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First description of deep benthic habitats and communities of oceanic islands and seamounts of the Nazca Desventuradas Marine Park, Chile

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Seamounts and oceanic islands of the Chilean Exclusive Economic Zone at the intersection of the Nazca and Salas y Gómez ridges lie within one of the least explored areas in the world. The sparse information available, mainly for seamounts outside Chilean jurisdiction and shallow-water fauna of the Desventuradas Islands, suggests that the area is a hotspot of endemism. This apparent uniqueness of the fauna motivated the creation of the large Nazca-Desventuradas Marine Park (NDMP, ~300,000 km²) around the small islands San Felix and San Ambrosio in 2015. We report for the first time a detailed description of benthic microhabitats (i.e., centimeter to meter scale), macrohabitats (i.e., meter to kilometer-scale) and associated megafauna within the NDMP. Descriptions were based on analysis of fauna collected by trawling and ROV video observations from ~50 to 370 m depth. Rocky, coarse sand and silty sediment bottom habitats were observed at island slopes. In contrast, rocky and coarse sandy bottom habitats with a predominance of rhodoliths, thanatocoenosis, and other biogenic components were observed at seamounts. Mobile fauna and predators dominated the oceanic islands and nearby seamounts, whereas seamounts farther from the islands were dominated by sessile and hemisessile fauna that were mainly suspension and deposit feeders. Based on the register of 118 taxonomic units, our results provide an expanded and updated baseline for the benthic biodiversity of NDMP habitats, which seemed pristine, without evidence of trawling or anthropogenic debris.

Seamounts are topographic elevations that rise more than 1000 m above the seafloor1, and in some cases, they reach the euphotic zone or the surface (i.e., oceanic islands)2. These ecosystems are considered vulnerable marine habitats because they are physically fragile or inherently rare3,4. Studied seamounts and oceanic islands are generally considered to play important roles by being highly productive locally, acting as regional centers of speciation or stepping-stones for dispersion. They comprise a diversity of substrates and thus habitats that support and provide refuge and feeding areas, not only for the benthic fauna but also for the associated pelagic and overlying surface water animals (e.g., birds, and marine mammals)5-7. Although seamounts are generally considered to play these important roles, each seamount experiences unique environmental conditions such as current characteristics and water-column environmental conditions (i.e., temperature, salinity and pressure) that differ with depth and current dynamics6. They also have unique characteristics such as height and morphology that result in unique physical dynamics that can result in increased nutrient availability relative to the surrounding...

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The Pacific Ocean basin is characterized by the existence of several relatively long quasi-linear chains of oceanic islands and seamounts. The oceanic islands and seamounts of the southeast Pacific lie within one of the most unexplored areas in the world. Most of the ~940 southeast Pacific seamounts are located along the Salas y Gómez (SGR) and Nazca (NR) ridges, and only 24 (~3%) of the SGR and NR seamounts have been studied. Most of these studies were conducted by expeditions of the former USSR between 1973 and 1987 in international waters from ~80°W to 101°W at 162 to 1900 m depth. They reported unprecedented rates of endemism for benthic communities (e.g., ~41% for fishes and ~46% for invertebrates) that were similar to those rates observed for seamounts of the remote Norfolk Ridge, near New Caledonia. Despite studies being conducted on SGR and NR seamounts, only one of the many seamounts within the Chilean EEZ adjacent to the Desventuradas Islands (San Felix and San Ambrosio islands) has been investigated. In addition to this seamount, known as Stockman Guyot, the Desventuradas Islands were studied on two expeditions: Marine Research Cruises in Remote Areas (CIMAR 6) conducted by the National Oceanographic Committee of Chile (CONA) in 2001 and the ’Pristine Seas Expedition’ carried out by the National Geographic Society and Oceana in 2013. These studies, which were conducted at 40 to 2300 m, revealed that the fauna of these islands are unique and irreplaceable, granting these areas a high conservation value. These considerations prompted the creation, in 2015, of the large Nazca Desventuradas Marine Park (NDMP), protecting an area of ~300,000 km² including the Desventuradas Islands and seamounts located northwest of them. This marine park provides enormous advances in safeguarding the unique biodiversity of actual or past threats such as pelagic fishing of tuna and swordfish, as well as bottom trawling.

Of the available studies in the region, none has explored the importance of substrate type on species composition, nor the role of the habitat at different scales from centimeters to meters. Because distinct environmental conditions, such as internal tides and heterogeneity of substrates and oceanographic conditions (i.e., temperature, salinity and oxygen gradients), can differ considerably among and within seamounts, these and other variables can play a critical role in the distribution and behavior of megabenthos, operationally defined here as organisms with a body size > 1 cm. Differences in these environmental conditions can generate a mosaic of micro- and macrohabitats, with breaks in species distributions that can enhance biodiversity and drive changes in community composition within or among seamounts. The heterogeneity and topographic complexity of seamounts is affected by the presence of organisms that can change spatial conditions and, directly or indirectly, affect the availability of habitat and resources for other species. These organisms are called habitat-forming species and are characterized by being small-scale engineers of autogenic ecosystems. These organisms, and the biogenic structures they produce, contribute to increasing spatial complexity in soft-sediment benthic systems, promoting spatial heterogeneity on seamounts, but they are often easily overlooked because seamounts are sampled at much more general spatial scales. In recent years, the importance of sampling at smaller scales has been accentuated with the understanding that the characteristics of the bottom and the presence of habitat-forming species increases the heterogeneity of the habitat and fulfill the function of a structural habitat.

Several studies of continental shelf, slope and submarine canyon habitats have specified relationships of megafauna with certain microtopographic (microhabitat) characteristics (e.g., depressions, burrows and sessile fauna). Because many of these studies lacked a standard habitat classification scheme, these observations cannot be compared efficiently among ecosystems and studies. To explore the importance of seabed habitat, Greene et al. proposed a standardized classification, which divides the habitat according to depth, size and biogenic and abiotic variables, for in situ observations of the seabed. Within the size category are the subcategories of macrohabitat and microhabitat. Macrohabitats range in size from one to ten meters and include seafloor features such as boulders, crevices, cracks, caves, scars, sinkholes and bedrock corals (solitary and reef-building). Meanwhile, microhabitats operate at centimeters and smaller scales and include seafloor features such as sand, silt, gravel, pebbles, small cracks, crevices and fractures.

To explore relationships among micro- and macrohabitats and the fauna living on the summit of the seamounts and upper slope of oceanic islands of the NDMP, we describe the benthic habitats and associated fauna of the upper slope (50–370 m) of Desventuradas Islands and the summits and upper slopes (150–305 m) of seven nearby seamounts. We conducted remotely operated vehicle (ROV) surveys complemented with benthic fauna collections using an Agassiz trawl, aiming to achieve the following objectives: (1) to describe the benthic habitats of the oceanic islands and seamounts of the NDMP at different spatial scales (i.e. at centimeter to meter scale), (2) to describe the composition and the diversity of the benthic megafauna on these oceanic islands and seamounts, and (3) to evaluate the relationships between macrohabitat and megafauna species diversity and composition as well as feeding mode and movement type of the benthic communities. To our knowledge, this study is the first to describe benthic habitats and associated fauna at seamounts and oceanic islands of the NDMP.

**Materials and methods**

**Study area.** The NR and SGR together form a sequential chain of seamounts of volcanic origin with an extension of ~2900 km that is ~100 km wide along the SGR and ~300 km wide along the NR. The Desventuradas Islands, constituted by San Felix and San Ambrosio islands (~26°S, 80°W), are located ~970 km off the coast of the Atacama Region, northern Chile. Seamounts of the Desventuradas Islands region are located northwest of these islands at the intersection of SGR and NR (Fig. 1).
Data collection. From 22 October to 1 November 2016, benthic surveys were performed at five stations on the upper slope of the Desventuradas Islands and the summits of seven nearby seamounts of the NR (Fig. 1). A Commander MK2 (Mariscope Meerestechnik, Kiel, Germany) ROV equipped with an HD Camcorder (Panasonic SD 909, resolution 1920×1080, 30 fps), a GoPro Hero camera (resolution 2704×1520, 60 fps) and laser pointers (10 cm apart) was used to survey benthic habitats and communities. A total of 11 ROV dives were conducted at ~40 to 370 m depth (Table S1); five on the slope of Desventuradas Islands (5 h of total bottom time) and six on the seamounts (6 h of total bottom time). The ROV observations were descriptive and did not aim to obtain quantitative data due to the potential overlapping of the paths of the surveys.

Benthic trawling was performed at stations where either multibeam or ROV observations indicated suitable soft bottoms. Trawls were conducted for ~4 to 15 min (bottom contact) with a constant speed of ~3 knots at each station (Table S1). The gear used was a modified Agassiz trawl, with a mouth of 1.5 m × 0.5 m (width × height) fitted with a net of 12 mm mesh at the cod end. A total of 10 trawls were conducted; four on the slope of the Desventuradas Islands and six on the seamount summits, with sampling depths ranging from 133 to 340 m (Table S1). Both trawl and ROV deployments were possible at all stations, except at ST18 and SF2 (only ROV data because the bottom was too rocky to safely conduct trawls) and at SF5 (only trawl data because strong currents prohibited ROV deployment) (Fig. 1).

Environmental data (i.e., temperature, salinity and oxygen) used in our analysis were obtained from the global three-dimensional CSIRO Atlas of Regional Seas (CARS) climatology (2009 version) as presented by Mecho et al.37.

Habitat description based on ROV videos. The oceanic islands (OI) and seamounts (SM) were considered as two different environments (corroborated by statistical analyses presented below) and were referred to as subsystems, based on differences in physiography and depth. The characteristics of the seafloor habitats for each subsystem were described based on ROV data. Videos for each dive were analyzed in a time-lapse mode at half normal speed in VLC media Player 3.0.1. Habitats were classified at different spatial scales: (1) macrohabitats (i.e., meter-scale) and (2) microhabitats (i.e., centimeter-scale). The habitat types were described by geomorphology, including by slope (i.e., flat = 0°–5°, sloping = 5°–30°, steeply sloping = 30°–60°, vertical = 60°–90°), sediment type (i.e., rock, silty sediments, mixed substrate, coarse sand), texture (i.e., low rugosity, moderate rugosity, high rugosity) and “modifier” elements (i.e., biological communities, sedimentation and bio-perturbation) following Greene et al.31,32. The sections of the videos in which the ROV was steadily moving between 30 cm and 1 m above the ground along the bottom were used for the description of the macrohabitats (field of view per frame ~ 3 m²), and the sections in which the ROV remained sitting on the bottom (field of view per frame ~ 0.05 m²) were used.
for the description of the microhabitats. The field of view per frame was estimated using the laser pointers of the ROV (positioned 10 cm apart).

**Benthic and demersal fauna description.** Specimens collected with the Agassiz trawl were preliminarily sorted, counted, and preserved onboard in 95% ethanol. Definitive counts and identification to the lowest possible taxonomic unit (hereafter operational taxonomic units, or OTUs) were performed at Sala de Colecciones Biológicas Universidad Católica de Norte (SCBUCN), where specimens were then assigned an ID number and cataloged. The observed fauna was classified according to relevant literature and previous reports for the area (e.g.,15, 39–45). Taxonomic assignments were further validated with resources such as the World Register of Marine Species (Worms, 2020. [http://www.marinespecies.org](http://www.marinespecies.org)) and the Ocean Biodiversity Information System (OBIS, 2020, Intergovernmental Oceanographic Commission of UNESCO. [www.iobis.org](http://www.iobis.org)).

Semi-quantitative data of abundance for each OTU were calculated based on the swept area for each trawl. The swept area (\(A_{bi}\)) was established as the product of the trawling speed (\(V_t\)), effective trawl time (\(t_i\)) and width of the mouth of the trawl (\(A_{hi}\)) and abundance was standardized to 10 m\(^2\) following Barriga et al.\(^{46}\):

\[ Ab_i = t_i V_t A_{hi} \]

The ROV recordings followed an exploratory methodology which restricted the data to the presence/absence of OTUs at each station. Videos for each transect were viewed at half their normal speed in VLC. The VLC tool “Interactive Zoom” was used to magnify images to observe the diagnostic characteristics of the taxa. Observations that were blurry or too distant were omitted because they did not provide sufficient details for identification.

All the sampling was performed under permission Res. Ext N°3685/2016 from SUBPESCA (National Fishing Authority of Chile) to Universidad Católica del Norte.

**Data analysis.** All analyses were performed using the R software, version 4.0.3\(^{47}\) using the “vegan v2.5-6” package\(^{48}\). Because both trawl and ROV data were not available for all stations (Table S1), the analysis approach considered either only trawl data or combined trawl and ROV data as follows. Only trawl data was used for the estimation of Shannon diversity (\(H\)) and Pielou’s evenness (\(J\)) since abundance data is required. OTU richness (or total \(S\)) of each station was estimated based on the combined trawl and ROV data (except for ST18, SF2 and SF5 stations). In all cases, only "living" organisms were considered (i.e., empty shells or skeletons excluded) for the analyses. Species accumulation curves were constructed for each subsystem (OI and SM) and data gathering approaches (only trawl and combined trawl and ROV data) to estimate the ratified number of species and to assess sampling effort\(^{48}\). The OTU richness and diversity indexes of the two subsystems (OI and SM) were considered either only trawl data or combined trawl and ROV data as follows. Only trawl data was used for the estimation of Shannon diversity (\(H\)) since abundance data is required. OTU richness (or total \(S\)) of each station was estimated based on the combined trawl and ROV data (except for ST18, SF2 and SF5 stations), was conducted. The routine “adonis2” on the Bray–Curtis index of similarity of the raw OTU presence/absence data (10,000 runs) with subsystems (two levels: OI and SM) and maximum depth as factors was used. Patterns in the structure of benthic communities among subsystems and stations were visualized using a cluster analysis UPGMA hierarchical clustering (using the functions “desvest” and “hclust”) and non-metric multidimensional scaling (nMDS; using the function “metaMD”) analyses based on Bray–Curtis dissimilarity elaborated from OTU presence/absence data. To analyze differences in functional diversity among sampling stations, OTUs were assigned to feeding modes (i.e., suspension, depositor, grazer, opportunistic or predator) and movement type (i.e., sessile, burrower/tube dweller, crawler or swimmer) based on functional traits and associated categories as proposed by Jones & Frid\(^{49}\). A canonical correspondence analysis (CCA) was applied using the R function “cca” to relate the set of environmental parameters to: (1) OTUs presence/absence data, (2) feeding mode composition, and (3) movement type. Environmental variables included water hydrographic variables (temperature and oxygen), type of bottom (rock, mud and sand), depth, and geographic position (longitude and latitude). Salinity was not considered within the environmental variables in the nMDS and CCA because it co-varies with the oxygen. nMDS and CCA analysis were graphed using the library ggplot2 v3.3.2 in R\(^{40}\).

**Results.**

**Description of macrohabitats.** Oceanic island macrohabitats (~43 to 370 m depth) were classified to one of three types (Table 1): (1) cobbles and bedrocks, predominated by sea urchins (i.e., Centrostephanus sylviae, Fig. 2A), (2) coarse sand, with anemones (mainly Hormathia sp.) (Fig. 2B), and (3) silty sediments with the presence of bioturbation (e.g., burrows) ripples with a maximum height of ~ 10 cm (Fig. 2C).

Seamount macrohabitats (~150 to 305 m depth), except at SF2, consisted of coarse sand and rhodolith beds (Fig. 2D, E, Table 1) with large patches of anemones and sea pens. Seamount SF2 substantially differed from the others by the predominance of hard substrates and a steep slope of compact cemented rock, with small patches of coarse sand and large rock formations. The sessile fauna of seamount SF2 consisted of a multitude of hydrozoans, sea pens, and small corals, among other sessile fauna associated with rocky substrates. Also, the presence of longitudinal trenches in the cemented rock gave shelter to numerous fishes (e.g., Lotella cf. fernandeziana, Helicolenus lengerichi and Scorpaena thomsoni) and large crustaceans (e.g., the Chilean jagged lobster Projasus bahamondei and the Juan Fernández carrier crab Paromola rathbuni) (Fig. 2F).

**Description of microhabitats.** Oceanic island microhabitats were classified into one of three types (Table 1): (1) joints, cracks, crevices, and overhangs (differentially eroded) covered by incrusting algae, sponges and stony corals (Fig. 3A) at 43–50 m; (2) coarse sand with sea pens and anemone colonies, which provide
### Table 1. Description of benthic habitats of the oceanic islands (Desventuradas). Classification follows Greene et al. and Greene et al. Subsystem OI = oceanic islands (upper slope) and SM = seamounts (top).

| Stations | Subsystem | Class (macrohabitat) | Subclass (microhabitat) | Environmental variables | Modifiers |
|----------|-----------|----------------------|-------------------------|-------------------------|-----------|
| ST17 OI  | Flat bottom| Flat bottom          | Slope: flat (0–5°)      | Salinity: 3.4          | Bottom morphology: regular-continuous homogeneous bottom with little relief with organic debris (coquina) Biophysical processes: conspicuous microhabitats/communities of anemone, sea pens and kelps patch |
|          |           |                      | Texture: smooth surface | Temperature (°C): 13.9  |           |
|          |           |                      | Sediment types: mixed sediment, coarse sand | Oxygen (mL/L): 5 |           |
| ST18 OI  | Sloping bottom, with vertical sections | Type I: steep slope bottom | Slope: steeply sloping (30°–60°) | Salinity: 3.7 | Bottom morphology: irregular bottom with structures fractured, faulted and folder Bottom texture: occupied by clast or rock Biological processes: conspicuous microhabitats/communities of coralline encrusting algae, sponge and anemone |
|          |           |                      | Texture: moderate rugosity to high rugosity surface | Temperature (°C): 17.7 |           |
|          |           |                      | Sediment types: bedrock and boulder | Oxygen (mL/L): 5.5 |           |
| ST20 OI  | Flat bottom | Type I: steep slope bottom | Slope: flat (0°–5°) | Salinity: 3.4 | Type I Bottom morphology: irregular bottom with structures fractured, faulted and folder Bottom texture: occupied by clast or rock Biological processes: conspicuous microhabitats/communities of coralline encrusting algae, sponge and anemone |
|          |           | Hard substrates and steep slope of compact cemented rock | Texture: very low rugosity | Temperature (°C): 12.9 | Type II Bottom morphology: irregular bottom with structures fractured, faulted and folder Bottom texture: occupied by clast or rock Biological processes: conspicuous microhabitats/communities of coralline encrusting algae, sponge and anemone |
|          |           | Type II: flat bottom | Sediment types: mixed sediment, coarse sand | Oxygen (mL/L): 4.7 |           |
| ST21 OI  | Flat bottom | Steep slope bottom | Slope: flat (0°–5°) | Salinity: 3.4 | Bottom morphology: regular-continuous homogeneous bottom with little relief Biological processes: conspicuous microhabitats/communities of anemones and sea pens |
|          |           | Type I | Texture: smooth surface | Temperature (°C): 12.9 |           |
|          |           | Type II | Sediment types: mixed sediment, coarse sand | Oxygen (mL/L): 4.7 |           |
| ST22 OI  | Flat bottom | Sloping bottom | Slope: sloping (5°–30°) | Salinity: 3.5 | Bottom morphology: irregular bottom (Undulated surface - ripples) with sediment waves (10 cm to amplitude) Bioturbation: burrows and excavations |
|          |           | with bedform-sediment waves | Texture: moderate rugosity | Temperature (°C): 8.4 |           |
|          |           | Hard substrates and steep slope of compact cemented rock | Sediment types: silty sediments | Oxygen (mL/L): 1.3 |           |
| SF2 SM (top) | Steep slope bottom | Steep slope bottom | Slope: steeply sloping (30°–60°) | Salinity: 3.5 | Bottom morphology: rock bottom with smalls accumulation of coarse sand Biological processes: conspicuous microhabitats/communities of sponges, sea pens and white corals |
|          |           | Type I | Texture: moderate rugosity to high rugosity surface | Temperature (°C): 10.4 |           |
|          |           | Type II | Sediment types: mixed sediment, coarse sand | Oxygen (mL/L): 1.6 |           |
| SF6 SM (top) | Flat bottom | Flat bottom | Slope: flat (0°–5°) | Salinity: 3.4 | Bottom morphology: regular-continuous homogeneous bottom with little relief Biological processes: conspicuous microhabitats/communities of anemones, hydroiden colonies, biocenosis (sea urchin skeletons) |
|          |           | Texture: smooth surface | Sediment types: mixed sediment, coarse sand | Temperature (°C): 13.5 |           |
|          |           | Flat bottom | Oxford: occupied by clast or rock | Oxygen (mL/L): 4.4 |           |
| SF7 SM (top) | Flat bottom | Flat bottom | Slope: Flat (0–5°) | Salinity: 3.4 | Bottom morphology: regular-continuous homogeneous bottom with little relief Biological processes: conspicuous microhabitats/communities of anemones, rhodoliths, sponges, thanatocoenosis (coquina- Pteropod shells) |
|          |           | Texture: smooth surface | Sediment types: mixed sediment, coarse sand | Temperature (°C): 13.5 |           |
|          |           | Flat bottom | Biological processes: thanatocoenosis (coquina- bivalve shells); Bioturbation (burrows and excavations) | Oxygen (mL/L): 4.4 |           |
| SF8 SM (top) | Flat bottom | Flat bottom | Slope: Flat (0–5°) | Salinity: 3.4 | Bottom morphology: regular-continuous homogeneous bottom with little relief Biological processes: thanatocoenosis (coquina- bivalve shells); Bioturbation (burrows and excavations) |
|          |           | Texture: smooth surface | Sediment types: mixed sediment, coarse sand | Temperature (°C): 10.3 |           |
|          |           | Flat bottom | Biological processes: thanatocoenosis (coquina- bivalve shells); Bioturbation (burrows and excavations) | Oxygen (mL/L): 2.1 |           |
| SF9 SM (top) | Flat bottom | Flat bottom | Slope: Flat (0–5°) | Salinity: 3.4 | Bottom morphology: regular-continuous homogeneous bottom with little relief Biological processes: conspicuous microhabitats/communities of anemones, amphinomid polychaetes and detrital patch |
|          |           | Texture: smooth surface | Sediment types: mixed sediment, coarse sand | Temperature (°C): 10.3 |           |
|          |           | Flat bottom | Biological processes: conspicuous microhabitats/communities of anemones, amphipod polychaetes and detrital patch | Oxygen (mL/L): 4.3 |           |
| SFX SM (top) | Flat bottom | Flat bottom | Slope: Flat (0–5°) | Salinity: 3.4 | Bottom morphology: regular-continuous homogeneous bottom with little relief Biological processes: conspicuous microhabitats/communities of anemones, amphipod polychaetes and detrital patch |
|          |           | Texture: smooth surface | Sediment types: mixed sediment, coarse sand | Temperature (°C): 11.5 |           |
|          |           | Flat bottom | Biological processes: conspicuous microhabitats/communities of anemones, amphipod polychaetes and detrital patch | Oxygen (mL/L): 2.6 |           |
Cnidarians and sponges are the most conspicuous biological components of seamount microhabitats (~ 150 to 305 m depth), which included fields of sea pens (Protoptilum sp. and Scleroptilum sp.) and colonies of anemones (Hormathia sp. and Cerianthid), except at SF2. Besides, we also reported biogenic structures on coarse sand beds such as coquina of pteropod (Fig. 3D) and rhodoliths (Fig. 3E). Although the SF2 seamount is characterized by a hard and fractured substrate (faults and folds) covered with small corals (Stylaster cf. marenzelleri) and green
sponges, small patches of coarse sand were observed between the rocks with sea pens of the genus *Scleroptilum* (Fig. 3F).

**Figure 3.** Benthic microhabitats on the upper slope of Desventuradas islands (A–C) and summits of seamounts (D–F) at the Nazca-Desventuradas Marine Park. (A) Rocky bottom dominated by incrusting red algae, sea urchin *Centrostephanus sylviae*, the cracks and faults of the rocky bottom, are used as habitats for moray eels (*Gymnothorax porphyreus*) and small fishes (*Pseudolabrus cf. gayi*), (B) coarse sand flat bottom dominated by anemones (*Hormathia* sp.), (C) soft-sediment with burrows and excavations, (D) microhabitats of cerianthid anemones and hydrozoan colonies, (E) unattached nodules of crustose coralline red algae (Rhodoliths), demosponges, and coquina of pteropod shells, (F) irregular rock bottom with structures fractured, faulted and folded, characterized by sea pens (*Scleroptilum* sp.) and hydrozoan corals (*Stylaster* sp.). Scale bar: 10 cm. Image credits: ESMOI/OCEANA.

**Benthic community.** In total, 2414 individuals (only living specimens) were collected by trawling and assigned to 95 OTUs (OI: 44 OTUs and SM: 75 OTUs, 24 OTUs shared between subsystems), belonging to nine phyla (Table S2). In terms of total abundance, Cnidaria was the predominant major faunal group, comprising 29% of the total capture, followed by Porifera (26%), Arthropoda (13%), Echinodermata (13%), Mollusca (7%) Annelida (7%), Sipuncula (5%), Chordata (1%) and Bryozoa (0.2%). ROV observations resulted in a total of
61 OTUs (OI: 46, SM: 38, shared between subsystems: 23), of which 23 OTUs were observed only with this approach, 17 of these 23 OTUs were fish.

Combining collected specimens and ROV observations allowed allocation of a total of 118 OTUs (OI: 65, SM: 84, and shared between subsystems: 31). An additional 13 OTUs were identified just by shells or skeleton remains (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4). Chordata (25%), Arthropoda (23%), Mollusca (13%) (e.g., pteropod or other mollusk shells), but were not included in the analyses. Invertebrates represented 75% of the OTUs, whereas vertebrates represented 25% (Fig. 4).
Figure 4. Representative OTUs observed at the upper slope of Desventuradas islands and seamounts within the Nazca-Desventuradas Marine Park. (A) Sea pen Protoptilum sp. and anemone Hormathia sp., (B) anemone (Hormathia sp.) and hermit crab Paragopagurus boletifer, (C) Cryptogemma praesignis, (D) Anthenoides sp., (E) Clypeaster isolatus, (F) Notopogon fernandezianus, (G) anemone colony Hormathia sp., (H) Chloea sp., (I) Paromola rathbuni, (J) Streptocidaris nascaensis (left) and Scrippsechinus fisheri (right), (K) Squalus mitsukurii, (L) Gonorhynchus greyi, (M) tube anemone Ceriantharidae, (N) Chryseofusus kazdailisi, (O) Projasus bahamondei, (P) Pseudarchaster sp., (Q) Tetronarce sp., and (R) Lotella fernandeziana. Laser pointers, when visible, are 10 cm apart. Image credits: ESMOI/OCEANA.
Seas Expedition” at depths of 20 to 350 m at the Desventuradas Islands and reports of substrates on other seamounts. These observations are consistent with the description of the macrohabitat made by “Pristine patches of habitat-forming sessile species and rhodoliths was the most commonly observed at oceanic islands and seamounts of the SGR15, 19 as well as of the eastern Pacific Ocean52, northeast Atlantic53 and equatorial Atlantic9. For example, Parin et al.15 reported, based on collections and observations made from a manned submersible, that the upper slopes of SGR seamounts located >400 km NW of Desventuradas Islands had a soft bottom composed of biogenic sands derived from shells of local mollusks with some pelagic pteropods, foraminiferal material and fossil corals. We observed a change in the kind of sediment/ bottom type with predominantly coarse sands at the 150–180 m stations and predominantly fine sands at 220–370 m. This pattern of sediment change with depth has also been recorded in other deep-sea areas54–57.

The rocky macrohabitat observed on oceanic island ST18 (Fig. 2A) is similar to other islands located in the southwest Pacific. For example, Lord Howe Island (~33°S, 159°E, ~600 km E of Australia) is also an isolated, endemism hotspot with several similarities to Desventuradas Islands20. The macrohabitat of Lord Howe Island at a depth of 50 m is characterized by having a rocky bottom covered with encrusting red algae and being dominated by urchins (Tripneustes and Centrostephanus)20,50. The rocky substrate (i.e., steep slope of compact cemented rock) observed at seamount SF2 (Fig. 2F) is consistent with the macrohabitat of other seamounts of the NR (e.g., Professor Mesyatzev, Soldatov, Ikhtiandr and Ekliptika; ~81–83°W) reported by Parin et al.15. This macrohabitat is characterized by the presence of a longitudinal trench in the cemented rock, which gives shelter to numerous species of fishes (e.g., Helicolenus lengerichi and Scorpaena thomsoni) and large crustaceans (e.g., the Chilean jagged lobster Projasus bahamondei and the Juan Fernández carrier crab Paromola rathbuni) (Fig. 2F).

Until recently, most seamount research related to benthic habitat heterogeneity and complexity has focused on larger-scale variations (macrohabitats)58. Unlike hard-bottomed habitats, soft-bottom habitats have generally been considered unstructured, homogeneous environments; consequently, these habitats have been studied primarily from a landscape perspective (usually at a kilometer scale)59. Hence, Clark et al.59 suggested that the concept of seamounts as a single, relatively well-defined habitat type appears outdated, giving way to a growing recognition that within seamount variability can have different spatial scales. Although not statistically tested, our results suggest a higher faunal diversity associated with biogenic microhabitats compared to sites with few or no biogenic microhabitats (e.g., SF8 and SFX), further supporting the importance of such small-scale differences in understanding the mechanisms involved in maintaining species diversity and the linkages between habitat-forming species and users of these habitats (Table S4). The presence of multiple distinct morphologies of the deep seabed, such as, scars, channels, mud, rocks and sand, together with habitat-forming species (e.g., sponge, anemones and stylasterids corals) provide an environment that is home to numerous species, resulting in increases in diversity60. Besides, habitat-forming species are known to promote local complexity and

| Site  | Subsystem | OTUs richness (S) | Total S (trawl + ROV) | Diversity (H’) | Evenness (J) |
|-------|-----------|-------------------|-----------------------|---------------|-------------|
| ST17  | OI        | 4                 | 15                    | 1.3           | 1.0         |
| ST18  | OI        | –                 | –                     | –             | –           |
| ST20  | OI        | 27                | 35                    | 2.5           | 0.8         |
| ST21  | OI        | 13                | 15                    | 1.3           | 0.5         |
| ST22  | OI        | 6                 | 11                    | 1.6           | 0.9         |
| Mean  | OI        | 12                | 17                    | 1.7           | 0.8         |
| SF2   | SM        | –                 | –                     | –             | –           |
| SF5   | SM        | 32                | –                     | 2.2           | 0.6         |
| SF6   | SM        | 19                | 27                    | 2.2           | 0.7         |
| SF7   | SM        | 19                | 35                    | 2.5           | 0.9         |
| SF8   | SM        | 6                 | 8                     | 1.6           | 0.9         |
| SF9   | SM        | 45                | 50                    | 1.9           | 0.5         |
| SFX   | SM        | 11                | 13                    | 1.3           | 0.6         |
| mean  | SM        | 22                | 24                    | 1.9           | 0.7         |

Table 2. OTU richness based on trawl data, total S (trawl + ROV) data and diversity and evenness indexes obtained from relative OTU abundances of only trawl data. Subsystem OI = oceanic islands and SM = seamounts. Only ROV (***).

Discussion
This study constitutes the most complete and updated description of benthic habitats and fauna for the upper slope of Desventuradas Islands and summits of nearby seamounts within the NDMP. ROV videos allowed the first description of benthic habitats of the Desventuradas Islands and their surrounding seamounts at a fine scale (meters to centimeters). Although we are aware of the limitations of the present study (e.g., only one ROV dive and/or trawl per site), we consider that our information presents a fundamental base-line knowledge of the benthic fauna and environment in this relatively understudied region of the Pacific Ocean, with a high value for conservation.

Of the three macrohabitats (Fig. 2, Table 1) observed in this study, relatively homogeneous coarse sand with patches of habitat-forming sessile species and rhodoliths was the most commonly observed at oceanic islands and seamounts. These observations are consistent with the description of the macrohabitat made by “Pristine Seas Expedition” at depths of 20 to 350 m at the Desventuradas Islands and reports of substrates on other seamounts of the SGR15,16 as well as of the eastern Pacific Ocean15, northeast Atlantic20 and equatorial Atlantic6. For example, Parin et al.15 reported, based on collections and observations made from a manned submersible, that the upper slopes of SGR seamounts located >400 km NW of Desventuradas Islands had a soft bottom composed of biogenic sands derived from shells of local mollusks with some pelagic pteropods, foraminiferal material and fossil corals. We observed a change in the kind of sediment/ bottom type with predominantly coarse sands at the 150–180 m stations and predominantly fine sands at 220–370 m. This pattern of sediment change with depth has also been recorded in other deep-sea areas54–57.

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Figure 5. (A) Cluster analysis (UPGMA method) based on Bray–Curtis dissimilarity, (B) non-metric multidimensional scaling (nMDS) ordination plot based on presence/absence data of the benthic megafauna, and (C) canonical correspondence (CCA). Analysis based on the community structure of benthic megafauna, grouped at major taxa level, from stations sampled at Desventuradas Islands (blue markers) and seamounts (red markers) of the Nazca Desventuradas Marine Park. Vectors in (B) and (C) represent contribution of environmental descriptors (salinity, oxygen, temperature, substrate type, depth, latitude and longitude), and ellipses in (B) represent the 95% confidence interval. Image generated using R software (version 4.0.3)47.
heterogeneity of the seafloor at small (microhabitat) to large (macrohabitat) scales and to provide suitable refuge and nursery zone for smaller mobile benthic organisms\cite{15, 19, 20, 60, 61}. Consistent with this pattern, it appears that OTU richness may be higher where habitat-forming species, such as sea pens (\textit{Protoptilum} and \textit{Scleroptilum}), anemones (\textit{Hormathia} sp.), tube-dwelling anemones and stylasterids corals were present (Table S4). Microhabitats within and among seamounts differed based on small modifications in the seafloor substrate and the presence of habitat-forming species such as anemones (\textit{Hormathia} sp.), tube-dwelling anemones (cerianthids) and sea pens (\textit{Protoptilum} sp. and \textit{Scleroptilum} sp.). A marked pattern was observed between substrate type (soft vs. hard) and the type of habitat-forming species; anemones and sea pens of the genus \textit{Protoptilum} were observed frequently on soft bottoms, whereas sea pen of the genus \textit{Scleroptilum} and stylasterids corals were reported on hard bottoms. Similar patterns have been described for deeper habitats (> 400 m depth) of NR and SGR seamounts and oceanic islands\cite{15, 19} and also for New Caledonia, particularly on the Norfolk Ridge seamounts\cite{20}.

Habitat-forming species were distributed as small patches that supported a higher concentration of fauna compared to the surrounding seafloor, providing a structure that can support more species than habitats without such complexity\cite{20}. For example, at NDMP seamounts, squat lobsters (\textit{Munida dirita} and \textit{Phylladiorhynchus pusillus}), crabs (\textit{Latreillia} sp.) and juveniles of \textit{Caprodon longimanus} were observed hidden among anemones (Fig. 3D). This type of seamount microhabitat is mainly composed of coarse sand and rhodoliths with anemones, sea pens and tube-dwelling anemones, which likely provide nursery zones for some fishes, as suggested by ROV observations of the presence of juveniles of \textit{C. longimanus} in these anemone patches (SF6 and SF7 seamounts). Another role of microhabitats is contributing to predator–prey dynamics; for example, the use of microhabitats not only plays a role in predator avoidance by providing shelter but can also play a role in ambush tactics by providing a focal site where the prey may not recognize the predator\cite{21}. In our study, squat lobsters (\textit{Munida}...
similar resources at a low trophic level\textsuperscript{16, 23}. A similar pattern was described for the New Caledonian seamounts, might have short food webs and low guild complexity, i.e., the majority of the animals in seamounts consume \textit{Paragiopagurus} deposit feeders (e.g., \textit{Eisenia cf. zebra} and \textit{Mesocheaetopus minutus}), bringing the total to 15 genera and five species\textsuperscript{15, 21, 43, 67}; 17 genera and 15 species of crustaceans (e.g., \textit{Miersiella baswelli}, \textit{Zarenkolambrus minusus}, \textit{Z. ephranchialis}, \textit{Heteronida sp.}, \textit{Munida diritas} and \textit{Hispidolambrus mironovi}) (Table S2), bringing the total to 25 genera and 23 species\textsuperscript{44, 45, 72}, and two genera of fishes (\textit{Tetronarce} sp. and \textit{Callionymus} sp.). Fishes is the best documented group in the NDMP area, including reports by Sepulveda\textsuperscript{68}, Pequeño & Lamilla\textsuperscript{40}, Dyer & Wesneat\textsuperscript{39} and National Geographic & Oceana\textsuperscript{51} around the Desventuradas Islands from 5 to 2.215 m depth and the summit of the Stockman guayot (station SFX) at 200 to 370 m depth.

Therefore, it is probable that a greater sampling effort (i.e., higher area coverage and including flanks and bases of seamounts) will continue revealing substantial numbers of novelties for the region. Although rare invertebrate species and possibly new species were observed in the present study, none of the new records appear to be endemic to a particular seamount (Table S2). However, finer-scale studies may help to uncover diversity patterns of species within and among seamounts in this region. Furthermore, because of limited sampling across the southeast Pacific, available information is still insufficient to assess the high endemism and regional affinity of the NDMP fauna.

Although out of the scope of the present study, we provide records that would help to better assess the hypothesis of a faunal transition zone or ‘break’ proposed by Mironov & Detinova\textsuperscript{49} and subsequently by Parin et al.\textsuperscript{15} and Mecho et al.\textsuperscript{27} which divides the hard-bottom seamounts of south NR from the soft bottom seamounts of the east SGR. Parin et al.\textsuperscript{15} suggested a faunistic break at ~ 88°W. Mecho et al.\textsuperscript{27} observed remarkable turnovers of echinoderms at ~ 101° and ~ 86°W of the SGR, where assemblages tended to differ more across seamounts, suggesting the effects of physical barriers to dispersion (e.g., currents) and habitat changes. Our data suggests a transition zone located at the intersection of SGR and NR (~ 82.5°W), as indicated by the separation among stations in the nMDS (Fig. 5B) and CCA (Fig. 5C) coinciding with the initial position (~ 82–84°W) proposed by Mironov & Detinova\textsuperscript{49}. Differences among the communities can also be seen in the functional groups and composition of the fauna of the seamounts of the NDMP separated by this approximate longitude (Fig. S2). Sea-mount SF2 is the only hard-bottomed seamount explored, with a mobile fauna with a type of feeding associated with predators such as the spiny lobster \textit{Projasus bahamondesi} and shark \textit{Squalus mitsukurii}. These characteristics are shared with other seamounts such as Zvezda to Bolshaya further northeast in the NR\textsuperscript{15}. In contrast, the other seamounts studied coincide more with the characteristics reported for the SGR because they have a soft bottom and sessile/hemisessile benthic megafauna with a generalist feeding mode\textsuperscript{15}.

The CCA\textsuperscript{8} (Fig. 6) suggest that differences in feeding mode and mobility of the megafauna appear to be linked to habitat type, depth, temperature and oxygen. Such patterns have been observed in other seamounts or deep habitats reported in literature\textsuperscript{15, 70}. The megafauna of the Desventuradas Islands was characterized by a comparable high frequency of occurrence and diversity of fishes (e.g., \textit{Suezichthys rosenblatti}, \textit{Paratrimma sp.}, \textit{Parapercis cf. dockinsi} and \textit{Seriola lalandi}) and large predators such as the shark \textit{Squalus mitsukurii}. This predominance of fishes is likely the result of the islands having a biogenic structure that could support higher fish densities because of higher availability of nutrients, terrigenous contributions and eventual trophic subsidies by macroalgae (e.g., \textit{Eisenia cf. coker})\textsuperscript{96, 70}. In contrast, the seamount fauna was characterized by having hemisessile and sessile fauna that are opportunistic suspension feeders (e.g., \textit{Hormathia sp. Prototelmat sp. Scleroptilum, and Stylochera sp.}) or deposit feeders (e.g., \textit{Paragigapagurus} spp. and \textit{Munida diritas}). This pattern suggests that the seamounts of NDMP might have short food webs and low guild complexity, i.e., the majority of the animals in seamounts consume similar resources at a low trophic level\textsuperscript{16, 23}. A similar pattern was described for the New Caledonian seamounts, where it has been hypothesized that the length of the food chain in seamounts is shorter than in other aquatic systems\textsuperscript{16}. These authors also found that although the food web in seamounts is short, it is still relatively complex.
Conclusions
This study constitutes a first descriptive addition to the knowledge of benthic micro- and macrohabitats of the slope of Desventuradas Islands and summits of nearby seamounts within the NDMP, providing the most complete description of their benthic megafauna to date. The benthic habitats of oceanic island slopes and seamounts within the NDMP are home to a large diversity of habitats, including rock, rhodoliths, sandy bottoms, silty bottoms, vertical walls and caves. Our study highlights that faunal composition differed with seafloor habitat. For example, higher values of diversity and OTU richness were observed in areas with a predominance of habitat-forming species, which points to the need to study seamounts at finer scales (centimeters to meters) to better understand the links of habitat-forming species and faunal communities and the potential effects that would result from the loss of macro- and microhabitat-forming species. Currently, these habitats within the NDMP are in an apparent pristine state (i.e., without evident signs of human impacts, such as marine litter or trawled areas). Thus, these seamounts, now under protection, provide a regional unique opportunity to monitor effects of climate change without the confounding factor of human activities, such as fishing, deep seabed mining or bottom trawl fishing, and could also be useful for comparisons with other places in the world where such closures have been implemented for seamounts in the Azores, SW Indian Ocean, New Zealand, Hawaiian Islands and Palau, to mention a few.

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Author contributions
J.M.T. processed and identified specimens, analyzed the data, and wrote the manuscript. J.S., A.M., E.E.E. and M.G. developed the proposal and secured funding for participation in the CIMAR22 cruise. A.M., E.E.E. and M.G. conducted fieldwork, assisted in specimen identifications and other lab work, and contributed to writing and editing the manuscript. J.S. and M.A.G assisted in species identification, analyzed the data, contributed to writing and editing the manuscript. All authors reviewed the final version of the manuscript.

Competing interests
The authors declare no competing interests.

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