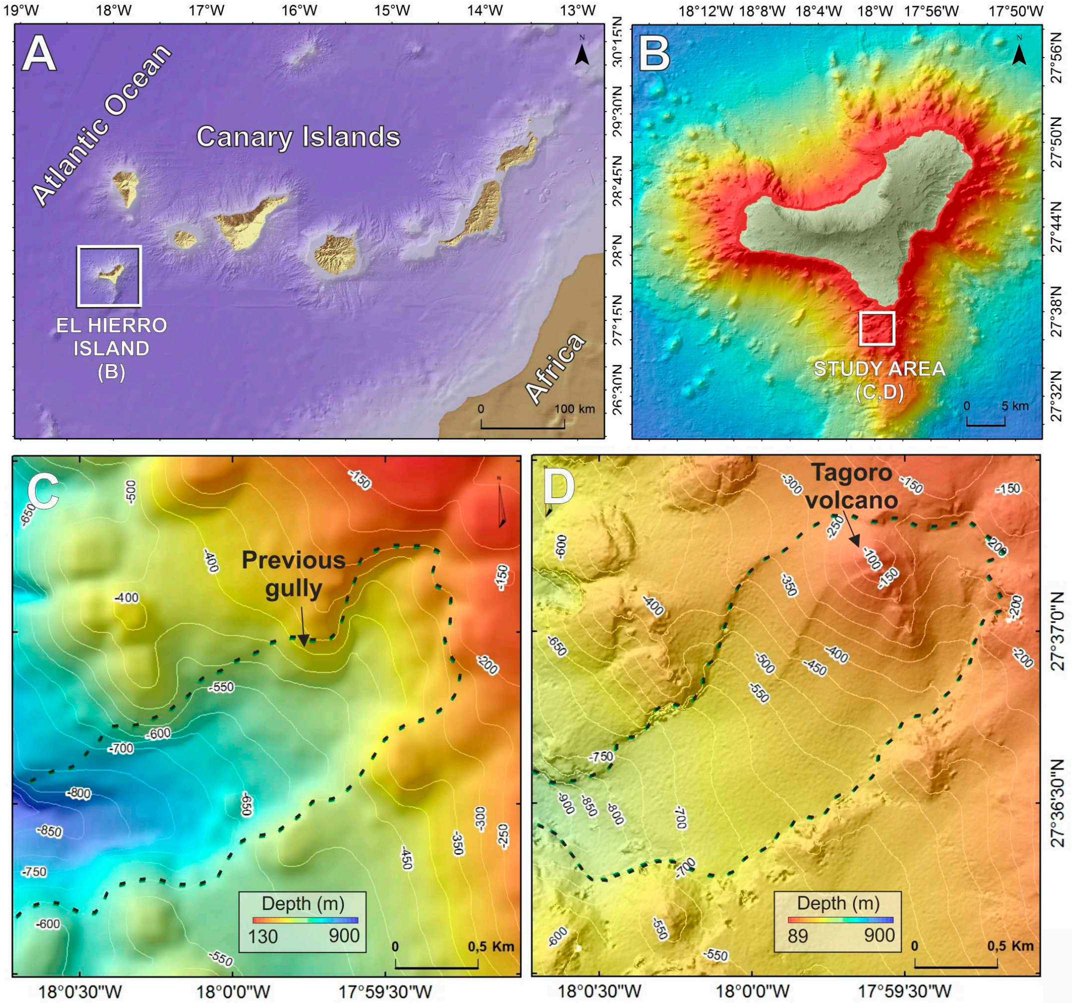

Figure 1. Overview bathymetric maps of the study area. (**A**) Geographical location of the El Hierro Island at the Canary Islands (Northeast, NE, Atlantic Ocean); (**B**) Study area location south of El Hierro Island; (**C**) Pre-eruption topography of the study area where the pre-eruption gully is highlighted; (**D**) Bathymetric map of the Tagoro volcano.

Tagoro is one of the Earth's shallowest submarine volcanoes being monitored and represents an ideal natural observatory for understanding the immediate and long-term impacts of volcanic eruptions, and their related hydrothermal fields in different ecosystem compartments. Geological natural phenomena have important impacts on marine environments; therefore, studying volcanic hazards over different ecosystems contributes valuable information on nature's behavior.

The Canary archipelago plays an important role as a natural laboratory for studying the biogeography and evolution of species, due to its geographical location and oceanographic characteristics in the Eastern North Atlantic Subtropical Gyre [13–15]. The islands edifices act as an oasis for sustaining life in the open ocean, and as an important corridor for species' dispersion and colonization of further new habitats [16]. Planktonic larvae dispersion has been identified as one of the main processes permitting new habitat colonization [17–20]. Larval flow is also closely related to the direction and intensity of ocean currents, topographic features, and substrate availability [17,21,22].

The Tagoro submarine volcano provides a truly valuable opportunity for studying submarine benthic and demersal colonization on newly formed habitats, in addition to understanding the resilience capacity of the disturbed environment in the context of the North Atlantic Ocean. This topic has been previously investigated; Danovaro et al. [8] explored the microbial habitat dominating bacterial mats around the craters. A few studies have been conducted on community diversity at shallow hydrothermal vents in other volcanic archipelagos, such as the Azores Islands [23], Iceland [24], and in Grenada (Caribbean) [25], which can be comparable, however, they do not describe the colonization components of the newly formed volcanic substrate.

The Tagoro volcano complex (TVC, Figure 2) comprises one main cone and thirteen secondary cones, with interspersed depressions, aligned North-Northwest–South-Southeast, NNW-SSE [26,27]. The main edifice extends 88–400 m deep and the lava debris apron spreads 1–1.3 km long south-west (Figure 2A). Different geomorphic features (scarps and crests) were constructed during the eruption, shaped by the pre-existing gully and the different slope gradients (Figure 2A,B), covering depths greater than 1000 m (Figures 1D and 2C). Information on the pre-existing biological communities was obtained by sampling near-by, non-buried areas (Figure 3A,B). Previous studies on underwater lava-substrate colonization have been mostly limited to sub-aerial eruptions that reached the ocean [28–30]. Consequently, only intertidal and shallow habitats have been considered. Nonetheless, in the Pacific Ocean, two submarine volcanoes were monitored after their most recent eruption—West Mata in the Tonga Trench at 1200 m depth in 2008–2009 [31,32], and the NW Rota-1 in the Mariana Trench at 517 m depth in 2006 [33]. Although the colonization process was not the main goal of those studies, two alvinocarid endemic shrimp species were identified at West Mata (*Opaepele loihi* and an unidentified species; [31]), and two similar shrimp species were detected as dominant macrofaunistic components at the NW Rota-1 volcano [31]. These were the only reported findings on colonizing macrofauna at the two sites, and the resilience ability of inhabiting species was not explored. However, colonization processes may sometimes depend on recruitment events from neighbouring communities [34,35], and on the survival rates of the disrupted habitat communities [36]. Clearly, scarce information exists on the settlement of benthic and demersal organisms as colonizers of newly erupted volcanic rocks, and further studies are then critically required.

Due to an overall lack of knowledge on the colonization process of the benthic and demersal fauna onto newly formed volcanic substrates in shallow submarine environments, this study aimed to investigate the survival and colonization components of benthic and demersal communities at the newly formed habitat types of the Tagoro volcano. Further, we evaluate the impact of the volcanic eruption on these communities by comparing them to those existing at similar depths in adjacent areas.

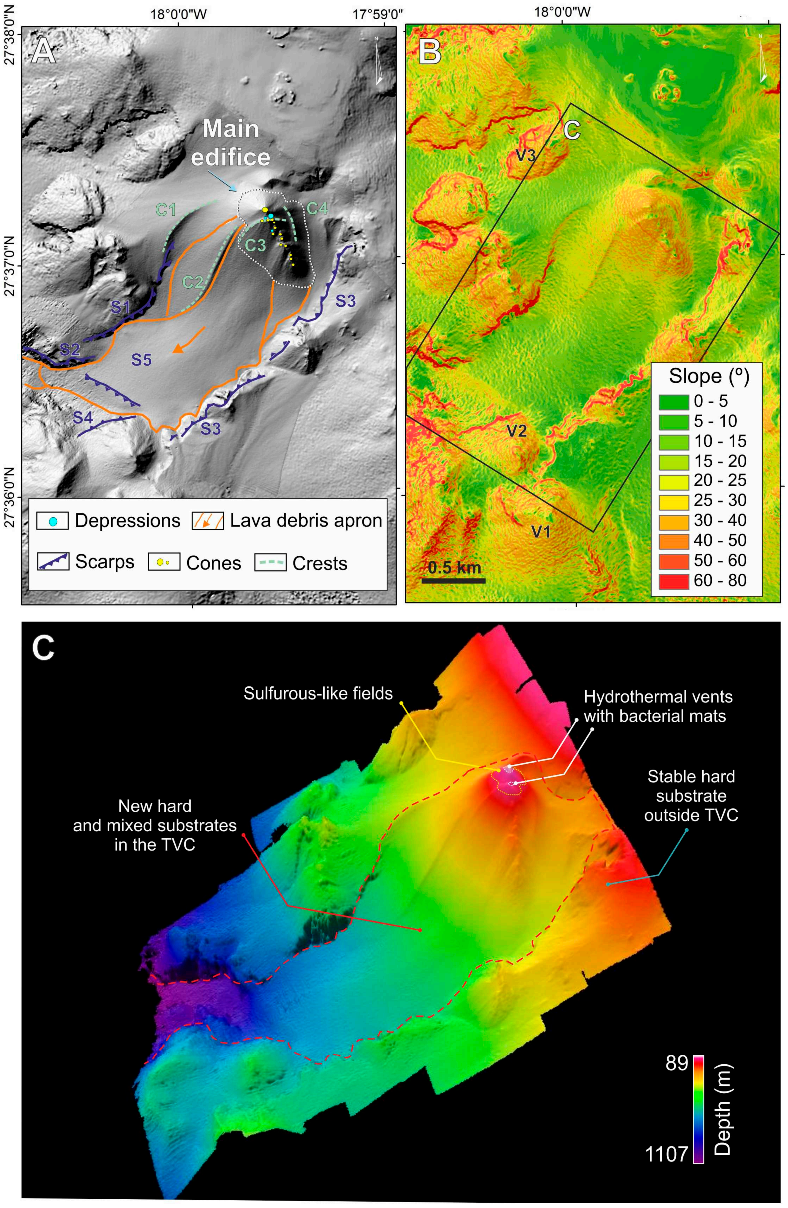

Figure 2. Main geomorphic features and related habitats of the Tagoro Volcanic complex. (**A**) Hillshade map showing the main geomorphological characteristics of the volcano. (**B**) Slope map highlighting similar volcanic cones (V1, V2, and V3) around the Tagoro Volcano. (**C**) 3D bathymetric map showing the location of the main habitats in and around the Tagoro Volcanic complex.

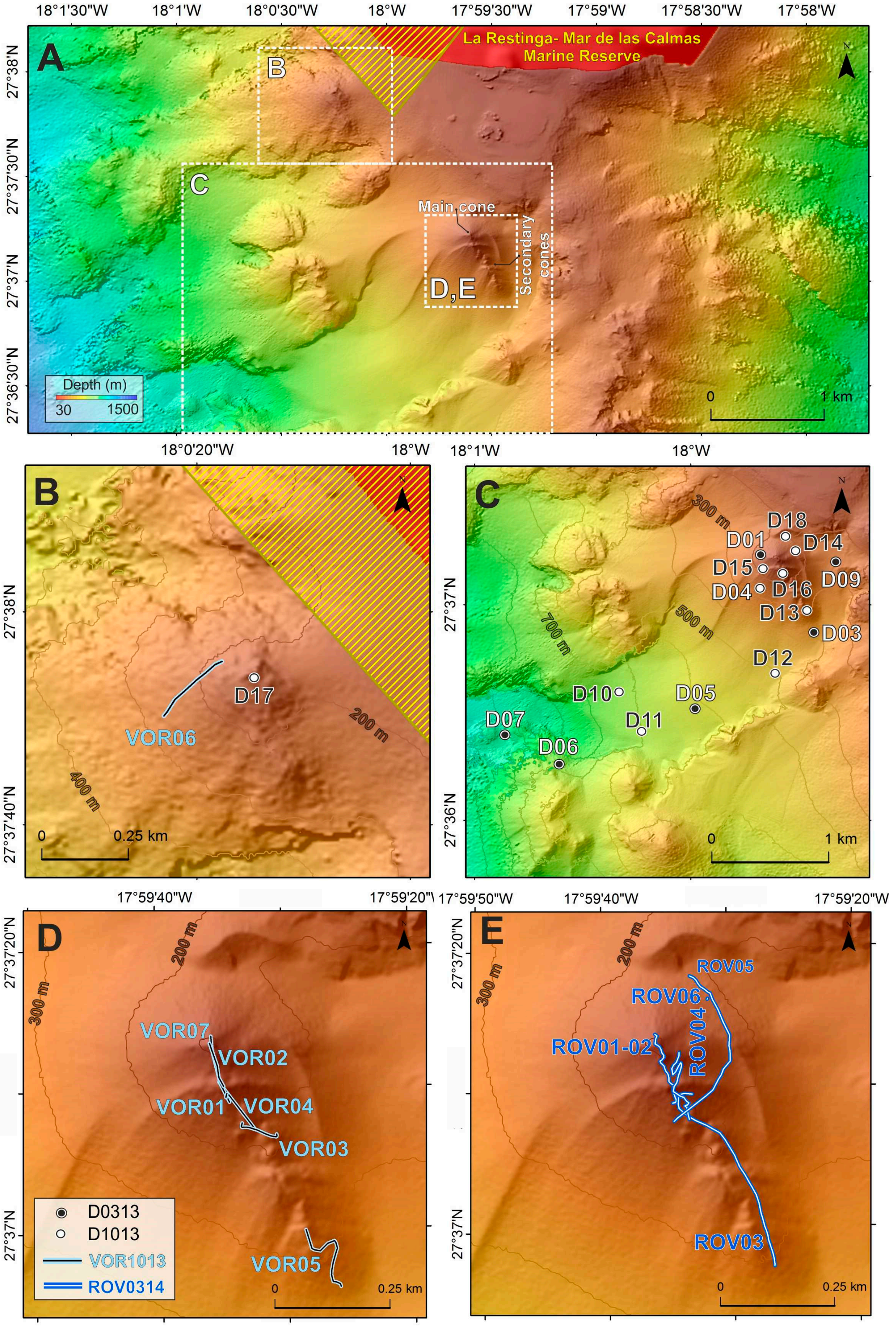

Figure 3. Sampling strategy (**A**) Bathymetric map showing south of El Hierro Island where the different sampling areas (**B–E**) are highlighted. (**B**) Unaffected eruption area close to the La Restinga-Mar de las Calmas Marine Reserve. (**C**) Tagoro volcanic complex, and (**D**,**E**) Main edifice and secondary cones of the Tagoro volcano. Dots represent dredge sites during the VULCANO0313 (black dots), and VULCANO1013 (white dots) oceanographic cruises. Lines indicate vehicle operated remotely (VOR) Aphia, (light blue) and remote operated vehicle (ROV) Liropus (dark blue double line) transects during the Vulcano1013 and Vulcano0314 oceanographic cruises.

2. Materials and Methods

Expeditions: the scientific dataset presented here was collected during four oceanographic expeditions on board the *R/V Ramón Margalef* (VULCANO0313, and VULCANA0417), and *R/V Ángeles Alvariño* (VULCANO0314, and VULCANO1013) between 2013 and 2017, being the earliest sample set less than two years after the end of the eruption. Sample collection was carried out off El Hierro Island, mainly at TVC (27°37′07″ N; 17°59′28″ W, Figure 3C–E), and at one adjacent unaffected area located close to "La Restinga-Mar de las Calmas" Marine Reserve (ca. 1.5 km from the main cone of Tagoro volcano) (Figure 3B).

Hydrography: hydrographic stations were carried out from the surface to 1200 m depth using a SeaBird 9/11-plus CTD (Conductivity-Temperature-Depth) with redundant sensors for temperature and conductivity, in addition to light transmission (Chelsea/Seatech), dissolved oxygen (SBE 43), pH and ORP (Oxygen-Reduction-Potential, SBE27, Figure 4A,B), pressure, and altimeter sensors. The accuracy of the temperature and conductivity sensors was 0.001 °C and 0.0003 S/m, respectively. Water samples were collected with a 24–10 L bottle rosette. The methodology followed has been previously described (Tow-yo and yo-yo techniques) [9,10]. Velocity data were obtained using a Vessel Mounted Acoustic Doppler Current Profiler (VMADCP) for the whole area.

Bathymetry and acoustic imagery: multibeam echosounder datasets were acquired using a Kongsberg-Simrad EM710 during VULCANA0417, which operates at sonar frequencies in the 70–100 kHz range, and were processed using CARIS HIPS & SIPS yielding bathymetric grid resolution of 5 m with 100% coverage.

Seafloor and benthic–demersal characterization: underwater imagery and benthic dredging were used for spatial characterization of the habitats, and their associated benthic and demersal communities. Submarine high quality video images were recorded using an Underwater Camera Sled (UCS) Aphia 2012 (VULCANO1013) and the Remote Operate Vehicle (ROV-Liropus 2000) from the Spanish Institute of Oceanography (VULCANO0314) (Figure 3B,D,E; light blue, VULCANO1013; and strong blue, VULCANO0314). A total of four and thirty-six hours of video were recorded, respectively. Underwater images were analyzed for the presence/absence of species, and the organism identification was done to the lowest possible taxonomic level.

Benthic (and some demersal) species were sampled using a benthic dredge (horizontal opening of 1 m, net mesh size of 1 cm). Samplings were mainly performed to carry out a geological characterization of substrate types in these areas, in order to collect small species that were not detected by underwater images and also to support species already identified in the images. Some dredges were towed at different depths to increase the spatial characterization of the communities at the TVC (Figure 3B,C). A total of 18 dredges were towed during the VULCANO0313 and VULCANO1013 cruises (Figure 3B,C; white and black points, respectively).

To contrast the effects of eruption on the biological community within the shallowest areas (around 200 m depth), a dredge sample and underwater video transect (Underwater Camera Sled-Aphia2012) were obtained in an almost pristine area outside the volcano-affected region (Figure 3B). Due to the invasiveness of the used sampling methodology, only one replicate was obtained in the non-buried (nearly pristine) area outside TVC. Moreover, some patches with slow-growing habitat-forming species were detected in deep areas of the TVC, which was useful for studying the survival of some organisms and alterations caused by the eruption. Collected organisms were separated from seafloor basaltic rocks and sedimentary material, identified to the lowest possible taxonomic level, photographed, and quantified. Sessile organisms attached to lava rocks were also quantified and photographed. Faunistic and geological materials were properly labeled and preserved dry or with 70% ethanol until further processing in the laboratory, to improve species identification when possible.

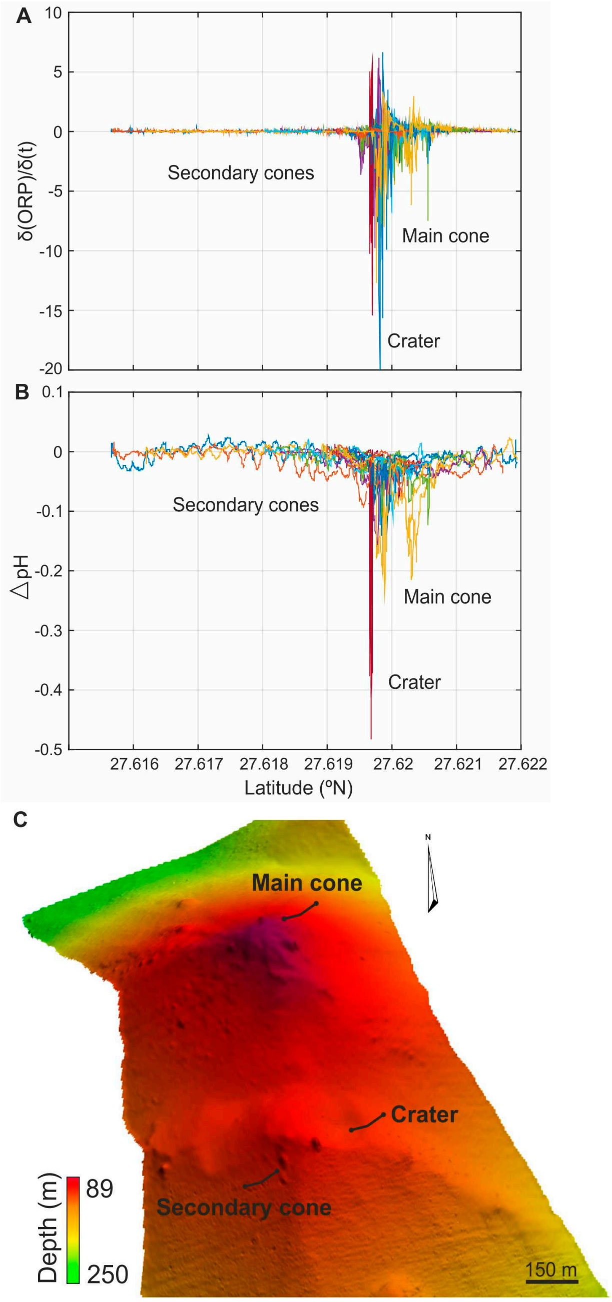

Figure 4. Plots of (**A**) Magnitude of oxidation-reduction potential (ORP) changes throughout time, δ (ORP)/δ t and (**B**) The increment of pH, ΔpH, versus latitude obtained from different meridional tow-yo transects (colored lines) over the main volcanic edifice in October 2017, (methodology described in [9,10]. (**C**) Three-dimensional (3D) graph showing the main and secondary cones, as well as the crater.

3. Results

The present study was based on a data set collected from 2013 and 2017, two years after the eruption's onset (2011). During the survey study period, the Tagoro submarine volcano was in an active degassing phase, emitting heat, different gases, and volatile components—mainly CO_2 [6,10]. Important physical–chemical anomalies were detected in the water column as δ(ORP)/δt up to −20 mV and pH anomalies up to −0.5 units (Figure 4A,B). In the same way, and for the interior of the main crater, the physical-chemical anomalies were more pronounced as: (i) thermal increase of +2.55 °C, (ii) salinity decrease of −1.02, (iii) density decrease of −1.43 ($kg \cdot m^{-3}$), and (iv) pH decrease of −1.25 units [9]. These alterations were concentrated 0.5 km around the crater (Figure 4A–C).

Pre-existing and newly formed habitat types were classified according to their location inside or outside the TVC-affected area, and substrate types. Within the TVC area, a distinction between the main edifice—which extends 88–400 m deep—and the natural prolongation of the SW flank of the main edifice was based on substrate type (Figure 5A). The main shallower edifice contained two newly formed habitats: hydrothermal vents with bacterial mats and sulphurous-like fields, both associated to the volcanic cones (Figure 2). The former was concentrated around hydrothermal vent sites, displaying a 10 cm yellow band of bacterial mats. However, the sulphurous-like fields were less restricted and extended around the main and secondary cones, and formed sulphur-looking light and sparse material that were easily re-suspended as shown by the underwater images (Figure 5B). Two other habitats conformed to the lava-debris flown apron that covered the SW flank of the volcano were named as new hard substrate and new mixed substrate. The new hard substrate habitat was composed of abundant pyroclastic rocks (from tens of cm to meters) that were deposited around the main cone during the eruption, forming an ideal area for colonizers that generally inhabit small cavities and hard substrate crevices (Figure 5C,D). The new mixed substrate habitat surrounds the previously described habitat type, and was conformed by small to medium size rocks and gravel sediments, offering distinct colonizing substrates (Figure 5E). Basaltic rock dimensions ranged from tens of centimetres (the largest rocks) to centimetres (the finer grained erupted material), creating a bed of rather fine sediment spotted with bigger size rocks. This habitat was less compact and stable than the new hard substrate due to its natural instabilities.

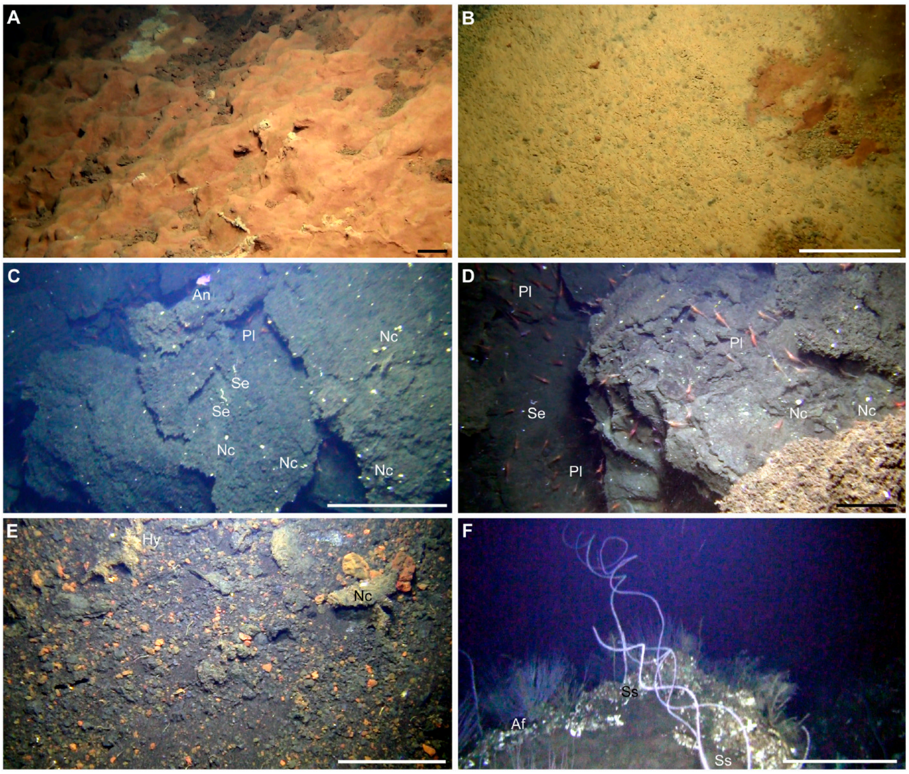

Figure 5. Images of the different habitat types within the Tagoro volcano complex (**A**–**E**), and at an undisturbed area (**F**). (**A**,**B**) Seep habitats with extensive bacterial mats close to the main and secondary craters. (**C**,**D**) Newly formed pyroclastic rocks harboring *Neopycnodonte cochlear* (Nc) (Mollusca: Bivalvia) and *Hyalopomatus* sp. (Hy) (Annelida: Polychaeta) individuals, together with *Anthias anthias* (An) (Chordata: Actinopterygii), and high densities of *Plesionika* sp. in the crevices (Pl) (Arthropoda: Decapoda). (**E**) New mixed substrates with small rocks colonized by individuals of *N. choclear* and *Hyalopomatus* sp. (**F**) Stable undisturbed hard bottoms colonized by fan-shaped *Antipathes furcata* (Af), and twisted whip-shaped *Stichopathes* cf. *setacea* (Ss) (Cnidaria: Anthozoa). Scale bars represent 20 cm.

Outside the TVC-affected area a single habitat—named Stable hard substrate—comprised of different substrate types, including some soft sediment dispersed within the rocky bottom (Figure 5F). This habitat, even though being close to the eruptive zone, remained undisturbed thanks to the ocean current direction [12], which flowed south-southwest preventing from any volcano derived burial. This habitat provides comparative pre-eruption conditions due to its undisturbed natural state. It consists of a crumble of solid and well-established rocks, and sediments of different sizes, with finer sediments that had been deposited previously to the eruption along the years. This habitat provides an interesting comparative baseline to investigate the physical and biological recovery of the newly formed shallow habitats.

Diversity of the benthic and demersal species colonizing the aforementioned habitats was set by coupling the analyses of underwater images (VOR and ROV data; Figure 3D,E) and dredge samples (Figure 3C). Determining the abundance was only possible from data collected using the dredges. A total of 6451 individuals, accounting for 116 taxa and nine phyla, were identified over the entire study (Table 1).

Table 1. List of all taxa identified in different habitat types of the Tagoro volcanic complex (TVC), with adjacent non-buried bottoms in the underwater images (ROV, VOR) and benthic dredges. Abundance is only shown for dredge-sampled taxa. X indicates the presence of taxa in the underwater images.

		Inside TVC				**Outside TVC**
		Hydrothermal Vents with Bacterial Mats	**Sulfurous-Like Fields**	**New Hard Substrate**	**New Mixed Substrate**	**Stable Hard Substrate**
Porifera	*Geodia* sp.	-	-	-	-	3
	Pachastrella sp.	-	-	-	-	2
	Axinella sp.	-	-	-	X	3
	Aplysina sp.	-	-	-	-	3
	Ircinia sp.	-	-	-	-	2
	Heteroscleromorpha 1	-	-	-	2	-
	Demospongiae 1	-	-	-	-	2
	Demospongiae 2	-	-	-	-	2
	Demospongiae 3	-	-	-	-	1
	Demospongiae 4	-	-	-	-	2
	Demospongiae 5	-	-	-	-	24
	Demospongiae 6	-	-	-	-	3
	Demospongiae 7	-	-	-	-	7
	Demospongiae 8	-	-	-	-	10
	Demospongiae 9	-	-	-	X	X
	Demospongiae 10	-	-	-	-	X
	Demospongiae 11	-	-	-	-	X
	Demospongiae 12	-	-	-	-	X
	Demospongiae 13	-	-	X	-	-
	Euplectellidae 1	-	-	-	1	-
	Porifera 1	-	-	-	-	X
Cnidaria	*Aglaophenia* sp. 1	-	-	1	-	12
	Aglaophenia sp. 2	-	-	-	-	208
	Obelia sp.	-	-	-	-	1
	Sertularella cf. *gayi* (Lamouroux, 1821)	-	-	1	-	6
	Sertularella cf. *polyzonias* (Linnaeus, 1758)	-	-	-	2	-
	Sertularella cf. *tenella* (Alder, 1857)	4	4	3	18	12
	Sertularella sp.	-	-	X	X	3
	Lafoeidae 1	-	-	-	3	21
	Lafoeidae 2	-	-	-	-	1
	Plumulariidae 1	-	-	X	2	3
	Hydrozoa 1	X	-	X	8	-
	Hydrozoa 2	-	-	X	-	-
	Ceriantharia 1	-	-	-	X	-

Table 1. *Cont.*

		Inside TVC				Outside TVC
		Hydrothermal Vents with Bacterial Mats	**Sulfurous-Like Fields**	**New Hard Substrate**	**New Mixed Substrate**	**Stable Hard Substrate**
	Antipathes furcata Gray, 1857	-	-	-	-	7
	Stichopathes cf. *setacea* Gray, 1860	-	-	X	2	40
	Tanacetipathes cf. *cavernicola* Opresko, 2001	-	-	-	-	10
	Corallimorpharia 1	-	-	-	X	-
	Anomocora fecunda (Pourtalès, 1871)	-	-	-	-	1
	Caryophyllia smithii Stokes & Broderip, 1828	-	-	-	-	1
	Caryophyllia sp.	-	-	-	-	2
	Cladocora debilis Milne Edwards & Haime, 1849	-	-	-	-	1
	Madracis sp.	-	-	-	-	1
	Zoantharia 1	-	-	-	-	2
	Bebryce mollis Philippi, 1842	-	-	-	-	1
	Callogorgia verticillata (Pallas, 1766)	-	-	-	-	X
	Paralcyonium cf. *spinulosum* (Delle Chiaje, 1822)	-	-	-	-	X
	Villogorgia bebrycoides (Koch, 1887)	-	-	-	-	1
	Viminella flagellum (Johnson, 1863)	-	-	X	-	X
	Alcyonacea 1	-	-	X	-	6
Annelida	*Chloeia* cf. *venusta* Quatrefages, 1866	-	-	8	63	-
	Eunice sp.	-	-	-	-	1
	Glycera sp.	-	-	4	8	-
	Hyalinoecia sp.	-	-	-	1	-
	Leocrates atlanticus (McIntosh, 1885)	-	-	-	1	-
	Lumbrineris sp.	-	-	-	-	1
	Nereis sp.	-	-	-	4	3
	Onuphis sp.	-	-	5	3	1
	Syllidae 1	-	-	-	2	1
	Hyalopomatus sp.	-	-	9	33	-
	Placostegus sp.	-	-	2	-	-
	Protula sp.	-	-	3	3	5
	Semivermilia cf. *torulosa* (Delle Chiaje, 1822)	-	-	-	4	30
	Serpula vermicularis Linnaeus, 1767	-	-	-	-	1
	Spio sp.	-	-	-	1	-
	Spiochaetopterus sp.	-	-	2	6	-
	Vermiliopsis sp.	-	-	1	-	-
	Sabellidae 1	-	-	-	-	1
	Serpulidae 1	X	X	X	8	50
	Terebellidae 1	-	-	-	2	1
Mollusca	*Mitrella* sp.	-	-	-	1	-
	Onoba sp.	-	-	-	2	-
	Tritia denticulata (A. Adams, 1852)	-	-	-	X	-
	Nudibranchia 1	-	-	X	X	-
	Asperarca nodulosa (O. F. Müller, 1776)	-	-	-	-	1
	Neopycnodonte cochlear (Poli, 1795)	-	-	13	178	245
	Pteria hirundo (Linnaeus, 1758)	-	-	-	-	41
	Arcidae 1	-	-	-	1	-
	Octopus vulgaris Cuvier, 1797	X	-	-	-	-
	Cephalopoda 1	-	-	X	-	-

Table 1. *Cont.*

		Inside TVC				Outside TVC
		Hydrothermal Vents with Bacterial Mats	**Sulfurous-Like Fields**	**New Hard Substrate**	**New Mixed Substrate**	**Stable Hard Substrate**
Arthropoda	*Heteralepas cornuta* (Darwin, 1851)	-	-	-	-	3560
	Megabalanus tulipiformis (Ellis, 1758)	-	-	-	3	-
	Acanthephyra eximia Smith, 1884	-	-	-	2	-
	Alpheus macrocheles (Hailstone, 1835)	-	-	1	1	-
	Alpheus sp.	-	-	8	12	-
	Homola barbata (Fabricius, 1793)	-	-	-	1	-
	Macropodia sp.	-	-	-	-	2
	Monodaeus couchii (Couch, 1851)	-	-	10	21	-
	Munida sp.	-	-	1	1	-
	Munidopsis sp.	-	-	-	1	-
	Plesionika edwardsii (Brandt, 1851)	-	-	-	X	-
	Plesionika martia (A. Milne-Edwards, 1883)	-	-	1	-	-
	Plesionika narval (Fabricius, 1787)	-	-	X	4	-
	Plesionika sp.	-	-	1	-	-
	Velolambrus cf. *expansus* (Miers, 1879)	-	-	-	5	-
	Decapoda 1	-	-	X	X	-
Echinodermata	Ophiuroidea 1	-	-	-	-	6
	Centrostephanus longispinus (Philippi, 1845)	-	-	-	-	1
	Coelopleurus floridanus A. Agassiz, 1872	-	-	-	1	-
	Stylocidaris affinis (Philippi, 1845)	-	-	X	1	-
	Diadematoidae 1	-	-	-	1	-
Brachiopoda	*Megerlia truncata* (Linnaeus, 1767)	-	-	-	-	9
	Pajaudina atlantica Logan, 1988	-	-	-	-	25
Bryozoa	*Hornera* sp.	-	-	-	-	8
	Reteporella sp.	-	-	-	-	15
	Frondiporidae 1	-	-	-	-	1362
	Bryozoa 1	-	-	-	-	X
Chordata	Clavelinidae 1	-	-	-	-	X
	Ascidiacea 1	-	-	-	-	X
	Anthias antias (Linnaeus, 1758)	X	X	1	11	X
	Conger conger (Linnaeus, 1758)	-	-	X	X	-
	Scorpaena sp.	-	-	-	X	-
	Seriola sp.	X	X	-	-	-
	Serranus atricauda Günther, 1874	X	X	X	X	-
	Perciformes 1	-	-	X	X	-

Biodiversity was distributed differently across the habitats (Figure 5). At the TVC's shallowest areas, the biological community of hydrothermal vents with bacterial mats and sulphurous-like fields, were mainly composed of scares of a low number of species including small hydrozoans (*Sertularella* cf. *tenella*; size up to 2–3 cm; Figure 5A,B; Figure 6 and Table 1). Underwater images further detected the presence of some cephalopods, small serpulid polychaetes, and fishes, though at very low densities. In addition, previous studies investigated abundant bacterial mats occurring in these areas, which comprised mostly of a recently described genus and species of the order Thiotrichales, commonly known as Venus´s hair (*Thiolava veneris*) [8]. The bacterial mats concentrated around venting areas (Figure 2C), and were yellow-colored in underwater photographs, and oxidizers of the reduced sulphur that emanates from volcanic vents (Figure 5A).

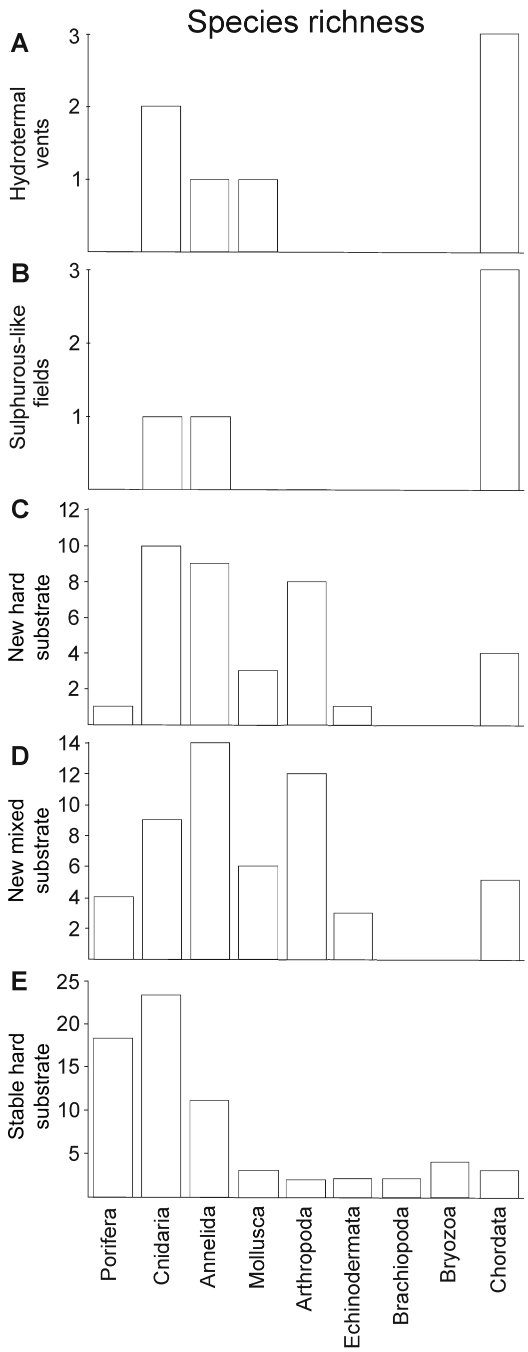

Figure 6. Species richness (number of species) in the different phyla identified in underwater images (ROV and VOR), as well as in the benthic dredges, within the different habitats at the Tagoro volcano complex (**A**–**D**) and at an undisturbed area (**E**).

In the deep areas of the TVC, new hard substrate and new mixed substrate displayed a larger biodiversity with seven different phyla in each habitat type, and a total of 38 and 55 taxa, respectively (Figure 6 and Table 1). Annelids, arthropods, cnidarians, and molluscs were the most diverse phyla in both habitats, generally present as small-sized specimens. The most represented taxa were similar in both habitats, although abundance differed significantly, with higher abundances in the mixed bottoms (Figure 7). Annelids were mainly represented by small sessile (*Hyalopomatus* sp.) and mobile species (*Glycera* sp., *Chloeia* cf. *venusta*, *Onuphis* sp.; Figure 8). *Monadaeus couchii* and *Alpheus* sp. were the dominant arthropod species (Figure 8). Cnidarians were mostly represented by scarce and small hydrozoan colonies (*Sertularella* cf. *tenella*; Figure 8). Finally, molluscs were mainly represented by the ostreid bivalve *Neopycnodonte cochlear* (reaching locally up to 100 individuals m^{-2}; Figure 8), with shell sizes ranging from less than a cm to more than 6 cm, and probably resembling different cohorts. This ostreid was one of the most dominant species in the large lava rocks deposited after the eruption. In deep areas of the TVC, patches with large antipatharian colonies (mainly *Stichopathes* cf. *setacea* and *Anthipathes furcata*), dead colonial scleractinians of unidentified species, *Sertularella* sp., Plumulariide, some sponges (*Axinella* sp.), and a few species of fish (*Anthias anthias*, *Conger conger*, *Scorpena* sp., and *Serranus atricauda*; Table 1) were detected in the underwater images.

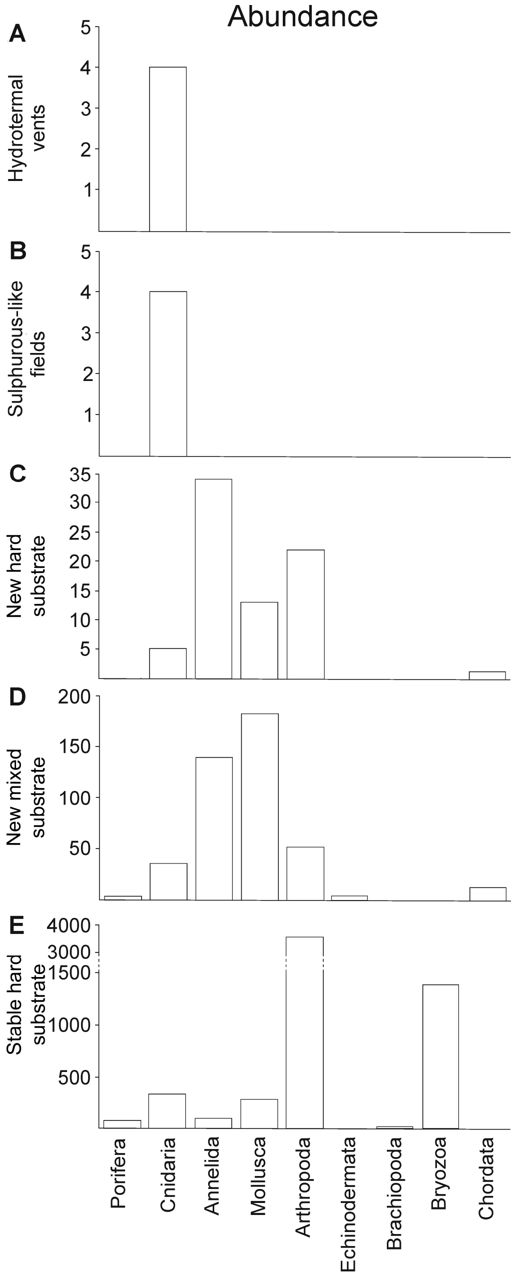

Figure 7. Abundance (number of individuals) in the different phyla collected in the benthic dredges, within the different habitats at the Tagoro volcano complex (**A**–**D**) and at an undisturbed area (**E**).

Figure 8. Biodiversity associated with new hard substrate and mixed substrate habitats within the Tagoro volcano complex (**A**–**L**), and with neighbouring stable hard substrates located at an undisturbed area close to "La Restinga-Mar de las Calmas" Marine Reserve (**M**–**V**). (**A**) Volcanic rock of new formation with small-size specimens of the ostreid bivalve *Neopycnodonte cochlear* (detailed in **B**) and serpulid worm (detailed in **C**). (**D**,**E**) Small colonies of the hydrozoan *Sertularella* cf. *tenella* colonizing newly formed volcanic rocks. Other dominant colonizers include the shrimp *Plesionika narval* (**F**); small-sized individuals of the echinoid *Coelopleurus floridanus* (**G**); the annelid *Chloeia* cf. *venusta* (**H**,**I**); small decapods such as *Monodaeus couchii* (**J**); *Velolambrus* cf. *expansus* (**K**); and *Alpheus* sp. (**L**). Vulnerable habitat-forming species were mainly represented by antipatharians, such as *Tanacetipathes* cf. *cavernicola* (**M**); *Antipathes furcata* (**N**); and *Stichopathes* cf. *setacea* (**O**), the latter being frequently colonized by different epibionts including the cirriped *Heteralepas cornuta* (**P**); the bivalves *N. cochlear* (**Q**); and *Pteria hirundo* (also colonized by small *H. cornuta*; **R**). Volcanic rocks from past eruptions were also colonized by small epibionts, dominating the brachiopod *Pajaudina atlantica* (Pa) and different serpulid species (Se; **S**,**T**), as well as large non-identified desmosponges (**U**,**V**). Scale bars represent 1 cm.

Outside the TVC, the biological community of Stable and hard bottoms not affected by the eruption comprised of nine phyla, with a total of 5774 identified individuals (Figure 6 and Table 1). Cnidarians were mainly represented by large and vulnerable slow-growing habitat-structuring species, including antipatharians such as *Stichopathes* cf. *setacea* (Figure 8; some of them with sizes of up to one m), *Antipathes furcata* (Figure 8), and *Tanacetipathes* cf. *cavernicola* (Figure 8), in addition to well-developed hydrozoan colonies, mainly *Aglaophenia* sp. 2, *Sertularella* cf. *tenella*, and *Sertularella* cf. *gayi*. Some of these antipatharians contained a wide variety of epibionts, mainly represented by cirripeds (*Heteralepas cornuta*; Figure 8), bryozoans (*Reteporella* sp.), and molluscs (*Neopycnodonte cochlear*, *Pteria hirundo*; Figure 8), which were the most abundant phyla of these non-buried habitats (Table 1). Annelids were dominated by *Semivermillia* cf. *torulosa* and an unidentified serpulid species (ca. 30 and 50 individuals, respectively). Some species of sponges (e.g., *Axinella* sp., *Aplysina* sp. and *Geodia* sp.; Figure 8) cohabited with the antipatharians, as well as taxa from phylla that were not detected in previous habitats of the TVC, such as brachiopods (*Megerlia truncata* and *Pajaudina atlantica*), bryozoans (e.g., Frondiporidae and *Reteporella* sp.), and ascidians.

4. Discussion

The study of the macrofauna at different sites of Tagoro volcano permitted to describe the primary biological evolution of new submarine habitats, with the possibility of identifying fast colonizing organisms as well as survivors to submarine eruptions.

The formation of the Tagoro volcano complex (TVC) included extrusion of magmatic material and the formation of new hard bottoms, as well as changes in the physical–chemical characteristics of water masses in the area [6,10,26,27]. This eruptive process locally impacted pre-existing habitats through burial, mainly those conformed by antipatharians (*Stichopathes*, *Antipathes*, and *Tanacetipathes*), which when detected were considered survivors of the eruption and the water column anomalies [37]. Black corals grow at relatively slow rates (maximum longevities ranging from decades to millennia), with long life spans and older age of maturity [38]; extended longevity of some detected individuals may represent an indicator of resilience to environmental changes, such as the Tagoro eruption is in this case. The impact produced by the physical–chemical anomalies may have also affected other species, for example, no live colonies of scleractinians were detected in the dredge samples (which contained some remains of dead ones) and in the underwater images.

Habitats of hydrothermal vents with bacterial mats and the sulphurous-like fields were the most extremophilous, and were basically colonized by bacteria that oxidizes reduced sulphur emanating from volcanic vents [8]. Nevertheless, very small hydrozoan colonies began to colonize the hard substrates of those habitats, and were also detected on the newly formed hard substrates away from the crater. Hydroids have also been detected as common components in shallow hydrothermal vents (<200 m depth) in the NE Atlantic [24,39,40]. These could represent early colonizers of extremophilous environments. In general, the metazoan biodiversity in these vents and sulphurous fields was very low when compared to the remaining habitats. Usually, hydrothermal vents are impoverished in comparison to other substrates located at similar depths, due to toxic and extremophilous environments that are noxious to most metazoans [40,41].

Regarding the two other new habitats conformed by the erupted lava rocks (new hard substrate and new mixed substrate; Figure 2C), the highest diversity was held by annelids, arthropods, cnidarians (only hydrozoans), echinoderms, and molluscs (Figure 6C,D), some of which are considered to be successful benthic colonizers of new substrates. Part of the identified species are mobile and may have planktotrophic development [42], even though larvae mobility could be influenced by different factors, such as larval mortality [43], pelagic larval duration [44], larval output [45,46], and geography [47,48]. Successful recruitment events of some of these species could have been enhanced because they are dominant components of undisturbed, stable hard bottoms located close to the TVC (Table 1). Additionally, some annelid and mollusc species are opportunistic organisms, and may have high larval settlement success in free empty substrates, a variable determining the spatial pattern of their distribution [49,50]. In the newly formed lava rocks (new hard substrates, Figure 2C), one of the first dominant colonizers was the bivalve *Neopycnodonte cochlear* (Figure 8A,B) that is a non-selective filter feeder that grows attached to rocks and to some organisms (e.g., antipatharians in this study), adapting its shape to irregular substrates. This ostreid is a very common species in circalittoral hard bottoms of the Canary Islands. It is also one of the whip black corals dominant epibionts (reaching densities of six per *Stichopates* cf. *setacea* colony) on the stable hard-bottoms located close to the Marine Reserve (ca. 1.5 km from the main cone of the Tagoro volcano) [51]. The presence of large populations of this fouling bivalve at the undisturbed area, the availability of uncolonized hard substrates, and the high concentration of Fe(II) and inorganic nutrients (natural fertilization event aforementioned; [10]), probably favoured successful recruitment of these ostreids at the TVC. Other common colonizers of the new hard substrates were hydrozoans (basically dominated by *Sertularella* spp; Figure 8D,E) that have planktonic larvae during their life cycle, which may permit their settlement in remote places. These hydroids are also very common circalittoral hard bottom species, and probably favoured by the same aforementioned reasons as *N. cochlear*. Another dominant colonizer was the shrimp *Plesionika narval* (Figure 8F and Table 1), represented by adult and juvenile individuals (high visualization rate in the underwater images), and it is also a common component of the Macaronesian circalitoral bottoms. In this context, its presence in the TVC could be primarily due to horizontal movements of individuals from nearby habitats [52,53]. This could also be the case for the few fish species observed in the TVC and its surrounding areas, *Anthias anthias* being by far the most abundant species.

In the new mixed substrates, a higher number and abundance of taxa were detected compared to the previously discussed habitats (Figure 8C,D). In these mixed bottoms, combining different types of substrates promotes the presence of a higher number of microhabitats, food sources, and species. A phenomenon that has been generally detected in mature complex communities [54]. The species colonizing lava rocks included most of those detected at the new hard substrates (Table 1). In this habitat, molluscs, annelids, and arthropods were the dominant groups in terms of abundance. Annelids were primarily represented by mobile predators and scavengers with a planktotrophic larval development, high dispersal potential such as *Glycera* sp. and *Chloeia* cf. *venusta* (Figure 8H,I; [55]), and both adults and juveniles (post-eruptive recruitment) were found in the samples. In this case, it remains unclear whether the colonization was only through larval settlement or also through adult and juvenile individuals coming from adjacent habitats with similar substrates that were not buried. Arthropods were mostly represented in the new mixed substrates by species with planktotrophic development that are common in circalittoral soft bottoms, inhabiting crevices and small burrows, such as *Monodaeus couchii* (Figure 8J), *Alpheus* sp. (Figure 8L), *Munida* sp., and *Velolambrus* cf. *expansus* (Figure 8K) [56]. Some of those decapods were represented by adults and juveniles (e.g., *M. couchii*, *Alpheus* sp.) and they generally inhabit crevices. Therefore, they may not be as mobile as other colonizing decapods with a demersal life style that colonized the TVC (e.g., *Plesionika*). Those species could have colonized the TVC through larval settlement and were probably favoured by the wide availability of unoccupied crevices of the new substrates (Figure 5C–E). Finally, cnidaria, molluscs, and echinoderms were also quite diverse. Cnidarians and mollusca showed the same pattern as in the new hard substrate, although some species displayed higher abundances (Figures 5 and 6), and echinoderms were mostly represented by echinoid—mainly cidaroids (Figure 8G)—which generally are opportunistic species with broad tolerance ranges, able to live in very diverse substrates as detected in the current study [57]. Moreover, cidaroids are slow-moving species so their presence in the TVC is more likely due to larval settlement than to horizontal movements because only small-sized individuals were detected in the samples and in underwater images.

In the present study, the highest biodiversity was detected at the neighbouring hard and stable hard bottoms, located at a non-disturbed area close to the Marine Reserve "Punta de la Restinga—Mar de las Calmas" (Figure 3B). Taxa from all phyla detected in this study were observed in this undisturbed area, and the biodiversity distribution reflects well-established circalittoral hard bottom communities, with dense antipatharian aggregations and large sponges [58]. Although the sampling effort performed in this highly pristine habitat was smaller (e.g., only one dredge and one video transect outside the TVC) than in newly formed ones, a larger number and abundance of taxa was detected in these non-buried habitats. Antipatharians and large porifera are not considered pioneer colonizers of new substrates due to their slow growth rate and their fragility, making these groups more diverse and abundant at the undisturbed habitats (Figure 5E). Black corals (mainly *Stichopates* cf. *setacea*; Figure 8O and Table 1) were the most dominant habitat-forming species within those habitats, acting as habitat-structuring agents hosting different species of bryozoa and brachiopoda, e.g., Frondiporidae unid., *Reteporella* sp., and *Pajaudina atlantica* (Table 1). Moreover, these structurally complex organisms, together with large sponges or scleractinians, enhance three-dimensional habitats, which provide other organisms with settling substrates and shelter from predators [59,60]. Indeed, a wide variety and abundance of epibionts with planktotrophic larval development (e.g., *N. cochlear* (Figure 8Q), *Heteralepas cornuta* (Figure 8P), serpulids, and hydroids) occurred in *Stichopates* cf. *setacea* colonies and on rocky substrates (Figure 8S,T). Some of these epibiotic organisms were later found as key colonizers of the newly formed substrates in the Tagoro volcano. Conversely, the black corals detected in the underwater images at the newly formed habitats, were definitely survivors from the eruption, mainly due to the fact that they were half buried by the erupted volcanic materials, and were located in specific areas of the TVC away for the crater and lava debris apron.

In general, benthic and demersal macrofauna biodiversity and abundance were low close to venting areas, and increased away from the main and secondary cones where TVC structure is sharper and vertical, however, further decrease of biodiversity was detected relative to increasing depth. Species zonation along a depth gradient and between habitat types is known to be affected by several factors, such as temperature [61], pressure [62], currents and topography [63,64], sediment characteristics [65], in addition to biological factors including free-predator substrates, species competition, predation, and trophic levels [66,67]. A lower number of species generally occurred in the deeper parts of the lava debris apron, as higher biodiversity is expected where slope gradient is higher as shown by Gori et al., [68]. At deeper parts of the TVC colonization and recovery will probably occur slowly, since substrate variety, vertical gradient and depth [68] of that zone are curbing the metazoan community diversification. Dispersal capabilities of larvae and early stages might also affect species distribution when colonizing new substrates, as has been discussed for different species [16,69,70].

5. Conclusions

During the eruption of the Tagoro submarine volcano in March 2011, volcanic sediments and lava and gas emissions resulted in important disturbances in the surrounding grounds and on the water column. The results of this study highlight that the eruption first buried most of the previously existing habitats, except some patches with antipatharians that survived the event, and secondly created a highly unstable environment that affected some slow-growing organisms (e.g., cold-water corals), but not others (e.g., antipatharians). Nevertheless, our results indicate that the submarine eruption provided uncolonized hard and soft seafloor substrates to different organisms. These, together with the high concentration of Fe(II) and inorganic nutrients emitted by the volcano, which promoted a natural fertilization event in the area, could have enhanced the establishment and development of sessile suspension feeders (e.g., *N. cochlear*, hydrozoans) in the newly formed hard and mixed substrates, representing common components in nearby unaffected habitats.

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