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Megabenthos and benthopelagic fishes on Southeast Atlantic seamounts

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In a descriptive study of megafauna of several Southeast Atlantic seamounts, multiple video-transects on upper slopes and summits documented the occurrence of benthic invertebrate taxa, primarily corals, regarded as indicators of vulnerable marine ecosystems (VMEs) as defined in international guidelines. At Schmitt-Ott Seamount there was a pronounced dominance of gorgonian corals (seafans, Alcyonacea). In all other study areas the diversity was greater, and more scleractinians (stony corals, Scleractinia) were observed. Scleractinian corals were mainly dead, and much of the coral framework and rubble may have been ancient. In the Valdivia complex and on Ewing Seamount, which are open to fisheries, scleractinians seemed restricted to some slopes of knolls, and on Valdivia Bank and the subarea denoted Valdivia West the summit substrate was mostly bare rock. Pelagic armourhead *Pseudopentaceros richardsoni* and splendid alfonsoino *Beryx splendens* (two targets of commercial fisheries in the area) were observed at a few sites, but did not appear to be abundant in the main former fishing areas of the Valdivia area. Orange roughy *Hoplostethus atlanticus* was common in video records around the summit at Ewing Seamount. The deep-sea red crab *Chaceon erythraeus* was abundant in the Valdivia area and at Ewing Seamount, and crabs were distributed across a more extensive depth range than the fishes. In areas with high densities of live coral, the video records suggested that the benthic communities were intact and not impacted by fishing. Evidence of past fishing activities included observations of lost pots and rope at Vema Seamount and in the Valdivia area.

Keywords: acoustic survey, coral, deep sea, fisheries resources, high seas, video observation, vulnerable marine ecosystems

Online supplementary material: Supplementary Figures S1–S6 (available at <https://doi.org/10.2989/1814232X.2019.1571439>) show echograms from crossings of the summits at the five selected Southeast Atlantic seamounts visited by the RV *Dr Fridtjof Nansen* in January–February 2015

Introduction

The myriad seamounts of the World Ocean are recognised as diverse features in terms of location, geomorphology, size and summit depth, reflecting geological origin, age and evolution through geological history (e.g. Wessel 2007). Seamounts are also very diverse in terms of biological communities and ecological characteristics (Rogers 1994; Consalvey et al. 2010). Common assertions that seamounts are unique environments, hotspots of biodiversity and endemism, and fragile ecosystems of exceptional ecological worth, have been questioned by some (Rowden et al. 2010), partly because only a few hundred seamount ecosystems have been sufficiently studied to draw firm conclusions. However, it is well documented that many seamount communities have biota that have been negatively impacted by fishing with bottom-contact fishing gear (e.g. Clark and Koslow 2007), and

seamounts are thus features likely to need special protection. Many seamounts are inhabited by communities regarded as vulnerable marine ecosystems (VMEs) by pertinent UN General Assembly resolutions (e.g. UNGA 61/105 and later), and the associated FAO International Guidelines for the Management of High-Seas Bottom Fisheries (FAO 2009).

Numerous seamounts with summits within the operational depths of bottom fisheries were never studied at relevant spatial scales, and information on biological communities remains very scarce or non-existent. Even in such virtually unknown areas, exploratory and regular fishing activities have taken place. While the exact documentation of the scales and locations of past activity is often poor, it is likely that most seamount summits shallower than 1 000–2 000 m have been visited and explored during the extensive

international exploratory efforts starting in the 1970s onwards (e.g. Clark et al. 2007). This is also likely to be the case in the oceanic areas beyond national jurisdiction (ABNJ) in the Southeast Atlantic. This region has hundreds of seamounts, a subset of which have summits shallower than 2 000 m and thus range into fishable depths. Past fisheries have targeted seamount resources (fish and deep-sea crustaceans) using trawls, pots and longlines, but, whereas current fisheries are monitored well by the intergovernmental regional fisheries management organisation (i.e. South East Atlantic Fisheries Organisation [SEAFO]), the historical record prior to around 2000 is probably incomplete.

For most of the seamounts in the Southeast Atlantic, very few data exist, or the documentation of benthic communities is missing. Coarse data on likely benthic communities can be derived from biogeographic analyses (e.g. Stocks and Hart 2007) and habitat suitability models predicting occurrence of benthic invertebrates on wide geographical scales (e.g. Bryan and Metaxas 2007; Tittensor et al. 2009; Davies and Guinotte 2011). Model predictions have relatively low spatial resolution, however, and are rather strongly influenced by bathymetry, which is not well mapped at local scales (Jacobs and Bett 2010). In limited subareas of the Southeast Atlantic some spatially resolved data on geomorphology and biota were acquired by recent Spanish–Namibian research activity on the Valdivia and Ewing seamounts (López Abellán and Holtzhausen 2011; Durán Muñoz et al. 2012). An earlier Spanish study of decapod crustaceans at the Valdivia Seamount complex described seven new species (Macpherson 1984). For other features, such as the prominent, previously fished Vema Seamount, only basic mapping with single-beam echosounders and various benthos samplers was conducted in the past (Simpson and Heydorn 1965; Mallory 1966; Berrisford 1969). There are also earlier records of various invertebrate taxa from bottom-trawl studies (e.g. scleractinian corals by Zibowius and Gili [1990]), and some distribution data on deep-sea red crab *Chaceon erythraea* are available from fisheries records (SEAFO Scientific Committee reports at www.seafo.org).

Furthermore, there is a shortage of data on the seamount-associated fishes inhabiting the Southeast Atlantic. This includes species presently or previously targeted by commercial fisheries, primarily Patagonian toothfish *Dissostichus eleginoides*, pelagic armourhead *Pseudopentaceros richardsoni*, splendid alfonso *Beryx splendens* and orange roughy *Hoplostethus atlanticus*. The assessments of the status of these target fish (and crab) stocks of the currently minor seamount fisheries in the area remain unsatisfactory because of a lack of appropriate time-series data and research-vessel surveys monitoring the stocks (e.g. see SEAFO Scientific Committee reports, www.seafo.org).

SEAFO introduced comprehensive measures to protect VMEs (as defined in FAO [2009]) and resources in the ABNJ (Figure 1). Commercial harvesting in the SEAFO Convention Area (SEAFO CA) is currently restricted to certain subareas ('existing fishing areas,' as defined in SEAFO Conservation Measure [CM] 30/15, www.seafo.org), and is further regulated by other measures, such as species-specific annual total allowable catches (TACs), gear restrictions and a measure to conserve sharks. Since 2006, SEAFO has implemented and refined subareas that

are closed to all fishing activity in order to protect VMEs. CM 30/15 was most recently revised in 2015, and now includes 11 closed areas, shown as SEAFO closed areas in Figure 1 (a very small closure south of Valdivia Bank is not included in the figure). Recognising that protective actions had to be taken despite insufficient knowledge, the approach selected was to close a set of potential fishing areas that represented the range of features likely to have VMEs within the major biogeographical and surface productivity zones of the region (Longhurst 1998).

However, the scientific basis for selecting candidate areas to close to fishing was recognised as rather weak, and evaluations of appropriateness of current closures are to be made as and when new scientific information becomes available (van Zyl et al. 2016). New scientific investigations were called for to supplement and extend knowledge and databases on VME indicators as well as fisheries resources. Specifically, some of the fishing closures should be surveyed to document presence–absence of VME indicators and to describe distribution patterns. Data from these targeted studies would enhance the quality of fish stock assessments and help analyse the appropriateness of VME closures currently implemented solely based on feature characteristics and biogeographical patterns.

To enhance regional knowledge and data on seamount communities and the impact of fisheries, an international investigation of the Southeast Atlantic was initiated in 2014. The study included a 29-day research cruise on the RV *Dr Fridtjof Nansen*, conducted in January–February 2015. The main objective of this study was to map and analyse occurrence and abundance of benthopelagic fish and sessile epibenthos on selected Southeast Atlantic seamounts. The new data generated should inform management advisory processes. A supplementary objective was to provide an improved basis for future cross-basin comparisons of seamount biota for which the potential has been enhanced through recent studies at the Rio Grande Rise in the Southwest Atlantic (Perez et al. 2018).

This article presents results on VME-indicator-organism presence, fishes and deep-sea red crab, and evidence of fisheries 'footprints' in the different study areas. The results of associated bathymetry and substrate mapping efforts are provided in Bergstad et al. (2019 [this issue], <https://doi.org/10.2989/1814232X.2019.1571439>).

Materials and methods

Study area

The investigation included studies at the following features representing seamounts or seamount complexes: Schmitt-Ott Seamount, Wüst Seamount (two summits), Vema Seamount, the Valdivia area (four locations) and Ewing Seamount (Figure 1). Of these, Wüst, Valdivia and Ewing are features associated with the Walvis Ridge. Schmitt-Ott, Wüst and Vema seamounts are closed to fishing by SEAFO, while the Valdivia area and Ewing Seamount are classified as 'existing fishing areas' and thus remain open to fishing (SEAFO CM 30/15, www.seafo.org).

Sampling methods

Hydrographic observations

Vertical hydrographic profiles were sampled with a Sea-Bird

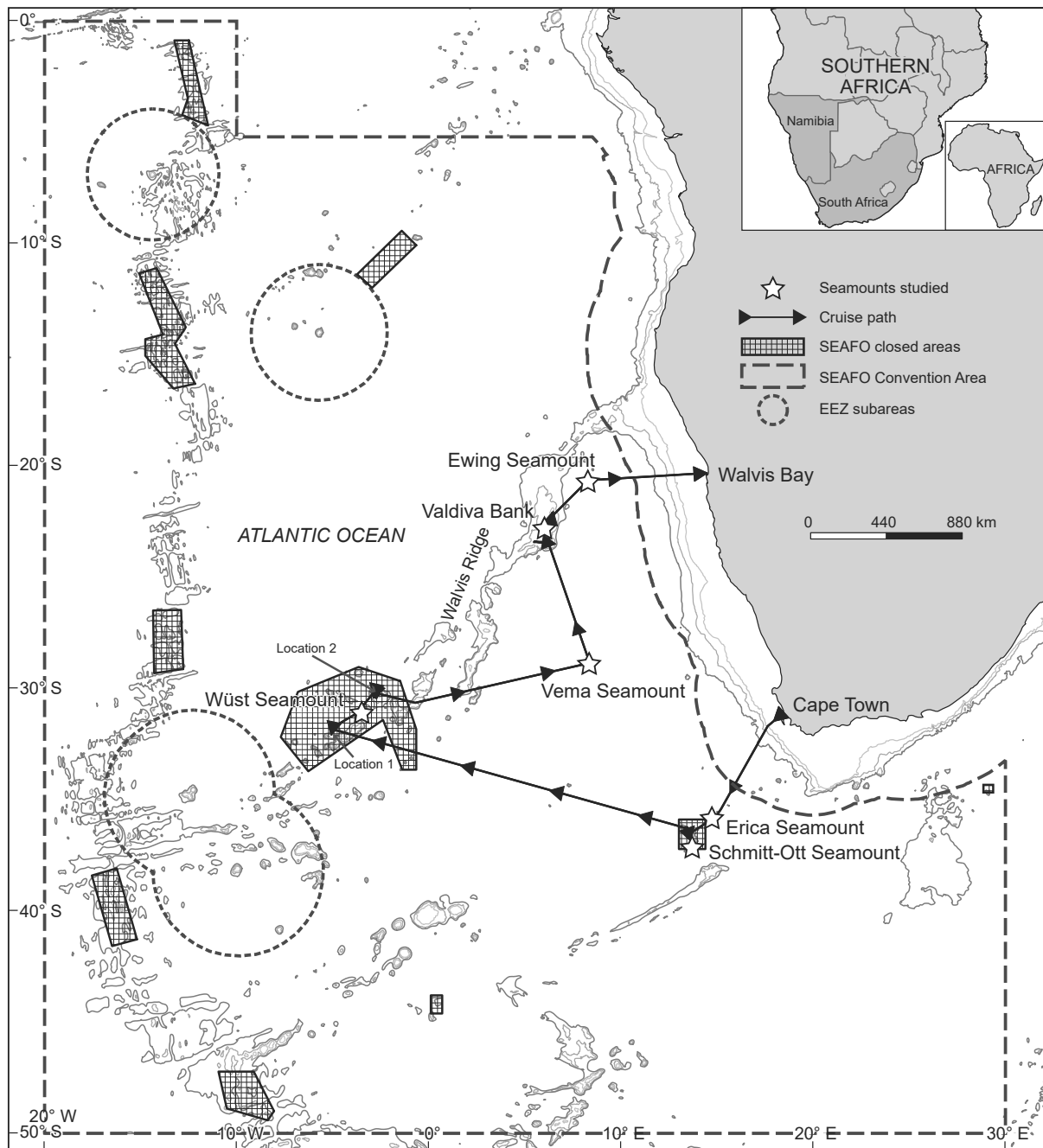


Figure 1: Track of the RV *Dr Fridtjof Nansen* off southern Africa during the January–February 2015 study of seamounts in the South East Atlantic Fisheries Organisation (SEAFO) Convention Area. The Convention Area comprises the sea area bounded by the broken line, except the circular areas represent exclusive economic zones of UK Overseas Territories; hatched subareas within the Convention Area are closed by SEAFO to fishing

Electronics (SBE) conductivity-temperature-depth (CTD) profiler to 1 000 m. Due to time constraints and priority on biological studies the effort was restricted to conducting at least one surface-to-1 000-m profile in each of the target sampling areas.

Acoustics

The vessel's Simrad multibeam (EM710) and single-beam (EK60) multifrequency echosounders were used to map bathymetry and midwater sound scatterers, such as fish

and zooplankton. Before running acoustic surveys at a new location, the sound-velocity data derived using the CTD data were used to adjust the sound-velocity profile settings of the echosounders. Mapping was restricted to depths shallower than 1 500 m. The results of the bathymetry mapping are provided in Bergstad et al. (2019, this issue).

Mapping of scattering layers and shoals by the EK60 utilised both the 38-KHz and 18-KHz transducers. The sounders were run continuously, but to gain further information on distribution

and identity of the scattering layers and the shoals associated with target locations, special surveys, including acoustic mapping and targeted trawl sampling, were run during the nighttime. Primary focus was placed on the shallower hills (i.e. depths of <1 000 m), assumed to represent the main distribution areas of the fish resources.

Visual observations

The main equipment for studying benthic megafauna was a 'CAMPOD' towed video rig consisting of a tripod frame with a centrally placed pan-tilt HD video camera, two 400-W strobe lights, four laser pointers showing a 10×10-cm square for size calibration, and a backward-looking camera added mainly to monitor performance and avoid snagging. The CAMPOD is an instrument designed solely for recording video and has no facilities for sampling objects from the seabed.

Upslope transects with distances ranging from 0.5 to 0.9 nautical miles (0.9–1.7 km) were run along paths determined after bathymetry mapping had been conducted with the vessel's multibeam echosounder. The maximum depth of operation was 1 000 m. The rig was towed at 0.5–1.5 knots (~15–46 m min⁻¹) with the forward-looking continuously recording HD camera at a fixed tilt angle (~45°). The camera was kept at a preferred height of 1–2 m off the seabed by the winch operator who constantly monitored the video stream. While conducting the pre-selected transects, efforts were made to maintain a constant speed and direction. The vessel did not have a dynamic positioning system, and hence safe navigation and towing was restricted to calm seas with little or no swell.

Replicate dives of approximately one hour were conducted on most selected summits. The aim was to approach the summits from the north, east, west and south. In addition, dives were made on summit plains or knolls when this was considered necessary to obtain a better understanding of the biota associated with the selected features.

Identification of organisms observed from the CAMPOD footage was challenging, and while higher taxa were recognisable, only rarely was identification to species level possible. Numerical data were recorded either during the dive or when re-examining the videos during reviewing sessions. This work was conducted by a team of observers with the necessary taxonomic skills, normally with each person being responsible for counting a specific taxon. Emphasis was placed on quantifying taxa regarded as indicators of VMEs, hence numbers of colonies of scleractinian corals, gorgonians (seafans) and sponges were recorded, as well as numbers of individual echinoderms and fish.

A constraint was that the available version of the CAMPOD did not provide continuous information on vehicle depth. After the dive, the depth profile of the dive was reconstructed based on data from the vessel's EK60 sounder and the recorded start and stop time of the dive. Depth was recorded every 0.001 nautical miles (1.85 m).

Trawls and grab sampling

The bottom trawl used was a Gisund Super two-panel otter trawl towed on two warps (for details see Axelsen and Johnsen 2015), and the pelagic trawl was an Aakrehamn design (see Krakstad et al. 2017). To sample bottom habitats and benthic biota, a Van Veen grab was used at selected sites.

Bottom trawling was restricted to plains where bottom conditions were considered suitable and snagging unlikely. Midwater trawling was conducted when echograms showed concentrations of sound-scatterers, which required identification and sampling of specimens. Towing speed was 3 knots (93 m min⁻¹), but towing distance varied with conditions. Grabs were mainly deployed in attempts to recover some of the megafauna observed visually at sites first explored with the towed video system.

Vessel and itinerary

The RV *Dr Fridtjof Nansen* (since replaced by a new vessel of the same name) was a 57-m custom-designed vessel for fisheries research and oceanography. Rigged as a stern trawler, the ship could deploy large midwater and bottom trawls to 1 200 m, as well as carry out many other types of sampling with biological samplers.

The coarse track of the vessel's voyage from Cape Town, South Africa, to Walvis Bay, Namibia, during the period 15 January–12 February 2015, is shown in Figure 1. The study locations along the track are indicated and named, and detailed vessel tracks for each of the study locations were provided in the cruise report (FAO 2016) and are illustrated in the separate article on bathymetry and substrate (i.e. Bergstad et al. 2019, this issue). Also, tracks for the small-scale EK60 surveys are provided with the accounts of the results shown in Supplementary Figures S1–S6.

Statistics, data management and curation

The CAMPOD video dataset, and data derived therefrom, constitutes the most important dataset in relation to the objective of the study. The CAMPOD did not have facilities for recording position of the vehicle, and hence counts of organisms could not be related directly to exact geographical positions or distances travelled.

Only crude estimates of densities of individual taxa could be generated. The counts of recorded taxa for each 5-min interval of the dive were converted to densities based on estimated areas viewed in each 5-min interval along the dive transects. The area viewed was calculated as the distance travelled multiplied by the mean width of the swath viewed by the camera. Distance travelled per 5-min interval was extracted from the ship's log. The mean width of the swath observed was estimated to be 4.5 m (SD 1.55) based on 81 comparisons between the total width of the video image and the 10-cm distances between laser points.

In order to describe distribution patterns, the density estimates per 5-min interval were related to the depth profiles of the dives, illustrating the position of the estimates along the dives extending from the slope to the summit plateau of the study sites. The geographical positions and tracks of the transects are illustrated on maps of individual sites.

The EK60 data were processed onboard using the scientific Large Scale Survey System (LSSS) post-processing software (<https://www.marec.no>), resulting in presentations of echograms but not abundance estimates. The post-processing of multibeam bathymetry data is described in Bergstad et al. (2019, this issue).

All raw data, video records and metadata were deposited in databases with SEAFO as data owner and the Institute

of Marine Research (IMR), Norway, as data custodian. Access is regulated in accordance with the data policy of the Ecosystem Approach to Fisheries (EAF)–Nansen Programme. Biological samples were labelled and preserved in accordance with standard procedures and sent to the IZIKO South African Museum, in Cape Town, South Africa, for conservation and curation.

Results

Sampling data and materials generated

In total, 41 CAMPOD dives were completed on the five deep-sea features investigated. A full list of dive details is provided in Table 1. The number of dives was highest in the more-extensive seamount complexes that have several summits, namely the Wüst and Valdivia areas, where two or more summits/locations were selected for further study.

In total, 14 trawl stations were visited (Table 2). The conditions for bottom trawling were generally poor due to steep slopes and rugged, hard substrate; hence only five bottom trawls were made, of which one was unsuccessful due to snagging. Exceptions were trawls on flat sedimented areas at the bases of the seamounts or adjacent to the main (shallowest) summits. Trawling was generally impossible in slope areas, where most of the CAMPOD dives were made. Midwater trawling (nine stations) was mainly carried out to identify echosounder recordings assumed to reflect fish concentrations near the summits or slopes of seamounts, but this also proved difficult or unsuccessful. The trawling efforts did, however, generate the bulk of the samples for the specimen collection resulting from the cruise.

In all study areas, Van Veen grab sampling stations were established in an attempt to sample the sediments and benthos. In total, 60 grabs were deployed, but many were replicates in roughly the same position. Only 11 of the grabs yielded material, and the samples were included in the IZIKO museum collection. Grab sampling produced some material at all study sites except the Vema and Ewing seamounts.

A total of 240 invertebrate samples were collected from trawls, 25 from grabs (including sediment samples), and 212 fish samples from trawls. In addition, a few samples were obtained (by accident) from the CAMPOD video rig, including during an encounter with an old pot rope. Samples of fauna attached to a pot captured in the bottom trawl were also collected.

At the end of the cruise the fish records comprised 74 species and 22 genera belonging to 34 teleost families, whereas the chondrichthyans were represented by 6 species of sharks belonging to 2 families. Lists of the fishes and invertebrates observed and sampled are provided in the cruise report (FAO 2016). Ten species of corals were identified to species level and another seven to genus level. Further analyses of several of the invertebrate taxa are, however, ongoing and a refined identification will be published elsewhere. The present list of invertebrate taxa at family level or higher (except Anthozoa, which are given at the lowest possible level) is provided in Table 3.

Accounts for individual seamount locations

Erica and Schmitt-Ott seamounts

The Erica and Schmitt-Ott seamounts are neighbouring

features individually surrounded by abyssal depths (3 000–5 000 m). Erica Seamount was not studied in any detail, and most of the results presented here relate only to Schmitt-Ott Seamount. At Schmitt-Ott Seamount, where the summit depth is 920 m, the hydrographic profile from the surface to 1 000 m showed a decline in temperature, from 17.2 °C in the near-surface 100 m to 3.4 °C at the summit and beyond. The near-summit salinity was 34.41.

Two CAMPOD transects, from the NW and SE, respectively, were run upslope from 1 000 m to the 920-m summit of the shallowest feature of Schmitt-Ott (Table 1; Figure 3 in Bergstad et al. 2019, this issue).

Among the sessile invertebrates observed, corals were most frequent and widespread. Gorgonians (Alcyonacea) were common and prominent among the corals (Figure 2a, b), and at least four morphotypes were observed. However, identification to species was impossible based on video images alone. Particularly in Dive 1 (NW transect), gorgonian numbers appeared to increase towards the summit (Figure 3). However, the wide variation reflected rather patchy distributions of colonies. Scleractinians (stony corals, order Scleractinia), represented by small colonies, were frequent but insignificant compared with the extensive cover of dead coral (rubble) that would seem to be evidence of past extensive scleractinian presence. Small (1–2-cm high) white colonies of corals attached to hard surfaces were assumed to be hydrocorals and these were very frequent and widespread.

Invertebrates observed in small numbers were sponges (Porifera) and echinoderms (echinoids, crinoids, ophiuroids, asteroids) and most of the latter occurred attached to gorgonian corals. Crustaceans observed were unidentified crabs and shrimp, but only a handful of specimens were observed. The single grab sample collected (at 1 176 m) contained a hydrozoan (Stylasteridae) and sediment containing pteropod shells.

Fish taxa observed by video were the spiky oreo *Neocyttus rhomboidalis* and an unconfirmed specimen of Guinea oreo *Allocyttus guineensis*, grenadiers (Macrouridae), a lanternshark *Etmopterus* sp., and a few unidentified specimens of other taxa. The oreo dories showed increasing abundance up the slope towards the summit of the seamount (Figure 3) but the overall number was low. Observations of other fishes were too few to draw conclusions on abundance patterns.

No indication of the main SEAFO target species, namely the fishes alfonsino, armourhead, orange roughy and Patagonian toothfish or the deep-sea red crab were, found on Schmitt-Ott, neither by video nor echosounders. Due to rough ground, the summit appeared untrawlable with the bottom trawl, and no echosounder observations were made of fish to be targeted with the midwater trawl. No observations of lost gear or other footprints of fishing were recorded.

En route to Schmitt-Ott the vessel passed across the summit of the Erica Seamount. The shallowest point observed was 770 m, surrounded by a wider area of 800–850 m depth. A school of fish was observed near the summit (Supplementary Figure S1), but no fishing was carried out to determine species composition. A mesopelagic scattering layer was prominent at 400–500 m.

Table 1: List of the CAMPOD dives conducted during the 2015 SEAFO cruise to Southeast Atlantic seamounts by the RV *Dr Fridtjof Nansen*, Cruise 2015402

Seamount	Dive no. by location	Date	Depth and distance measurements (m)			Duration (min)	Comments
			Start depth	Stop depth	Dist.		
Schmitt-Ott	1	19 Jan	975	930	1 037	62	
Schmitt-Ott	2	19 Jan	995	935	963	59	
Wüst Location 1	1	24 Jan	1 040	1 000	926	49	Slope of knoll on plateau
Wüst Location 1	2	24 Jan	1 050	975	926	27	Slope of knoll on plateau
Wüst Location 2	1	26 Jan	708	572	1 241	71	Southwestern slope, 700+ m
Wüst Location 2	2	26 Jan	650	590	926	21	Knoll on plateau
Wüst Location 2	3	26 Jan	890	670	1 685	83	Northern slope, 800–670 m
Wüst Location 2	4	26 Jan	590	530	1 111	24	Knoll on plateau, 530 m
Wüst Location 2	5	27 Jan	765	640	1 667	85	Western slope, 770–64 m
Vema	1	31 Jan	750	145	1 667	70	Western slope
Vema	2	31 Jan	708	108	2 222	76	Southern slope
Vema	3	31 Jan	935	71	2 037	49	Eastern slope
Vema	4	1 Feb	95	91			Interrupted, rig snagged in rope
Vema	5	1 Feb	91	42	369	12	Plateau knoll
Vema	6	1 Feb	72	43	1 167	40	Plateau knoll
Vema	7	1 Feb	911	100	2 704	109	Northern slope
Valdivia	1	3 Feb	903	230	2 741	95	Valdivia Central, western slope of main plateau
Valdivia	2	3 Feb	805	230	3 185	109	Valdivia Central, western slope of main plateau
Valdivia	3	3 Feb	580	650	860	97	Valdivia Central, knoll southeast of main plateau
Valdivia	4	3 Feb	552	250	1 204	44	Valdivia Central, southeast slope of main plateau
Valdivia	5	3 Feb	562	655	2 019	55	Valdivia Central, knoll southwest of main plateau
Valdivia	6	4 Feb	640	595	1 333	40	Valdivia West
Valdivia	7	4 Feb	875	470	1 574	60	Valdivia West
Valdivia	8	4 Feb	934	490	2 111	65	Valdivia West
Valdivia	9	4 Feb	705	505	1 296	41	Valdivia Central, knoll southeast of main plateau
Valdivia	10	4 Feb	660	452	926	44	Valdivia Central, tongue of central plateau
Valdivia	11	5 Feb	735	550	1 111	46	Valdivia Middle, knoll south of main plateau
Valdivia	12	5 Feb	715	515	1 185	40	Valdivia Middle, western slope of main plateau (dive interrupted)
Valdivia	13	5 Feb	775	475	1 741	81	Valdivia Middle, western slope of main plateau
Valdivia	14	5 Feb	871	877	610	6	Valdivia Middle, sandy-plain dive (after trawling)
Valdivia	15	6 Feb	906	450	1 630	44	Valdivia Middle, northeastern slope
Valdivia	16	6 Feb	585	417	1 185	41	Valdivia Middle, southern summit
Valdivia	17	6 Feb	850	560	2 000	85	Valdivia North, southern slope
Valdivia	18	6 Feb	655	570	1 574	61	Valdivia North, eastern summits
Valdivia	19	7 Feb	880	885	1 833	30	Valdivia North, western plain
Valdivia	20	7 Feb	730	555	1 648	41	Valdivia North, northern slope of western summit
Ewing	1	8 Feb	1 021	787	1 796	61	Ewing, southern slope
Ewing	2	8 Feb	916	792	1 167	45	Ewing, western slope
Ewing	3	9 Feb	1 002	1 003	580	25	Ewing, western deep plain (trawl area)
Ewing	4	9 Feb	893	792	700	39	Ewing, northern slope
Ewing	5	9 Feb	923	833	600	40	Ewing, northeastern knoll

Table 2: List of trawl stations during Cruise 2015402 of the RV *Dr Fridtjof Nansen* to seamounts in the SEAFO Convention Area in January–February 2015. BT = bottom trawl; PT = pelagic trawl; i.t. = interrupted tow or damaged trawl caused by snagging; UTC = Coordinated Universal Time

Station no.	Date	Position at start of tow (decimal deg.)		Position at end of tow (decimal deg.)		Seamount	Sampler type	Time (UTC)		Tow duration (min)	Vessel log (nautical miles)		Tow distance (nautical miles)	Sampler depth (m)		Bottom depth (m)		Tow speed (knots)	
		Lon.	Lat.	Lon.	Lat.			Start	Stop		Start	Stop		Start	Stop	Start	Stop		
1	24 Jan	4.960 W	34.484 S	4.960 W	34.485 S	Wüst	BT	20:14:00	20:19:00	5	98.0	98.5	0.50	1066	1066	1066	1060	3.0	i.t.
2	26 Jan	2.837 W	33.054 S	2.801 W	33.083 S	Wüst	PT	20:11:08	21:05:18	54	494.7	497.4	2.69	460	750	778	800	3.0	
3	27 Jan	2.778 W	33.037 S	2.795 W	32.992 S	Wüst	PT	15:43:08	16:37:51	55	584.8	587.6	2.90	450	570	608	662	3.2	
4	31 Jan	8.377 E	31.662 S	8.395 E	31.636 S	Vema	PT	17:04:07	17:51:20	47	1383.8	1386.0	2.16	50	80	82	108	2.8	i.t.
5	31 Jan	8.377 E	31.621 S	8.385 E	31.616 S	Vema	BT	18:54:34	19:04:35	10	1390.4	1390.9	0.51	71	94	71	94	3.1	
6	3 Feb	6.354 E	26.134 S	6.294 E	26.163 S	Valdivia	PT	00:51:36	02:03:02	71	1793.1	1796.8	3.78	150	195	339	271	3.2	
7	3 Feb	6.341 E	26.206 S	6.320 E	26.217 S	Valdivia	PT	13:50:05	14:21:47	32	1822.7	1824.0	1.33	320	335	564	559	2.5	
8	3 Feb	6.278 E	26.214 S	6.335 E	26.155 S	Valdivia	PT	19:03:58	20:31:15	87	1836.0	1840.9	4.92	50	205	235	230	3.4	
9	5 Feb	6.081 E	25.526 S	6.102 E	25.538 S	Valdivia	BT	14:25:14	14:55:05	30	2031.3	2032.7	1.37	878	877	878	877	2.7	
10	5 Feb	6.211 E	25.615 S	6.192 E	25.624 S	Valdivia	PT	18:45:36	19:09:33	24	2048.2	2049.4	1.18	440	460	476	707	3.0	
11	7 Feb	6.450 E	24.887 S	6.434 E	24.902 S	Valdivia	PT	07:05:33	07:32:43	27	2185.2	2186.5	1.27	500	560	573	707	2.8	
12	7 Feb	6.411 E	24.817 S	6.424 E	24.794 S	Valdivia	BT	12:40:26	13:12:19	32	2202.8	2204.3	1.52	887	886	887	886	2.9	
13	7 Feb	6.456 E	24.882 S	6.463 E	24.888 S	Valdivia	PT	18:55:55	20:35:00	99	2225.4	2230.8	5.41	450	550	644	973	3.3	
14	8 Feb	8.229 E	23.175 S	8.249 E	23.188 S	Ewing	BT	17:13:10	17:44:27	31	2390.9	2392.2	1.33	1014	1023	1014	1023	2.5	

Wüst seamount complex

The Wüst seamount complex on the Walvis Ridge is very extensive. The two presumed shallowest summits were selected for this study (Figure 1), and are hereafter denoted Locations 1 and 2.

At Location 1 the hydrographic profile from the surface to 1 000 m showed a decline in temperature, from about 20 °C in the near-surface 100 m to 3.2 °C at the depth of the summit. The near-summit salinity was 34.41.

As illustrated in Bergstad et al. (2019, this issue), the summit at Wüst Location 1 is an extensive circular plateau approximately 1 050 m deep. Protruding from the plateau are several smaller shallower hills that we denoted knolls. At two of these knolls, two CAMPOD dives were carried out from the main plateau up the slope towards the summits of the knolls (Table 1; Figure 5 in Bergstad et al. 2019, this issue). In both dives, the presence of sessile macrobenthos was limited to a few whip-like gorgonian corals, and in Dive 2, which was the shallowest (975 m, as opposed to 1 000 m in Dive 1), the number of gorgonians increased towards the summit (Figure 4). Only in Dive 2 did a few small scleractinian coral colonies appear towards the summit (Figure 2c, d). Fishes at Wüst Location 1 comprised grenadiers (Macrouridae), which appeared most abundant at the base of the knolls, and a few unidentified specimens (Alepocephalidae, Synphobranchidae, and a shark).

Bottom trawling was attempted on the summit plateau at 1 060 m but resulted in an interrupted haul and torn net. Grab deployments were made in two locations west of the knolls, but despite several replicate grabs only a few minor samples of crustaceans (Decapoda), Hexactinellida, Polychaeta, Scaphopoda, Bryozoa and Hydrozoa were retrieved.

No observations of lost gear or other footprints of fishing were made. Supplementary Figure S2 shows results from a 24-h acoustic survey comprising multiple crossings of the summit. The mesopelagic scattering layer at 400–700 m, probably containing small fishes and zooplankton, was very prominent. Even during daytime, that mesopelagic layer never impinged on the 1 050-m-deep seamount summit.

Wüst Location 2 is rather flat-topped, with a plateau depth of ~650 m, and a few plateau knolls peaking at 550–600 m (Figure 7 in Bergstad et al. 2019, this issue). The hydrographic profile from the surface to 600 m showed a decline in temperature, from 23 °C in the near-surface layer to 8.2 °C near the seabed. The temperature curve was declining at the deeper end, hence it is likely that the surrounding deeper slopes would have a somewhat lower temperature. The near-summit salinity was 34.61.

Five CAMPOD dives were made at Wüst Location 2 (Table 1; Figure 7 in Bergstad et al. 2019, this issue). Three dives were upslope transects, starting at 708–890 m and approaching the main plateau from the southwest, west and north, respectively, reaching plateau depths of ~600 m. The remaining two dives were transects up the slopes of two central summit knolls (the very shallowest points of the seamount).

Corals were common at depths shallower than 740 m and comprised whip-like gorgonians, black corals (Antipatharia), and scattered small colonies of scleractinians (Figure 2c, e). On neither of the slopes did the corals form ‘gardens’ or reefs, but the occurrence was high as compared with

Table 3: List of macroinvertebrate taxa recorded in trawl catches and grab samples during the 2015 cruise of the *RV Dr Fridtjof Nansen* to Southeast Atlantic seamounts. Note that **Phylum Sipuncula** was also present, but not identifiable to lower taxonomic levels; identification is ongoing for all groups listed. For class Anthozoa the list includes some records specified as indeterminate (indet.)

Phylum Porifera	Phylum Cnidaria	Phylum Mollusca	Phylum Annelida	Phylum Arthropoda	Phylum Bryozoa	Phylum Chordata
Class Demospongia	Class Anthozoa	Class Gastropoda	Class Polychaeta	Class Pycnogonida	Family Aldeonidae	Subphylum Tunicata
Family Chalinidae	Subclass Octocorallia	Infraclass Opisthobranchia	Family Amphinomidae	Family Pycnogonidae	Family Aeteidae	Class Thaliacea
Family Desmacididae	Order Alcyonacea	Family Cavoliniidae	Family Chaetopteridae	Class Hexanauplia	Family Bitectiporidae	Family Pyrosomatidae
Family Esperipsidae	Family Alcyoniidae	Subclass Prosobranchia	Family Euniciidae	Subclass Copepoda	Family Bugulidae	Family Salpidae
Family Halichondrida	<i>Alcyonium elegans</i>	Family Calyptraeidae	Family Hesoniidae	Subclass Thecostraca	Family Candidae	Class Ascidiacea
Family Hymedesmiidae	Family Gorgoniidae	Family Capulidae	Family Maldanidae	Infraorder Cirripedia	Family Catenicellidae	Family Didemnidae
Family Mycalidae	<i>Leptogorgia viminalis</i>	Family Fissurellidae	Family Nereidae	Family Heteralepadidae	Family Celleporidae	Subphylum
Family Rhabderemiidae	Family Isididae	Family Velutiniidae	Family Orbinidae	Family Scalpellidae	Family Crepidacanthidae	Cephalochordata
Class Calcarea	<i>Keratoisis</i> sp.	Class Bivalvia	Family Oweniidae	Class Malacostraca	Family Hippothoidae	Family
Order Clathrinida	Family Melithaeidae	Family Arcidae	Family Sabellaridae	Subclass Eumalacostraca	Family Microporellidae	Branchiostomatidae
Family Sycettidae	<i>Melithaea rubra</i>	Family Pectinidae	Family Serpulidae	Order Euphausiacea	Family Petraliellidae	
Class Hexactinellida	Family Plexauridae	Family Walkeriidae	Family Spirorbidae	Family Euphausiidae	Family Phidoloporidae	
Family Farreidae	<i>Villogorgia</i> sp.	Class Scaphopoda	Family Syllidae	Order Decapoda	Family Schizoporellidae	
	Subclass Hexacorallia	Family Gadiliidae	Family Terebelliidae	Family Acanthephyridae	Family Scruparia	
	Order Actinaria	Class Cephalopoda		Family Alpheidae	Family Smittinidae	
	Actinaria indet.	Family Enoplateuthidae		Family Aristeidae	Family Trypostegidae	
	Family Hormathiidae	Family Cranchiidae		Family Benthesicymidae		
	Hormathiidae indet.	Family Enteropodidae		Family Geryonidae	Phylum Echinodermata	
	Order Corallimorpharia	Family Histiotethidae		Family Nematocarcinidae	Class Crinoidea	
	Family Corallimorphidae	Family Lycoteuthidae		Family Oplophoridae	Family Comatulidae	
	<i>Corynactis annulata</i>	Family Oegopsida		Family Pandalidae	Class Asteroidea	
	Order Zoantharia	Family Ommastrephidae		Family Paguridae	Family Asterinidae	
	Family Epizoanthidae	Family Onychoteuthidae		Family Parapaguridae	Family Luidiidae	
	<i>Epizoanthus</i> cf.	Family Pyroteuthidae		Family Pasiphaeidae	Family Stichasteridae	
	<i>paguriphilus</i>	Family Sepiolidae		Family Penaeidae	Class Ophiuroidea	
	Order Antipatharia	Family Spirulidae		Family Polychelidae	Family Amphiuridae	
	Family Myriopathidae			Family Sergestidae	Family Ophionereididae	
	<i>Antipathella</i> sp.			Family Thoridae	Class Echinoidea	
	Family Antipathidae			Order Lophogastrida	Family Clypeasteridae	
	<i>Stichopathes</i> sp.			Family Gnathopausiidae	Family Echinothuridae	
	Order Scleractinia			Order Amphipoda	Class Holothuroidea	
	Family Dendrophylliidae			Family Hiperiidae	Family Holothuriidae	
	<i>Enallopsammia rostrata</i>			Family Phronimidae	Family Mesothuriidae	
	Class Scyphozoa			Family Platyscelidae		
	Family Atollidae			Family Stegocephalidae		
	Family Periphyllidae			Order Isopoda		
	Class Hydrozoa			Family Janiridae		
	Subclass Hydroidolina					
	Order Siphonophora					
	Family Diphyidae					
	Order Anthoathecata					
	Family Bougainvilliidae					
	Family Corynidae					
	Family Eudendriidae					
	Family Oceaniidae					
	Family Pandeidae					
	Family Stylasteridae					
	Order Leptothecata					
	Family Campanulinidae					
	Family Campanulariidae					
	Family Haleciidae					
	Family Halopterididae					
	Family Lafoeidae					
	Family Plumulariidae					
	Family Sertulariidae					
	Family Tiarannidae					
	Family Tubulariidae					
	Family Zygophylacidae					

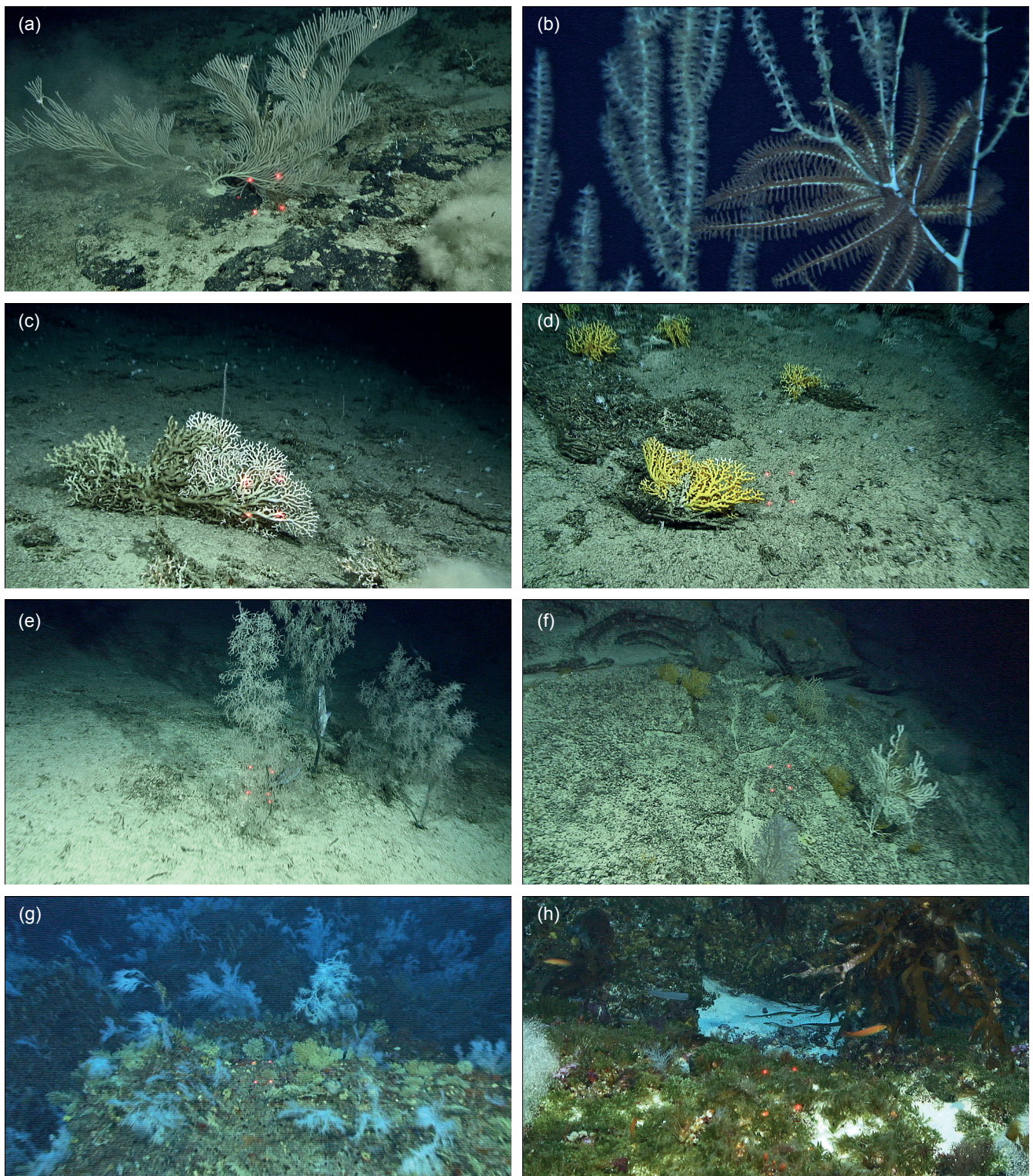


Figure 2: Photographs (frame grabs) of corals and other biota observed on Southeast Atlantic seamounts in 2015. (a, b) Schmitt-Ott Seamount: (a) fan-shaped gorgonian coral frequently observed; (b) bamboo coral (a gorgonian) with a species of Brisingidae (Echinodermata) attached. (c–e) Wüst Seamount: (c) scleractinian coral colony (partly dead) on hard ground, which may be ancient consolidated coral framework; (d) live scleractinian corals, probably *Enallopsammia rostrate*; and (e) a fish (probably *Tripterophycis* sp.) associated with colonies of black corals (Antipatharia, probably *Leiopathes* sp.). (f–h) Vema Seamount: (f) gorgonian (white) and scleractinian (yellow) coral colonies; (g) black coral garden on the rim of the seamount; and (h) kelp, green algae and yellow wrasses

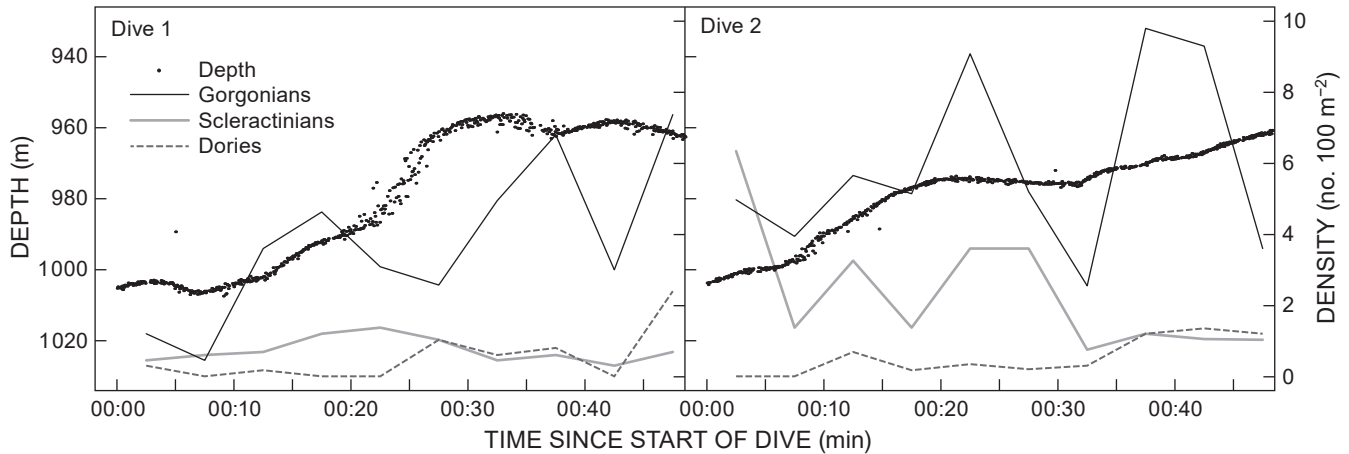


Figure 3: Megafauna density along two upslope video transects on the summit of the Schmitt-Ott Seamount, observed in January 2015. Estimated density by 5-min observation interval during Dives 1 and 2 was related to the depth profile of the tow of the CAMPOD video rig. Data are shown for three prominent taxa: gorgonian corals (*Alcyonacea*), scleractinian corals, and spiky oreo *Neocyttus rhomboidalis*

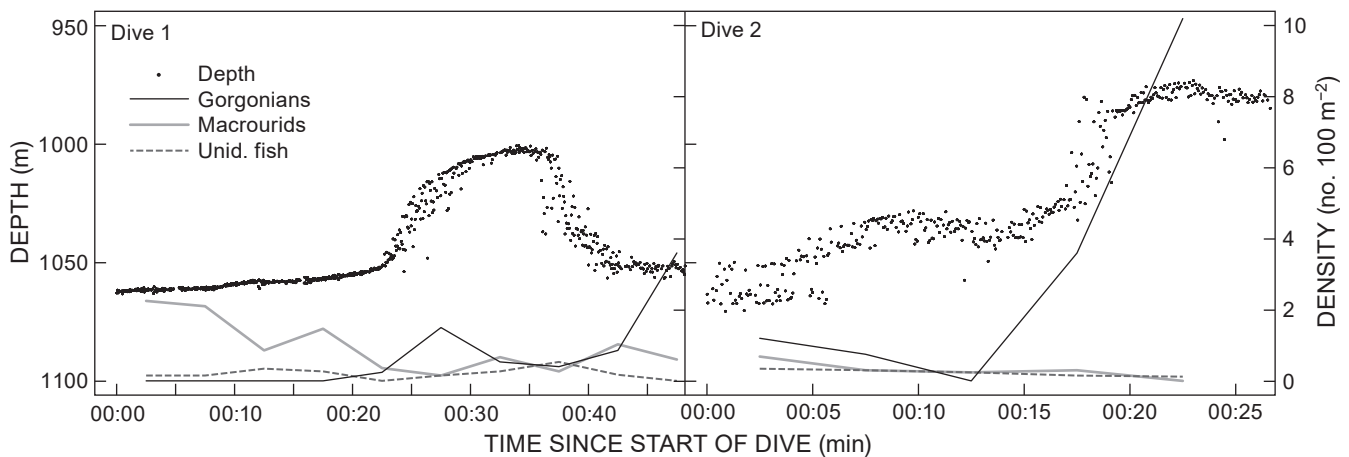


Figure 4: Megafauna density along two upslope video transects on the summit of Wüst Seamount, Location 1, observed in January 2015. Estimated density by 5-min observation interval during Dives 1 and 2 was related to the depth profile of the tow of the CAMPOD video rig. Data are shown for gorgonians (*Alcyonacea*), fish of the family Macrouridae, and unidentified fish (representing several non-macrourid species)

that on the previously explored seamounts. Densities along the transects are shown in Figure 5. The density of gorgonians was highest on the southern slope, where it increased upslope but seemed to reach a maximum, and then declined towards the summits. The scleractinians, probably mostly *Enallopsammia rostrata*, also increased in density up the slopes, but then decreased towards the summits. The recorded colonies were yellow (i.e. alive) or white (probably dying or recently dead). On the northern slope the first live scleractinians appeared at ~850 m, on the southern slope at ~700 m, and to the west at 730 m. However, in all cases the colonies were scattered and few as compared with the coral rubble and what appeared as consolidated coral framework, which occurred across wider areas and depth ranges. Exposed basaltic bedrock was not common.

The two knoll dives (Dives 2 and 4) explored the shallowest areas of Wüst Location 2, and transect depths ranged from approximately 620 to 550 m. On the hard substrate, whip-like gorgonians were very numerous. Live scleractinians occurred as scattered colonies, and, as observed on the summit slopes, the species appeared to be *E. rostrata* (Figure 2d). Also scattered on hard substrate were colonies of antipatharians, and the counts were particularly high on the knoll visited in Dive 2 (Figure 5). The density of coral was highest on the slopes of the knolls and declined at the summits, but the distributions in this area were patchy.

Three grabs were operated on the plateau and upper slope, at depths of 700, 630 and 560 m. These grabs produced a range of samples, including coral rubble identified as dead *E. rostrata*.

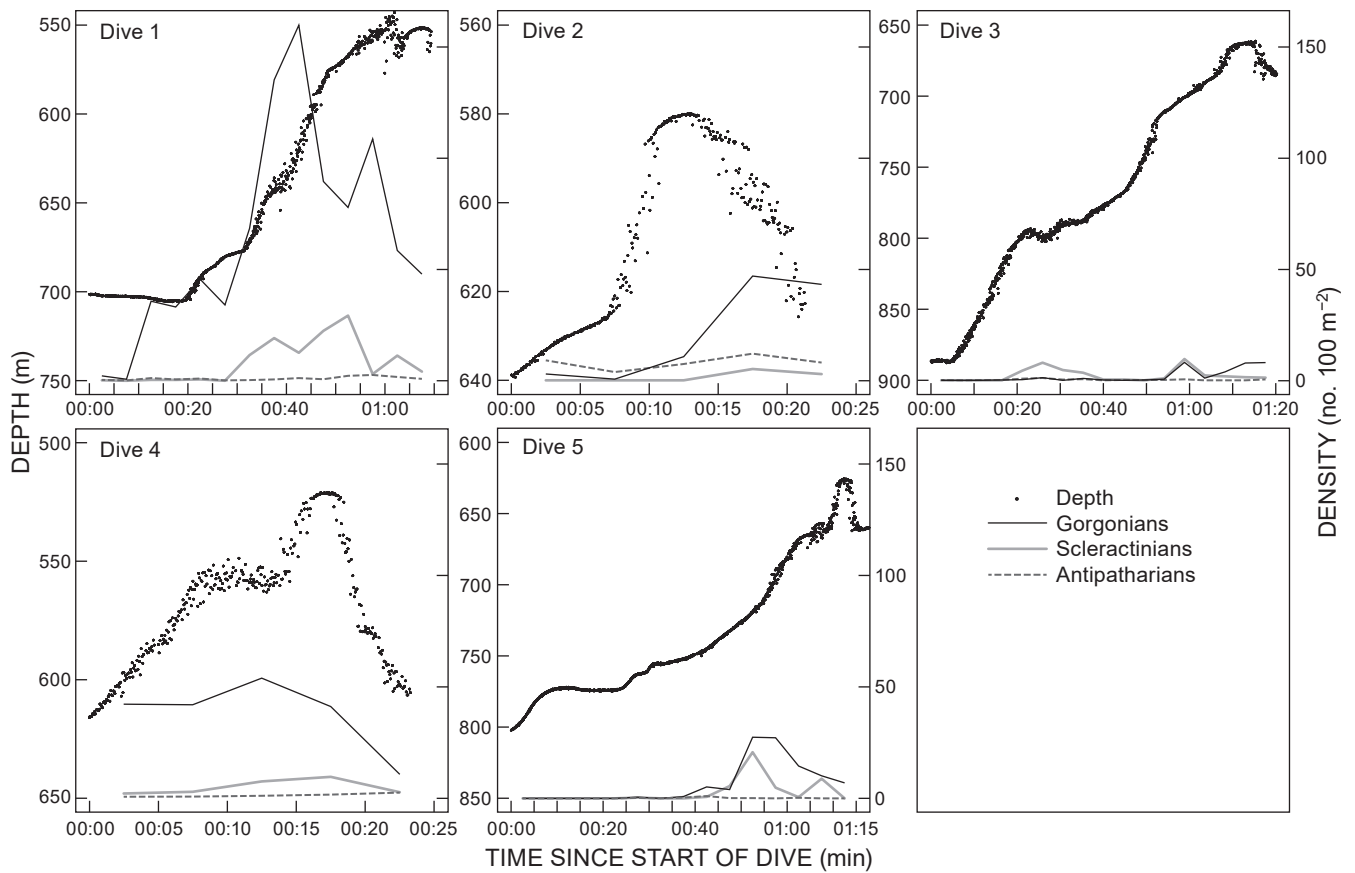


Figure 5: Megafauna density along five video transects on the summit of Wüst Seamount, Location 2, observed in January 2015. Estimated density by 5-min observation interval during Dives 1 to 5 was related to the depth profile of the tow of the CAMPOD video rig. Data are shown for three coral taxa: gorgonians (Alcyonacea), scleractinians, and black corals (Antipatharia)

Single specimens of alfonso *Beryx* sp. and the pelagic armourhead were observed in several of the dives, but aggregations occurred only towards the summit of the plateau knolls (Dives 2 and 4). These aggregations were small and not visible on echograms from the area, perhaps because of the rugged terrain and the distribution of the fish near the seabed. Other fish species that were common in the video records were grenadiers (probably *Tripterophycis* sp.), rosefish *Helicolenus* sp., and bellowsfish *Centriscomps* sp.

Two midwater trawls were made above plateau depths (Stations 2 and 3) (Table 2). In Station 2 the trawl was deployed at 460–750 m above bottom depths of 750–800 m, and the catch comprised 20 specimens of splendid alfonso, two specimens of sculpted lanternshark *Etmopterus sculptus*, an unidentifiable demersal fish, and some mesopelagic fishes (a specimen of *Diplophos* cf. *taenia* and 114 myctophids), plus at least four species of cephalopods. The second trawl, at depths of 450–570 m about 100 m off the seabed, produced only small numbers of mesopelagic fishes (*Diaphus* sp., *Hygophum reinhardtii*, *Protomyctophum* sp., *Argyropelecus hemigymnus*, *Stomias* sp.) and the squid *Lycoteuthis lorigera*.

A 24-h acoustic survey was conducted across the seamount, as shown in Supplementary Figure 3. The echograms show the prominent mesopelagic scattering layer impinging on the summit of the seamount throughout

the day. During the night a portion of the layer migrated into near-surface waters, particularly well reflected in the 18 KHz echogram (not shown). No observations of lost gear or other evidence of fishing were observed at Wüst Location 2.

Vema Seamount

In contrast with the multi-summit Wüst Seamount complex associated with the Walvis Ridge, Vema Seamount (31°38' S, 08°20' E) is a single-summit conical feature in the middle of an abyssal plain at 3 000 m deep or more. The now fully mapped seamount summit (Bergstad et al. 2019, this issue) was determined to be rather flat, with depths of 90–100 m. The subarea shallower than 150 m is ~11 km across in the east–west direction and 8.5 km across in the north–south direction and has several summit hills, with the shallowest estimated to be 21.5 m.

The hydrographic profile from the surface to 900 m showed a decline in temperature, from 21.8 °C at the surface to 16–18 °C at the depth of the seamount's summit (<100 m); down the slope, the temperature declined to ~5 °C at 900 m. The near-summit salinity was 35.6.

Seven CAMPOD dives were made on Vema Seamount (Table 1; Figure 9 in Bergstad et al. 2019, this issue), but Dive 4 on the summit was interrupted because the vehicle became snagged in an old pot rope. Dives 1, 2, 3 and 7

were upslope transects approaching the summit from different directions, and the other dives were comparatively short transects on the summit plateau or summit knolls. Since Vema Seamount is shallow, the slope transects starting at 708–935 m spanned a much wider depth range than dives in the other seamount locations described above.

Live coral colonies of seafans (*Alcyonea*), antipatharians and scleractinians (Figure 2f, g) appeared more prominent when approaching the summit (Figure 6). Only the antipatharians formed large aggregations (gardens). The scleractinians were small, yellow colonies, but not the same species as seen at deeper seamounts (e.g. *Wüst*). For all coral taxa, the numbers declined with depth on the slope (Figure 6).

The summit of Vema is in the euphotic zone, and sessile macroalgae, including prominent kelp forests, were observed in the shallow knoll dives (Figure 2h). The kelp resembled *Ecklonia maxima* but the identity was not confirmed with samples. The knolls were rugged and rocky, with intervening plains covered in coralline algae sometimes overgrown with green and/or brown macroalgae. Another prominent feature of the summit was extensive antipatharian (black coral) gardens (Figure 2g).

Among other relatively prominent invertebrate phyla at Vema Seamount were sponges (Porifera), which were comparatively common in deeper parts of the slope Dives 2, 3

and 7. Echinoderms, particularly echinoids, were widespread, and holothurians were common on the summit flats. A few scattered individuals of deep-sea red crab (*Chaceon* sp., probably *C. erythraea*, though the identity was not confirmed with samples) and other crustaceans were observed. Attempts to collect sediment samples using a grab were made extensively at four summit locations but did not produce samples, presumably because the substrate was too hard.

Low numbers of pelagic armourhead and alfonsino were present on the upper slope of Vema, but not at the summit. Only armourhead showed a relatively consistent pattern in all slope transects, with increasing numbers towards the summit depth and then disappearance at the shallow end of the dives (Figure 6).

The summit habitats were not sampled sufficiently to characterise the species composition. Shoals of epipelagic fishes were observed over the summit, and numerous unidentified fish species inhabited the kelp gardens.

Acoustic transects were run across the summit (Supplementary Figure S4), and near-bottom shoals of fish were observed above the rough untrawlable ground. These shoals may have been epipelagic species that were likewise occasionally observed during the CAMPOD dives. Two trawls were deployed, one 45-min midwater tow, and one 10-min bottom tow (Table 2). The former snagged and the trawl was

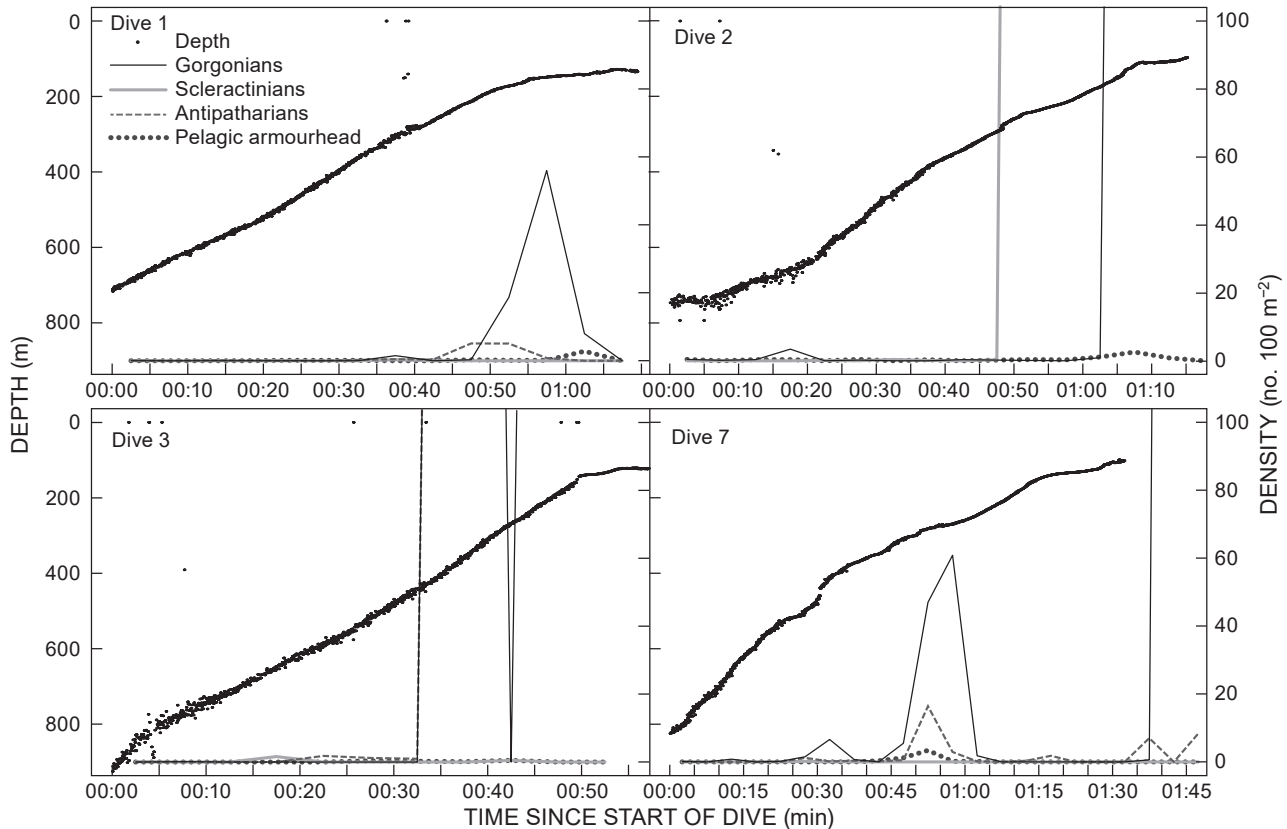


Figure 6: Megafauna density along four upslope video transects on the summit of Vema Seamount, observed in January 2015. Estimated density by 5-min observation interval during Dives 1, 2, 3 and 7 was related to the depth profile of the tow of the CAMPOD video rig. Data are shown for three coral taxa: gorgonians (*Alcyonacea*), scleractinians, and black corals (*Antipatharia*), as well as for one fish species, the pelagic armourhead *Pseudopentaceros richardsoni*. Coral records exceeding the density scale reflect very dense aggregations where the numbers of colonies were too high to be counted

ripped. The midwater catch was small (1.55 kg), comprising numerous pyrosomes and a few mesopelagic fishes. The bottom trawl also contained numerous pyrosomes and *Holothuria* sp., a single *Octopus magnificus*, 20 specimens of the eel *Gnathopis capensis*, and single specimens of blackbelly rosefish *Helicolenus dactylopterus* and a sparid.

Lost and old lobster or crab pots and rope were commonly observed in the video transects at Vema Seamount. The CAMPOD towed rig snagged in an abandoned rope during Dive 5 on the summit. No evidence of trawling activity was observed.

The abundance of lost pots may be illustrated by the following records from individual upper-slope CAMPOD dives—Dive 1: 7 pots and 4 ropes (incidence in terms of no. per km transect length: 6.6); Dive 2: 2 pots and 2 ropes (incidence: 1.8); Dive 3: 2 pots and 6 ropes (incidence: 3.9); Dive 7: 0 pots and 2 ropes and 3 other human items (incidence: 1.9).

Valdivia Bank and the associated seamount complex

Valdivia Bank and the surrounding seamounts lie on the northeastern end of the Walvis Ridge (Figure 1). Compared with the other seamounts visited, this is a complex area (Figure 7), and four widely spaced subareas were visited. The geomorphology of these subareas is described in Bergstad et al. (2019, this issue).

Profiles of temperature and salinity by depth were very similar in the four different subareas sampled. The temperature was ~23 °C at the surface and decreased to 4–5 °C at the summit depths of the deeper seamounts and adjacent plains. At the shallower Valdivia Bank and the summit of Valdivia West the near-bottom temperatures were appreciably higher, at 12–13 °C and 8 °C, respectively. In all the subareas near-bottom salinity was 34.9.

Valdivia Central — Valdivia Central was explored with seven CAMPOD dives up the slope of the flat bank (Dives 1, 2 and 4) (Table 1; Figure 13 in Bergstad et al. 2019, this issue) and on smaller and deeper knolls to the southeast and southwest of the bank (Dives 3, 5, 9 and 10). The upslope dives started on adjacent sedimentary flats, at 800–900 m on the northern side and at 550 m on the southeast side of the bank, and ended on top of the bank, at 230–240 m.

Figure 8a shows the densities of coral colonies and deep-sea red crab *Chaceon* sp. in the upslope dives on the northern and southeastern sides of Valdivia Bank. Live corals were very patchily distributed, and with the exception of numerous soft gorgonians on the summit in the southeast, the numbers declined markedly at the end of the dives when the vehicle reached the flat plateau. Live scleractinians were mainly observed in crevices of the steep rocky slope, but the colonies were small

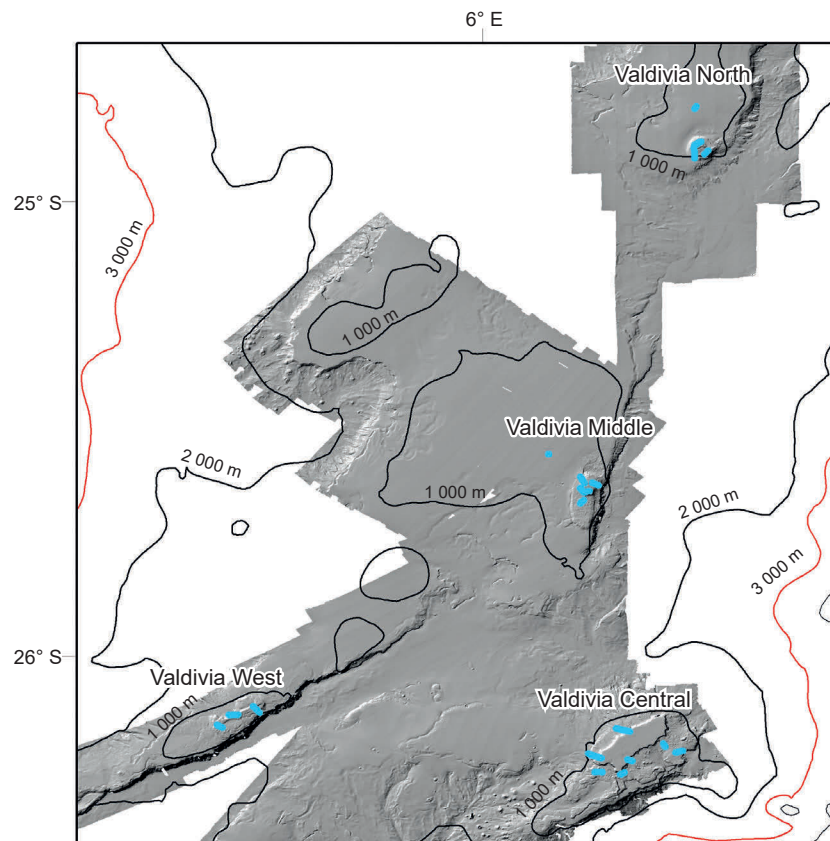


Figure 7: Relief of the Valdivia Seamount complex, on the Walvis Ridge in the Southeast Atlantic, and the four summits sampled by the RV *Dr Fridtjof Nansen* in 2015. Locations of CAMPOD dives associated with the shallower summits are indicated in turquoise. The relief (grey area) is based on bathymetry data sampled on Spanish–Namibian cruises (López-Abellán and Holtzhausen 2011) and our own data

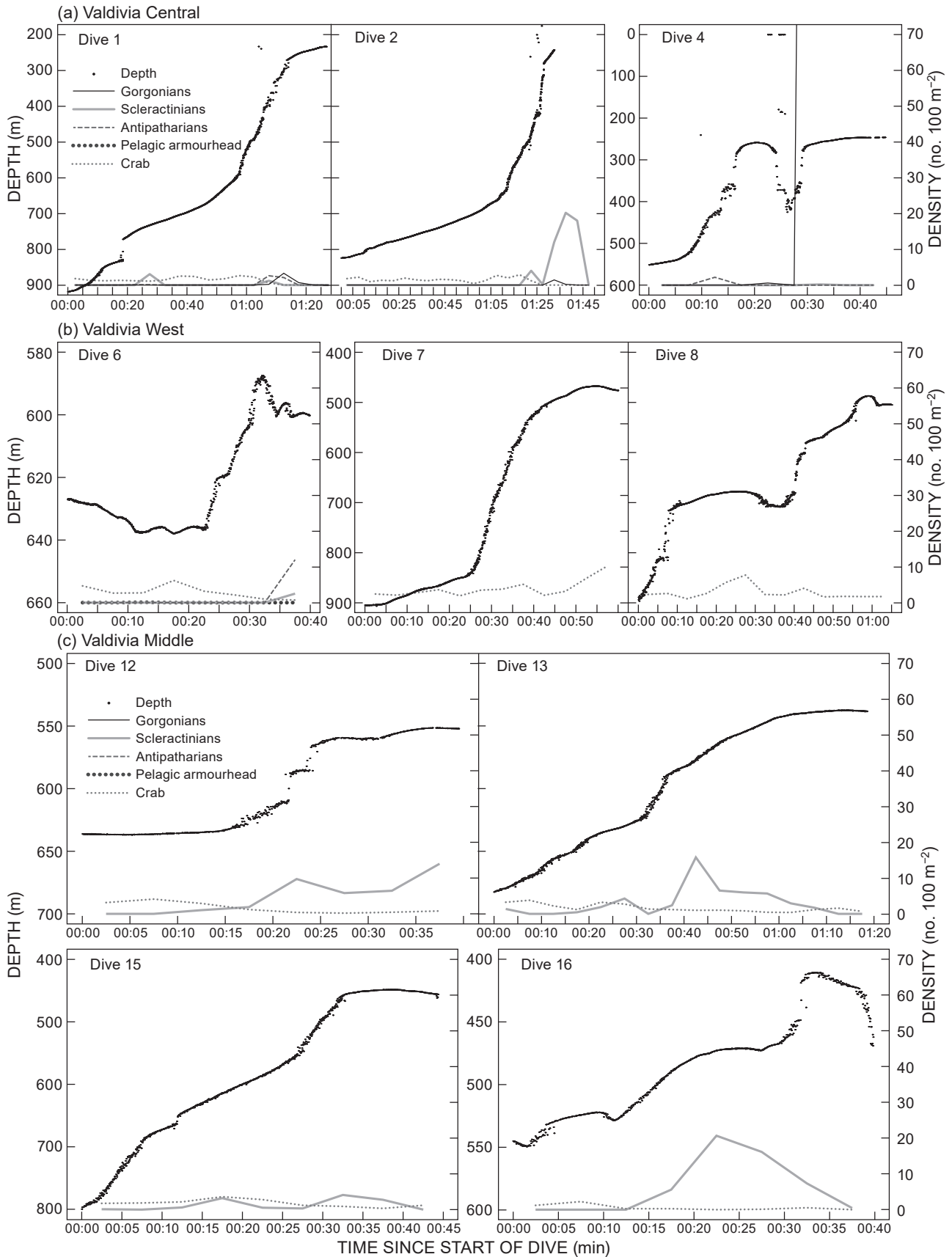


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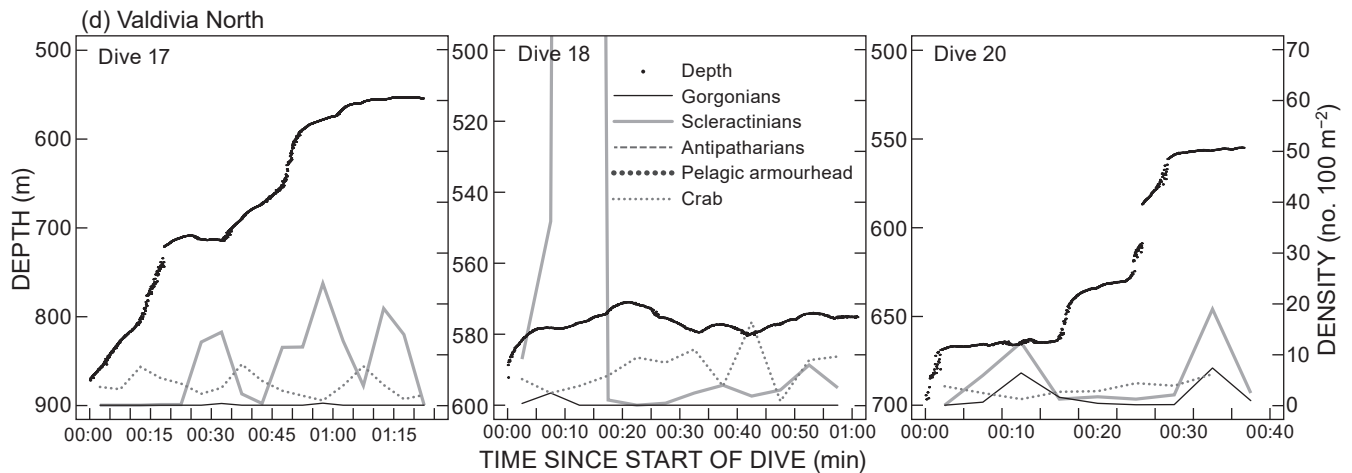


Figure 8: Megafauna density along video transects on the Valdivia seamount summits at the four subareas: (a) Valdivia Central, (b) Valdivia West, (c) Valdivia Middle, and (d) Valdivia North (see Figure 7), in January–February 2015. Estimated density by 5-min observation interval during the individual dives is related to the depth profile of the towed CAMPOD video rig. Data are shown for three coral taxa: gorgonians (Alcyonacea), scleractinians, and black corals (Antipatharia), as well as one fish species, the pelagic armourhead *Pseudopentaceros richardsoni*. Coral records exceeding the density scale reflect very dense aggregations where the numbers of colonies were too high to be counted

and scattered. In addition to the taxa shown in Figure 8, seapens (Pennatulacea) were quite abundant on relatively soft ground on the southeastern slope, but not on the much steeper northern slope. Many other invertebrate taxa were also recorded, but they were scattered and occurred in relatively small numbers. Deep-sea red crabs were numerous at the base and up the slope of Valdivia Bank, but not on the bare rocky plateau.

The dives on the lower slopes of deeper knolls to the south of Valdivia Bank (Dives 3, 5, 9 and 10) showed coral rubble composed of dead scleractinian fragments. The densities of several taxa of live corals (gorgonians, antipatharians and scleractinians) increased up the slopes, and particularly in Dives 5 and 9 the abundance was so high that the entire substrate was covered in live corals (Figure 9). The abundance of corals on these knolls was too high to facilitate enumeration and density estimation with the methods and technology available. The depth range of highest coral density differed between knolls: in Dive 5 it was 575–625 m, whereas in Dive 9 it was 460–475 m (near the summit).

Grab sampling was carried out in the locations of Dives 9 and 10. Only a single grab at 622 m on Dive 9 resulted in a significant sample, which included bryozoans, polychaetes, isopods and the scleractinian coral *E. rostrata*.

A zig-zag hydroacoustic survey was conducted across Valdivia Bank, but no fish shoals or aggregations were observed. During the CAMPOD dives, multiple individuals of armourhead were observed on the southeastern corner of the bank during Dive 10 at ~500 m depth, and during Dive 9 at the summit (465 m), but elsewhere only single individuals occurred. Only a few scattered alfonso specimens were observed. Three midwater trawls were conducted either above (Station 8, Table 2) or adjacent to (Stations 6 and 7) Valdivia Bank. The trawls produced small catches of cephalopods and mesopelagic fishes.

The CAMPOD dives revealed deep-sea red crab *Chaceon* sp. in all transects and across the depth range

investigated, but the highest densities were observed in the sedimented adjacent plains and on the lower slopes (Figure 8a). The densities appeared much lower in areas of rugged terrain and in coral gardens, but this observation is uncertain because crabs may be difficult to observe and count in such habitats.

Valdivia West — Three CAMPOD dives were made in the subarea denoted Valdivia West (Figure 7), namely Dives 6, 7 and 8 (Table 1; Figure 15a in Bergstad et al. 2019, this issue). All were upslope dives, yet only Dive 7 reached the shallowest summit, at 460 m. Densities of corals of all taxa were low (Figure 8b) and no features could be described as coral gardens. On the shallowest seamount explored in Dive 7 the summit was bare rock, as seen on Valdivia Bank.

On the summit explored by CAMPOD Dive 7 an aggregation of alfonso was encountered. The aggregation occurred above bare, rocky substrate. Deep-sea red crab was abundant in Valdivia West, at all depths and on all substrates (Figure 8b). The density was particularly high on the shallowest summit (Dive 7).

Valdivia Middle — The Valdivia Middle subarea is an elongate feature with the shallowest summit plateau occurring at the northern end (Figure 7). This northerly shallow area has several knolls, of which the shallowest is at ~415 m. To the west of the elongate shallowest area, there is a large plain with a plateau depth of 875–880 m.

Five CAMPOD dives were made on the shallower part of the seamount (Dives 11, 12, 13, 15 and 16) and one on the adjacent flat plateau (Dive 14) at 865 m (Table 1; Figure 15b in Bergstad et al. 2019, this issue). Scleractinian coral was common on the slopes deeper than 500 m (Figure 8c).

Only the knoll south of the main summit, visited on Dive 11, had a rich coral garden comprising primarily scleractinian corals. At depths shallower than 600 m during that dive the percentage cover of corals was 50% or more, and the summit depth was 555 m. On the shallower summits (depths of <500 m, Dives 13 and 15) to

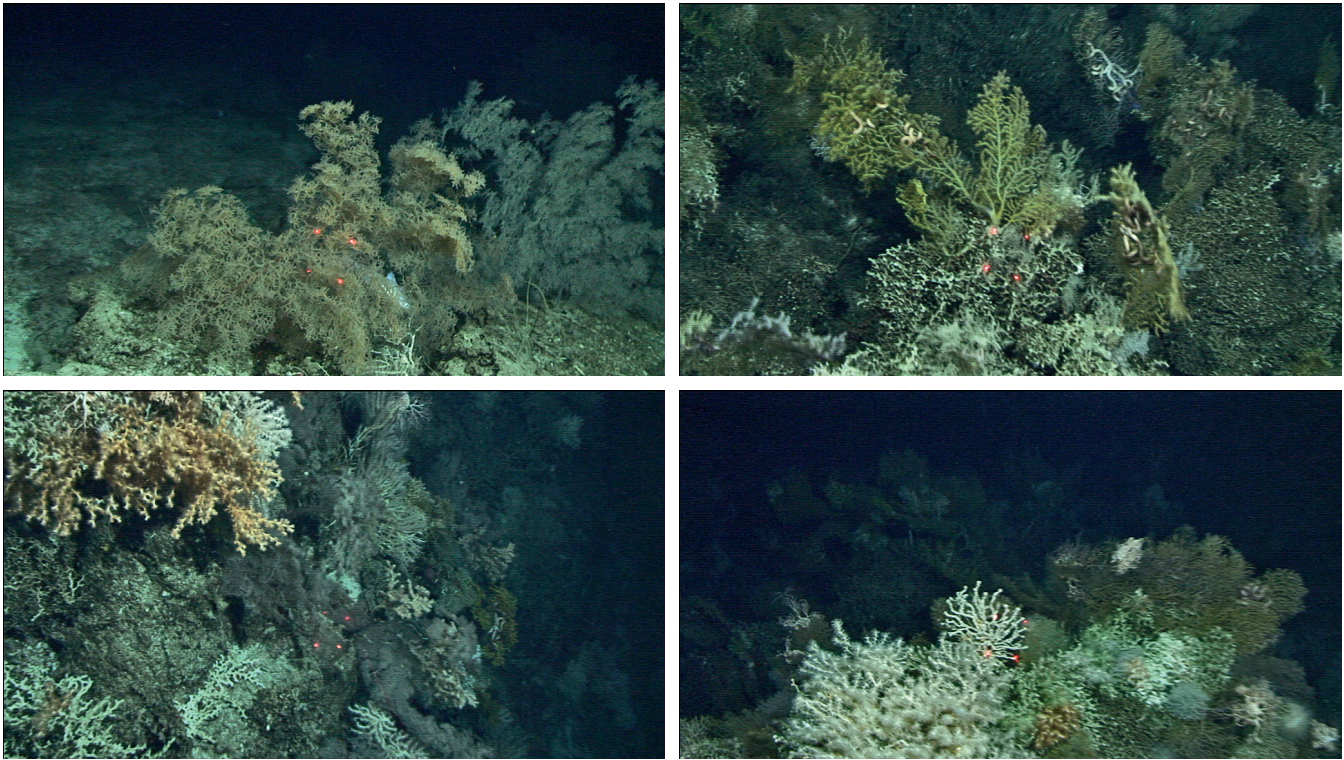


Figure 9: Photographs of coral gardens on a knoll adjacent to Valdivia Bank in the Valdivia Central subarea, from CAMPOD Dive 5. Observations from the RV *Dr Fridtjof Nansen* cruise, January–February 2015. Red dots from laser pointers indicate a 10×10-cm square

the north of this knoll the density of coral declined towards the summit, and the summit substrate was bare rock faces without coral.

Deep-sea red crab was common on the adjacent 865-m-deep plain and up the slopes, but the density of crabs appeared to decline towards the summit of the seamount. The crab density was high even at the deeper end of the dives, at ~900 m depth. Only scattered alfonso specimens were observed, but armourhead aggregations were encountered towards the end of the slope on Dives 15 and 16. In Dive 16, which was a summit dive targeting the shallowest knoll, the transect climbed the slope from 585 m to 415 m. The density of armourhead increased up the slope from ~530 m and was very high around the shallowest area towards the end of the dive (Figure 8c).

Valdivia North — At Valdivia North Seamount, the circular summit with a diameter of ~4.7 km lies to the southeast of a wide shallow area (Figure 7; Figure 15c in Bergstad et al. 2019, this issue). On the summit, three CAMPOD dives were carried out (Table 1), of which Dives 17 and 20 were upslope. The shallowest knoll is ~550 m. Dive 18 was made on the summit within a narrower depth range than the slope dives. Dive 19 was conducted in the flat, deep area to the northwest of the circular summit, at ~890 m.

In the two slope dives, Dives 17 and 20, areas of rich scleractinian coral were observed (Figure 8d), and in Dive 20 on the eastern side of the summit, rather high concentrations of gorgonians as well. Seapens (Pennatulacea) were also abundant in some areas. However, the corals seemed to disappear at the very summit of the seamount. In a grab

station associated with Dive 18 (three replicates) at 570 m, only black corals were retrieved. In the deep sandy plain to the west (885–890 m), no corals were observed but a rather rich fauna of other invertebrates and fishes. Deep-sea red crab was common along most dive transects but declined in abundance towards the summit of the seamount (Figure 8d). Crabs were also common on the deep plain to the west (Dive 19), but in lower numbers than on the summit. A sample of 49 crab specimens was obtained from the bottom trawl on the adjacent plain (Station 12, Table 2), and morphological examination of that sample confirmed that the identity of the crabs observed on videos was *Chaceon erythraeae*.

Scattered single specimens of alfonso were observed during Dives 17 and 18 (on the summit of Valdivia North), but none on the deep adjacent plain. Along and above the track of Dive 18 a rather prominent daytime aggregation of fish was observed on the echograms, and this was observed repeatedly in an 18-h experiment where the ship passed along the same track every hour (Supplementary Figure S5). The aggregation (shoal) was present throughout the series but changed in its character, configuration and depth distribution with time of day. At dusk the shoal appeared to lift off the bottom, and it stayed rather concentrated in the water column during the night. In the morning the shoal descended to the near-bottom zone and dispersed. To determine the identity of the sound scatterers, two unsuccessful attempts were made to sample the shoal with the midwater pelagic trawl; once in the morning (PT 11) and once in the early night (PT 13). Presumably the unidentified fish observed avoided the

trawl. The trawl captured some mesopelagic fish, and the echograms showed how a mesopelagic scattering layer impinged on the seamount (Supplementary Figure S5).

The bottom trawl at Station 12 (Table 2) on the 890-m-deep adjacent plain captured approximately 50 fish species, including orange roughy *H. atlanticus* (22 specimens), several macrourids, alepocephalids, oreos, and some demersal sharks.

Indications of fishing impacts in Valdivia

At Valdivia Central footprints of fisheries included lost ropes (one line in Dive 1; three lines in Dive 9), and what appeared as scour marks of trawl gear on the bare rock surface of Valdivia Bank. No impacts of fishing were detected on the adjacent knolls, including on the knolls with coral gardens. Scour marks from trawls were also observed at Valdivia West on the shallowest summit at depths of less than 590 m (Dive 7). No lost gear was encountered.

At Valdivia Middle, marks on the bare rock faces at the summit shallower than 525 m (Dive 16) were interpreted to be scour marks from trawl gear. At 420 m, during the same dive, a lost rope was observed. The summits had bare rock and little coral rubble, suggesting that corals never (or at least not recently) inhabited the shallowest areas. There was no obvious sign of destruction of coral by past or present fisheries.

A single lost pot was observed during Dive 17 at Valdivia North. No other footprints of fisheries were observed in the remaining dives in that area.

Ewing Seamount

Ewing Seamount lies on the northeastern section of the Walvis Ridge at 23°14.7' S, 08°16.0' E (Figure 1; Figure 17 in Bergstad et al. 2019, this issue). It has an irregular shape, and from the southeasterly summit area there is a rather wide and elongate deep plateau running northwestwards. The latter plateau is ~1 000 m deep whereas the shallowest summit is 780 m. The summit (<800 m) is only ~2.3 km across. The hydrographic observations showed that the temperature decreased from 23.3 °C at the surface, to near 5 °C at the summit depth, and further to 3.7 °C at the depth of the adjacent 1 000-m-deep plateau.

Four CAMPOD dives were made from different directions up the slope of the shallower parts of the seamount from ~900–925 m (Dives 1, 2, 4 and 5), and a further one on the plain to the northwest (Dive 3) (Table 1; Figure 17 in Bergstad et al. 2019, this issue). Scattered live corals (including scleractinians, gorgonians and antipatharians) were observed during all slope dives (Figure 10). The coral density seemed to decrease at the very summit of the seamount.

A bottom trawl tow was conducted at 1 023 m depth on the adjacent deep plateau along the same track as CAMPOD Dive 3 (Table 2). The catch was diverse in terms of both invertebrates and fishes (40+ species). Orange roughy was observed in all summit dives, from 925 m towards the slopes, but tended to be most abundant mid-slope (Figure 10). The density of orange roughy was particularly high in Dive 5. The trawl on the deep adjacent plateau (1 023 m), however, did not catch this species.

In view of the rather significant observations of orange roughy in the CAMPOD dives on the slopes, a repeat

acoustic survey was run across the summit. Three runs were made of a 'butterfly-shaped' track (Supplementary Figure S6), starting at local time 23:00, 01:30 and 05:30, respectively. Near-bottom records of what may have been orange roughy were made on several summit knolls, and the scatterers seemed to stay close to the seabed during the day and lift off into the pelagic zone at night. No attempt was made to trawl above the summit where the risk of snagging was high.

Deep-sea red crab was present on the slopes and appeared to increase with decreasing bottom depth (Figure 10). In Dive 3, on the northwestern plateau, 1–6 crabs per 5-min observation occurred, but the catch in the associated trawl was very low, at only 4 crabs in a 31-min tow.

Footprints of fisheries were a rope observed at 825 m in Dive 1, and some lost trawl gear at 889 m in Dive 2.

Comparisons among seamounts

A summary of VME indicator taxa and SEAFO target fish species observed in the different locations is provided in Table 4. Video-derived density for major coral taxa against depth in the different locations is shown in Figure 11. Noteworthy is the relatively low densities of corals and the extensive variation in abundance, the latter reflecting considerable patchiness in the distribution of all coral taxa. There are also distinctive differences between the seamounts. Scleractinians were most common and dense in the Valdivia area, and the density appeared to peak in the depth interval 350–800 m, where the few observations of coral gardens were also observed. Antipatharians were widespread, including at the shallow summit of Vema Seamount. Gorgonian corals (Alcyonacea) were most prominent at Wüst Seamount, and they were the only coral taxon at Schmidt-Ott Seamount. For all coral taxa the density seemed low in the deepest areas studied (i.e. at ~1 000 m).

Deep-sea red crab was not observed at Schmitt-Ott and the two locations at Wüst, and was only abundant in the Valdivia complex where it had an extensive depth range, from summits to the deepest areas observed. Scattered observations of alfonso and armourhead were made at Wüst, Vema, and in the Valdivia complex, mainly on upper slopes and on knolls associated with summits. Orange roughy occurred at Valdivia North (in a deep trawl catch) but was abundant only at Ewing Seamount, where it was observed in video transects from the shallowest areas of that seamount. A shoal observed on echograms at Ewing Seamount was suspected to be orange roughy, but the identity was not confirmed.

Discussion

All the seamounts visited lie westwards of the highly productive Benguela Current system and within the central subarea of what Longhurst (1998) denoted the South Atlantic Gyral Province (SATL). The sites appear as very minor 'shallow' systems in a deep and vast oligotrophic area of the ocean (Bergstad et al. 2019, this issue). Primary production is likely to be low. Vema Seamount is very different from all the other seamounts visited because the summit reaches into the euphotic zone, creating conditions for a sessile algal community, including kelp forests.

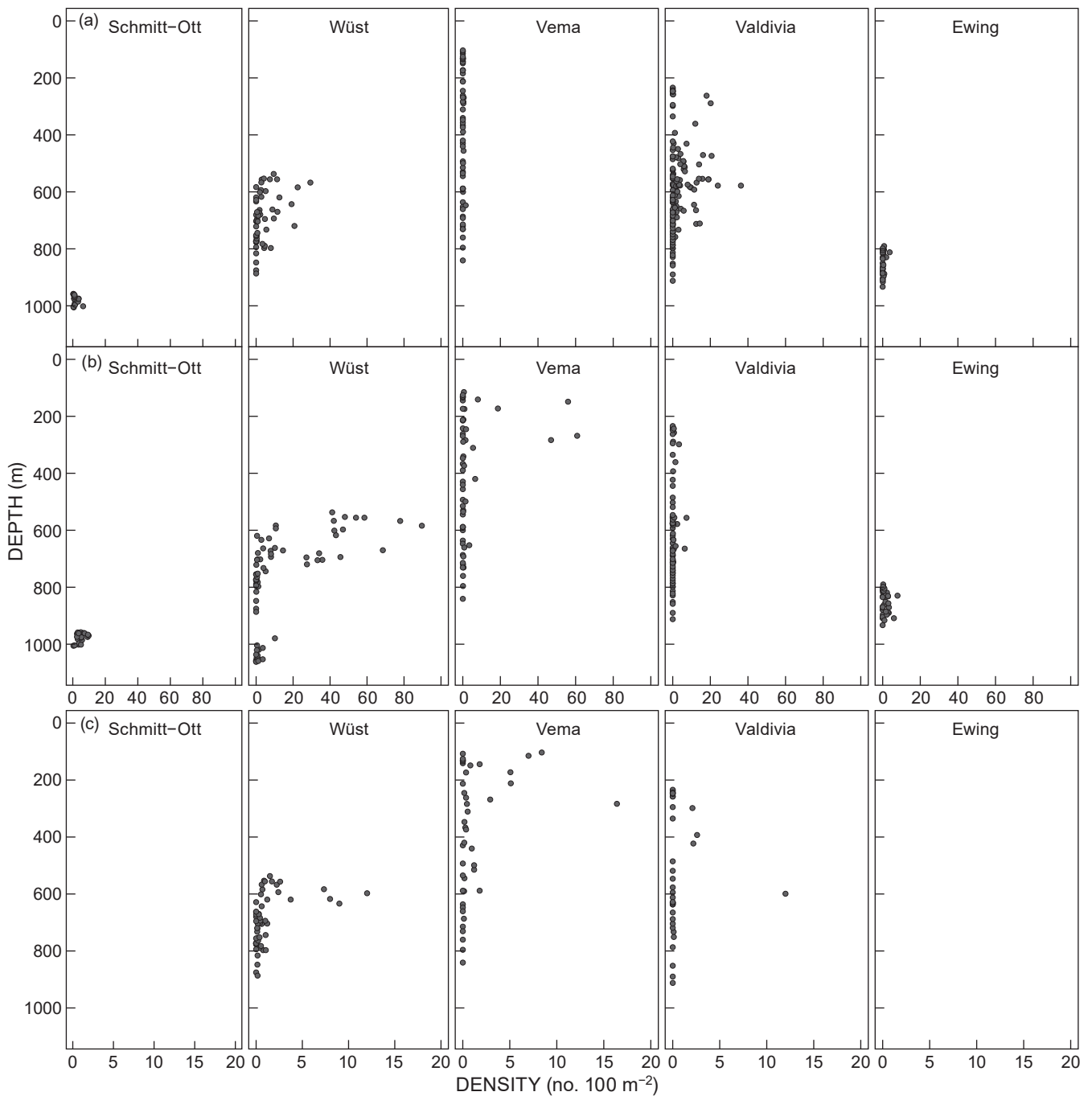


Figure 11: Estimates of density by depth of colonies of the three coral taxa, (a) scleractinians, (b) gorgonians, and (c) antipatharians, on seamounts studied by the RV *Dr Fridtjof Nansen* in January–February 2015. Results are visual enumerations from video footage obtained by the CAMPOD towed video vehicle. Dots represent density estimates by 5-min interval along transects; zero observations were included in the plots

With the exception of Vema Seamount, the summits of all seamounts visited are in the mesopelagic zone (200–1 000 m). The acoustic records suggest that a mesopelagic scattering layer at a daytime depth of 400–600 m was prominent across the study area. Several of the explored seamount summits were deeper than 400–600 m (i.e. Erica, Schmitt-Ott and Wüst Location 1), whereas others are likely to be shallow enough for mesopelagic organisms to impinge

on the summits or slopes during the daytime (e.g. Wüst Location 2, Vema, Valdivia and Ewing). Thus, in addition to inputs of energy from surface layers through sinking and sedimentation, it is likely that migratory import facilitated by the mesopelagic organisms is an important factor for the functioning of the seamount ecosystems in the area.

The study spanned a considerable latitudinal range (23°13'–38°40' S) and included summits varying in

terms of their shallowest depth, from 21 m to 1 000 m. Near-bottom temperatures at summits ranged from 3 °C (at Schmitt-Ott and Wüst Location 1) to 16–18 °C (at Vema). Considerable diversity in the megabenthic communities was expected and observed. Apart from the Valdivia area with its complex multi-summit geomorphology, all the other seamounts explored may be regarded as single-summit features. However, the flat-topped summits were found to be very small compared with the surrounding flanks and sedimented plains which had moderate depths (900–1 500 m). Only Vema Seamount can be regarded as a classical conical seamount with steep and even slopes leading from the summit margin to abyssal depths.

Taxa considered susceptible to significant adverse impacts from bottom-contact fishing gear, and thus regarded as indicators of vulnerable marine ecosystems (VMEs) as defined in the International Guidelines for the Management of Deep-sea Fisheries in the High Seas (FAO 2009), occurred on all the seamounts studied. However, the identity, distribution and density of the indicator taxa differed between locations. In SEAFO CM 30/15, corals and sponges are referred to as primary VME indicators. Corals were predominant in all locations studied, whereas sponges were very scattered and few (to the extent detectable by the methods applied). At the Schmitt-Ott and Wüst seamounts there was a pronounced presence and apparent dominance of gorgonians (Alcyonacea). In all other locations the diversity of VME taxa was greater, and more scleractinians and antipatharians occurred. However, in many cases the scleractinians were dead and probably ancient (entirely so at Ewing). Notably, at Valdivia and Ewing, scleractinians (dead and alive) seemed to be restricted to slopes of adjacent deep knolls within the depth range 350–800 m, and the more prominent shallower summits had no or only low densities of corals.

The most prominent scleractinian coral identified in grab samples and by video was *Enallopsammia rostrata*. The rubble also appeared to be composed primarily of *E. rostrata* skeletons. With few exceptions, live colonies were small and scattered and did not form prominent gardens or reefs. This was the common observation on the Wüst locations, on the slopes of Vema Seamount, and on most slopes of the Valdivia seamounts and Ewing Seamount; *E. rostrata* is a deep-living species (median depth 781 m in New Zealand) often associated with seamounts and low-productivity waters (Tracey et al. 2011). Global habitat suitability models suggest that *E. rostrata* is associated with habitats with limited particular organic carbon input, but the species accepts a wider temperature range than several other framework-forming scleractinians (Davies and Guinotte 2011). Compared with the model predictions showing a wide depth range, from surface waters to 1 000 m or beyond, the species' depth range in the Southeast Atlantic seems more limited. The species was absent from the deepest seamounts. In the shallow-summit seamounts where it was abundant, the species was absent from the deeper parts of the dive transects. In view of our depth range observations and considering the bathymetry and geomorphology of the Southeast Atlantic high seas (i.e. the SEAFO CA) (Bergstad et al. 2019, this issue), it is to be expected that only a minute proportion (probably less than 0.05%) of the area has suitable depth for this species.

Lophelia pertusa was recorded in previous studies in the Southeast Atlantic (e.g. the Spanish–Namibian surveys at Valdivia), and dead colonies were reported by Zibrowius and Gili (1990); but in the latter study it is noted that *E. rostrata* is the more common live species. The global habitat model of Davies and Guinotte (2011) predicts that *Madrepora oculata* and *Solenosmilia variabilis* would occur at the Walvis Ridge seamounts, but those species were not observed in this study.

It was only on knolls southeast of Valdivia Bank and on a knoll south of Valdivia Middle that well-developed multi-taxon coral gardens occurred on the slopes. These appeared as small and patchy sub-features of the seamounts. At Ewing Seamount, the density of dead but erect coral was comparatively high, suggesting that similar coral gardens may have inhabited this seamount in the relatively recent past.

Estimating the abundance of SEAFO fish resources (i.e. alfonsino, armourhead and orange roughy) expected to occur in the seamounts visited was very difficult due to rugged topography and the benthopelagic and aggregated distributions of the target species. Hydroacoustic mapping is potentially useful yet challenging in rugged areas, and it requires successful fishing with midwater trawls to facilitate identification of summit aggregations and scattering layers. Unidentified summit schools were observed at Erica, Valdivia and Ewing seamounts. At Ewing Seamount the school was likely to be orange roughy, whereas at Valdivia North a similar aggregation may have been alfonsino. These tentative conclusions were based mainly on observations of shoal patterns on echograms and occurrence of the species in video records. Bottom trawling was only possible on deep sandy plains, not in the main former fishing areas on slopes and summits (Bergstad et al. 2019, this issue).

Pelagic armourhead and alfonsino were numerous in only a few of the video transects, but in the majority of transects and locations these species were not observed at all. This is noteworthy because almost all summit dives were made in the depth ranges and habitats where these species were expected to occur. Distributions of the species appeared limited and abundances generally low. Very few armourhead were observed in the main fishing area of the Valdivia area, where trawl fisheries were recently conducted (SEAFO Scientific Committee reports, available at www.seafo.org). No armourhead were observed at Ewing Seamount. Orange roughy was common in video records around the summit of Ewing Seamount which, prior to the SEAFO moratorium introduced in 2006, used to be a main fishing area within SEAFO. A few juveniles occurred in a bottom-trawl catch on a deep plain in the Valdivia area.

Deep-sea red crabs *Chaceon erytheiae* were distributed across an extensive depth range in the Valdivia area and at Ewing Seamount. It is probable that the crabs observed at Vema Seamount were also this species. Video density records showed that Valdivia was a rich area for crabs, much richer than all others. There has been some doubt about the identity of the commercial crab catches from the Valdivia area; hence, it was clarifying that morphological examination of the scientific trawl samples supported the earlier observation that the main species in the area is *C. erytheiae* (Macpherson 1984).

Lost pots and ropes were frequently observed in video footage at Vema and Valdivia seamounts. These items could not be aged but may well have been abandoned or lost many years ago. At Ewing Seamount, lost trawl gear was observed in one of the summit dives. On Valdivia Bank and the Valdivia West summit what was suspected to be trawl-door scour marks were observed. These areas have flat rocky surfaces. No evidence of trawl impacts or pot fishing was observed in areas of soft sediments, or in the extensive areas with coral rubble. In areas with high densities of live (and dead) coral, such as in knolls adjacent to main summits in Valdivia, the video records suggest that the coral gardens are intact and not impacted by fishing.

On top of most of the summits there was very little coral and also little coral rubble. This was most prominent on upper slopes and summits of the Valdivia area where the main summits had bare pale-coloured rock and sheets that appeared as carbonates. Provisionally, these sheet-like features were classified as fossilised coral framework (Bergstad et al. 2019, this issue). The summit slopes had scattered colonies of scleractinians, and at the base extensive patches of coral rubble were observed. These observations are generally compatible with theories on the evolution of off-ridge eroded seamounts and guyots with extensive but largely extinct coral fringes or consolidated coral caps (e.g. US Geological Society 1978; Clague and Dalrymple 1987; Wessel 2007).

It is likely that the shallowest seamount summits, such as Vema Seamount, Valdivia Bank and Valdivia West, are presently not favoured habitats of cold-water scleractinians. Under the current environmental conditions and productivity regimes only relatively few species, such as *E. rostrata*, may be able to inhabit these seamounts. It is only at somewhat deeper knolls that extensive coral gardens still occur.

Comparisons between our information on observed depth distributions of scleractinian corals (and the extensive local patchiness of the corals) and the predictions from global habitat suitability models (Tittensor et al. 2009; Davies and Guinotte 2011) suggest that, for the Southeast Atlantic, the models generate areas of coral distributions that are too large. This emphasises the continued need for ground-truthing and probably also a need for science-based advice underpinning fine-scale spatial management, preferably based on observations. When good observations are not available, precautionary advice is warranted, taking into account the increasing understanding of VME distributions and geomorphology at the spatial scales relevant to current and perceived human impacts, as illustrated (Bergstad et al. 2019, this issue) for the seamounts considered here.

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