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From physics to fish: 50 Years of research at Great Meteor Seamount, NE Atlantic

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Abstract
Seamounts are among the most common physiographic systems in the global deep ocean, defining habitat for a hugely diverse biome. Great Meteor Seamount is located in the subtropical Northeast Atlantic and is considered one of the largest seamounts worldwide. Despite its remoteness, it remains one of the few seamounts globally with a long research history dating back more than 50 years. In this study, we aim to review the recent history of scientific research at Great Meteor Seamount, integrating multidisciplinary datasets of the entire seamount ecosystem, including data on plankton, benthos, fishes, and physical oceanography. The interaction of the seamount topography with background low-frequency and tidal currents creates a unique dynamical response due to its location at the critical latitude for seamount trapped diurnal waves, and the high amplitudes of semidiurnal tides. Biological observations show elevated patchiness on horizontal scales smaller than the seamount, which compares well to other seamounts with shallow summits. Regardless of ecosystem pressures associated with geographic isolation and the nutrient and organic matter deprivation inside the North Atlantic Subtropical Gyre, Great Meteor Seamount hosts a diverse species composition including megafaunal taxa such as sponges and corals, as well as species rich fish populations and meiofaunal groups of copepods and nematodes. Due to the ecological vulnerability of seamount habitats to unsustainable exploitation and their important role as open ocean hotspots of marine life, the Portuguese government plans to designate Great Meteor Seamount as a Marine Protected Area (MPA) under the European Marine Strategy Framework Directive. Here, we summarize and recount important results from the long history of research at Great Meteor Seamount in the context of present-day challenges and the initiatives to protect vulnerable ecosystems.

Keywords Seamount ecosystem · Deep-sea · Benthic and pelagic realms · Management and conservation · Biodiversity and Ecology · Oceanography

Introduction

The global seafloor is dotted with tens of thousands of seamounts (Wessel et al. 2010; Gevorgian et al. 2023), isolated or clustered, small or large, some of them rising several thousand meters from the seafloor into the photic layer. Seamounts host unique habitats and hotspots of marine life in remote areas with otherwise often low productivity and biodiversity (Rogers 1994). They are also hotspots of internal-wave generation and vigorous mixing, thus enhancing productivity, biomass, and biodiversity (Lavelle and Mohn 2010). Seamounts interact with the surrounding currents and alter ocean conditions locally and globally. They have attracted increasing scientific interest since the late 1950s when the presence of numerous seamounts in the world's oceans has become known to the scientific community (e.g., Uda and Ishino 1958; Herlinveaux 1971; Boehlert and Seki 1984; Uchida and Tagami 1984; Genin and Boehlert 1985; Eriksen 1998) However, significant advances in seamount research have only been achieved over the past three decades in the wake of growing commercial and conservation interest in deep-sea ecosystems (Consalvey et al.

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2010; Rogers 2018). Our perception of the complexity of deep-sea landscapes had radically changed over the past decades with access to remote sensing data, in situ depth soundings and processing techniques. As a result, we are rewarded with an unprecedented view of the true complexity of the seafloor. The estimated number of seamounts larger than 1000 m in height varies between 25,000 and 140,000, far exceeding previous estimates (Hillier and Watts 2007; Wessel et al. 2010; Yesson et al. 2011; Gevorgian et al. 2023).

Despite recent advances, a mechanistic understanding of seamount ecosystem dynamics at local seamount scales (several km or less) is still fragmentary and largely based on observations from only a few locations (Rogers 2018). Until a decade ago, fewer than 300 seamounts had been studied in sufficient detail to adequately describe seamount faunal composition, distribution, and ecology (Etnoyer et al. 2010a, b; Stocks 2010). The interaction of different environmental factors defines the effect of seamounts on populations of seamount biota, generates variability in the surrounding ocean and vice-versa, and makes each seamount a unique ecosystem. Early considerations on the interplay of seamounts and off-seamount currents led to the concept of stable Taylor caps (Taylor columns in a stratified fluid), which provided a first conclusive mechanistic view of particle aggregation and retention over seamounts driven by uniform impinging currents (Chapman and Haidvogel 1992; Goldner and Chapman 1997; Mullineaux and Mills 1997). Pioneering experiments combining in situ measurements with hydrodynamic models extended the spectrum of physical seamount processes to include higher frequency oscillatory currents generating topographically trapped waves, internal tides and turbulent mixing (Brink 1990, 1995; Beckmann and Haidvogel 1997). The Great Meteor Seamount (GMS) in the subtropical Northeast Atlantic is one such underwater island and one of the largest seamounts world-wide. In this review, we aim to summarize the key findings from 50 years of research at GMS and to discuss the results in the context of present-day deep-sea research challenges and conservation goals.

Geographic setting and seamount geomorphology

GMS is located in the subtropical Northeast Atlantic Ocean at 30° N and 28.5° W, approximately 1500 km west of the Canary Islands and 1000 km south of the Azores (Fig. 1a). It is the largest seamount in the North Atlantic with an elliptical plateau covering an area of 1400 km^2, roughly matching the size of the island of Gran Canaria (Von Rad 1974). It rises from 4200 m depth at the seafloor to a summit depth between 270 and 350 m below the surface (Hinz 1969). This shallow and flat summit (Fig. 1b) suggests, as for other southern Azores seamounts, that the original peak may have been eroded and flattened during a period when the seamount rose above sea level and descended later with tectonic movement (Gente et al. 2003). The flank is characterized by terraces (particularly at 450 m and 550 m depth), steep slopes with a typical inclination of 13° (maximum of 50°), and a surrounding lower rise region with an inclination smaller than 5° (Ulrich 1971). New high-resolution bathymetry surveys conducted by the Task Group for the Extension of the Continental Shelf (EMEPC-Portugal) reveal the fine-scale morphological characteristics of the steep slopes of GMS in great detail (Fig. 1c).

The summit and upper flank of the seamount are covered by a 150-m to 600-m-thick layer of carbonate and pyroclastic rocks of middle Miocene age, capped by heavily reworked, residual, and bioclastic sands (Von Rad 1974). The volcanic origin of GMS is reflected by the presence of basalt samples dredged from the top of the eastern and southeastern flanks (Wendt et al. 1976) and more recently from remotely operated vehicle (ROV) samples collected from the southern tip of GMS at 2700 m depth (Ribeiro et al. 2017). The GMS remained volcanically active until about 10 Myr before present (Von Rad 1974).

Material and methods

The summary of key findings at Great Meteor Seamount from different disciplines is largely based on a literature survey including scientific publications, reports, academic periodicals, and theses, as well as gray literature. A systematic review was also conducted in online databases, including Scopus (www.scopus.com, 86 records) and Web of Science (www.webofknowledge.com, 137 records) using the search terms "Great Meteor Seamount." The literature research was completed on the 4th of November 2022. The citations were cross-checked and duplicate records were removed (56 records); and additional relevant publications identified by the co-authors were included.

Other results presented in this review are based on the analysis of previously unpublished historical and new data. Data describing vertical distributions of physical water mass properties (temperature and salinity), nutrients, and chlorophyll-a (Chl-a) were collected in September 1998 on board RV "Meteor" at a total of 52 stations using conductivity, temperature, and depth (CTD) profiling and water sampling techniques (Mohn and Beckmann 2002; Kaufmann 2004; Pfannkuche et al. 2000). The phytoplankton biomass and community composition were characterized using various methods, including the determination of particulate organic carbon (POC) and nitrogen, analysis of phytopigments by high performance liquid chromatography (HPLC), microscopical analysis for the enumeration of microphytoplankton, scanning electron microscopy for the enumeration of nanophytoplankton (coccolithophores), and flow cytometry for the analysis of the picophytoplankton community. Zooplankton samples

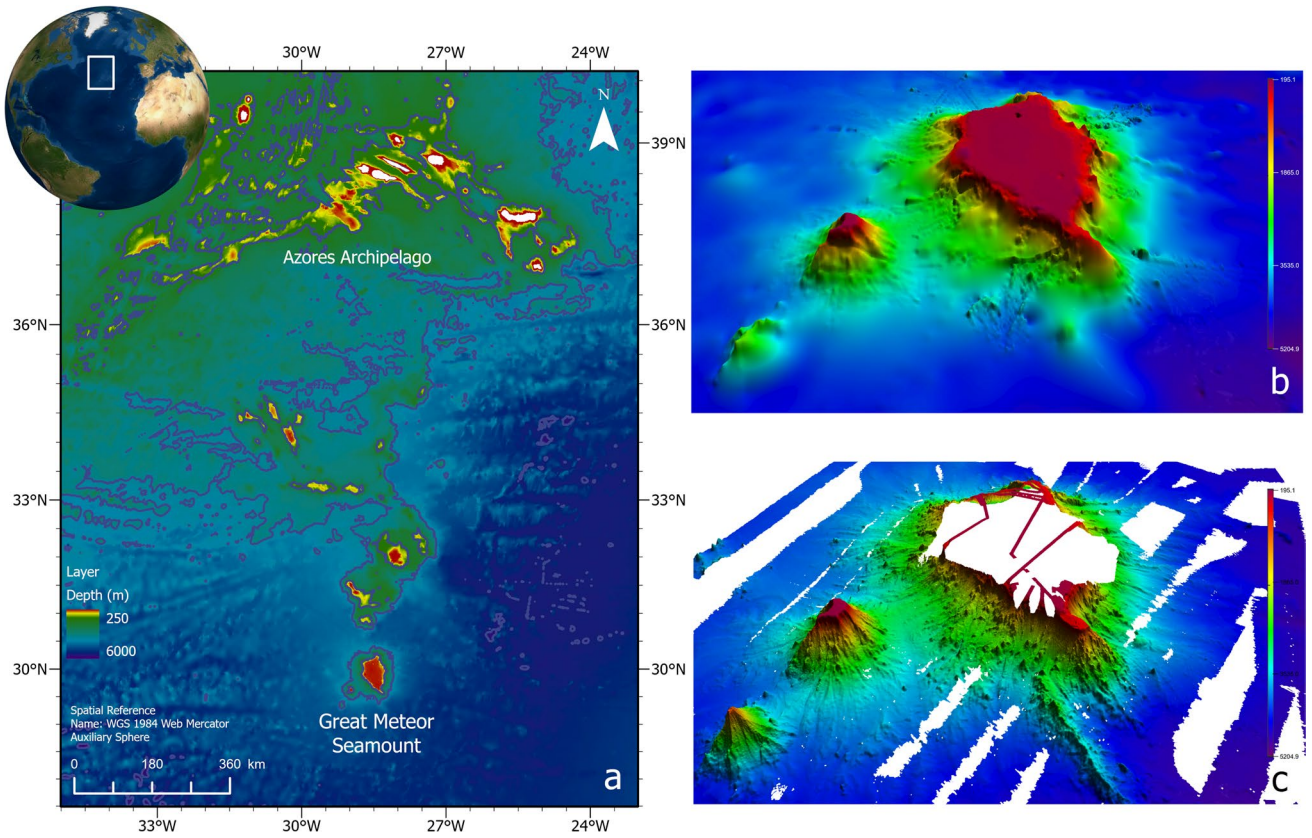

Fig. 1 **a** Geographic setting and morphology of Great Meteor Seamount (GMS) along the southern Azores Seamount Chain relative to Azores Archipelago in the North Atlantic Ocean; **b** 3D view of the GMS based on GEBCO_2022 bathymetry (GEBCO Compilation Group 2022); **c** 3D view of the GMS using the EMEPC-Portugal multibeam data acquired from 2005 to 2009: the high resolution bathymetry enabled detailed mapping, particularly evident on the GMS flanks, and on the Closs and Little Meteor seamounts (from left to right)

were gathered with a Longhurst-Hardy-Plankton Recorder (LHPR) (Longhurst et al. 1966); mesh size was at 200 µm and at different times of day on 11 stations above both the plateau and the slopes of the mount. The fixed samples were analyzed in the home laboratory for wet weight, abundance, composition, and distribution. Additionally, the acoustic scattering of organisms was observed using the ship's echo sounder (ATLAS DESO 25/RS) at a frequency of 33 kHz.

Bathymetric maps were compiled from multibeam data collected during different surveys between 2005 and 2009 and GEBCO_2022 data, respectively (Fig. 1b). A high-resolution multibeam bathymetry of the seamount was recorded on board the research vessels RV "Almirante Gago Coutinho" and RV "Kommandor Jack" between January 2005 and June 2009 by EMEPC-Portugal as part of the Portuguese Extension of the Continental Shelf project. Both ships were equipped with a Kongsberg EM120 multibeam operating at a frequency of 12 kHz, a beam width of 2°×2° and a depth resolution between 10 and 40 cm. On board RV "Almirante Gago Coutinho," an additional multibeam was used (Kongsberg EM 710) operating at frequencies between 70 and 100 kHz, a beam width of 1°×2° and a depth resolution of 1 cm. The multibeam data were processed using CARIS HIPS and SIPS® software to clean position and attitude data to correct the sound velocity and to filter the soundings using the total propagated uncertainty values and vertical distance to cube-based surface and to manual edit. The processed data was exported to an ASCII XYZ point cloud file.

Great Meteor Seamount: a timeline of exploration and discovery

GMS was discovered by the German research vessel "Meteor" (the first research vessel sailing under that name) in 1937, and it is one of the earliest seamounts ever discovered and described in the deep-sea (Nellen and Meincke 1999). A detailed bathymetry along with samples and photographs of the seafloor was later collected by the Woods Hole Oceanographic Institution (WHOI) on two distinct

cruises (Pratt 1963). In the years and decades following, additional data on the morphology, geophysics, geology, oceanography, and biology of GMS were collected making GMS not only one of the largest seamounts explored but also one of the most frequently visited seamounts worldwide (see Fig. 2 and Table 1).

Physical oceanography

The large-scale circulation surrounding GMS is dominated by the eastward flowing Azores Current to the North between 34 and 35° N latitude at velocities 25–50 cm s^{-1} in the upper few hundred meters east of the Mid-Atlantic

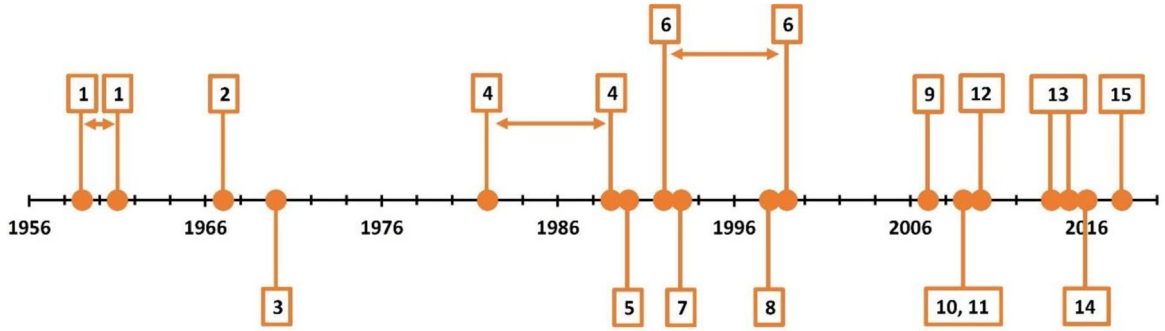

Fig. 2 Timeline of major research activities (numbers) at Great Meteor Seamount since the first cruise dedicated to research in 1959 (see Table 1 for a detailed description)

Table 1 Summary of major surveys and research activities at Great Meteor Seamount and surrounding areas since 1959 (for a detailed overview see Table S1 in the Online Resource 1)

Activity	Years	Area	Investigations
1	1959–1961	Great Meteor Seamount	Great Meteor Seamount reconnaissance surveys (USA): seamount morphology and benthos
2	1967	Great Meteor Seamount	Atlantic Seamount Cruises ("Atlantische Kuppenfahrten;" Germany): topographic surveys and seamount geology, water mass properties at different seamount locations, time-series of currents at individual mooring stations, fish larvae, and plankton using oblique tows
3	1970	Great Meteor Seamount	Supplement to data collected during the 1967 Atlantic Seamount cruises ("Roßbreiten Expedition;" Germany)
4	1982–1989	Atlantis—Great Meteor Archipelago	Various surveys (Russia): seamount geology, fish, and benthos
5	1990	Great Meteor Seamount	Trawling survey (France): fish fauna
6	1992–1999	Great Meteor Seamount	Oceanographic surveys (Spain): oceanography, phytoplankton, and primary production
7	1993	Atlantis—Great Meteor Archipelago	Seamount survey (France): benthic fauna and colonization of isolated seamounts by benthic species
8	1998	Great Meteor Seamount	Seamount Ecology survey (Germany): marine invertebrates, phyto-, zoo, ichthyoplankton, fishes, water mass properties, and currents
9	2007	Atlantis—Great Meteor Archipelago	Multidisciplinary expedition in order to supplement the process of extension of the continental shelf of Portugal (Portugal)
10	2009	Great Meteor Seamount	Sediment sampling (Germany): deep-sea protists, Amoebozoa
11	2009	Great Meteor Archipelago	Portuguese Continental Shelf Extension Programme (Portugal): seafloor mapping and benthic sampling
12	2010	Great Meteor Seamount	Benthic survey (Germany); benthic fauna
13	2014–2015	Atlantis—Great Meteor Archipelago	BIOMETORE Project (Portugal): demersal and deep-sea fish species and other marine invertebrates, benthic and pelagic fauna, mapping benthic communities, water mass properties, and currents
14	2016	Atlantis—Great Meteor Archipelago	Geological—Geophysical survey (Russia): tectonics and volcanism
15	2018	Great Meteor Seamount, Small Meteor Seamount	Benthic survey (Germany): benthic fauna

Ridge (Fig. 3a; Klein and Siedler 1989; Lozier et al. 1995). Although the Azores Current is described as a highly dynamic system with enhanced mesoscale variability from baroclinic instabilities along its zonal boundaries (e.g., Alves et al. 2002; Sangrà et al. 2009), early observations did not show evidence that shedding Azores Current eddies regularly propagate into the GMS region (Meincke 1971). The surface circulation around GMS often shows south-easterly to south-westerly currents at speeds < 10 cm − 1 with only little variability (Fig. 3a, b). However, analysis of long-term satellite altimetry data indicates that occasionally surface currents are amplified above the seamount and along its northern boundary (Fig. 3c). Barotropic tidal currents in the wider GMS region are much smaller in magnitude and vary between 0.1 and 0.3 cm s^{-1} (main diurnal tidal harmonics O_1 and K_1) and 1 and 3.5 cm s^{-1} (main semi-diurnal tidal harmonics S_2 and M_2), respectively (Siedler and Paul 1991; Mohn and Beckmann 2002).

Early observational data revealed systematic disturbances of water mass properties above the seamount, manifested as a well-pronounced cold and dense dome above the seamount summit (Meincke et al. 1971). Later observational and modeling studies provided a more complete picture highlighting a myriad of tidally dominated motions (Gerkema and van Haren 2007) but also confirming the large amplitude doming of isotherms and isopycnals above the summit at water depths of 200–300 m capped by a seasonal thermocline (see Fig. 4 a for water mass properties sampled along transects

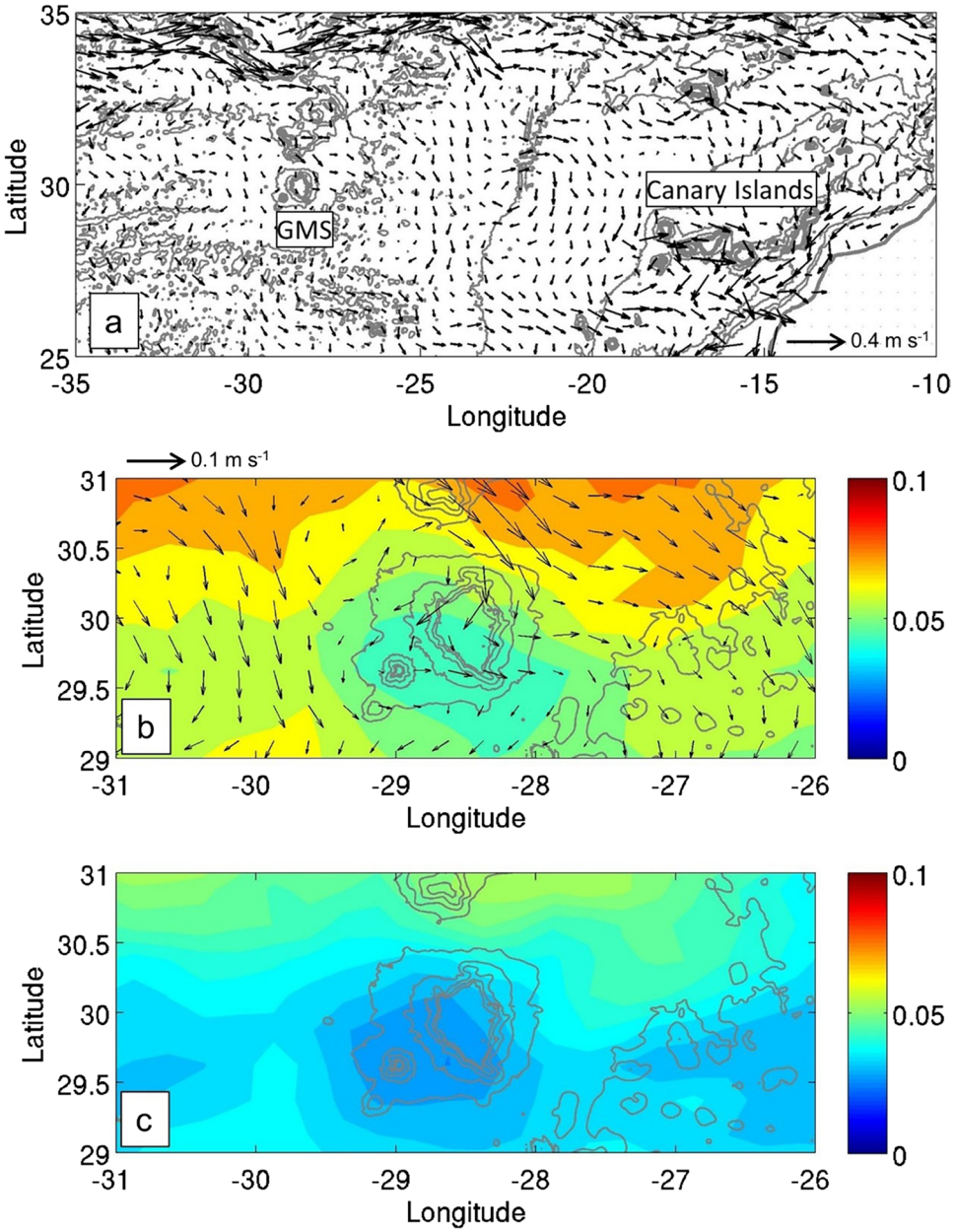

Fig. 3 **a** Surface currents in the NE Atlantic from satellite altimetry data (1998–2008 median of daily geostrophic velocities; https://data.marine.copernicus.eu/product/SEALEVEL_GLO_PHY_CLIMATE_L4_MY_008_057/description). A Great Meteor Seamount zoom of mean surface currents (m s^{-1}) and standard deviations from data presented in **a** are shown in **b** and **c**, respectively

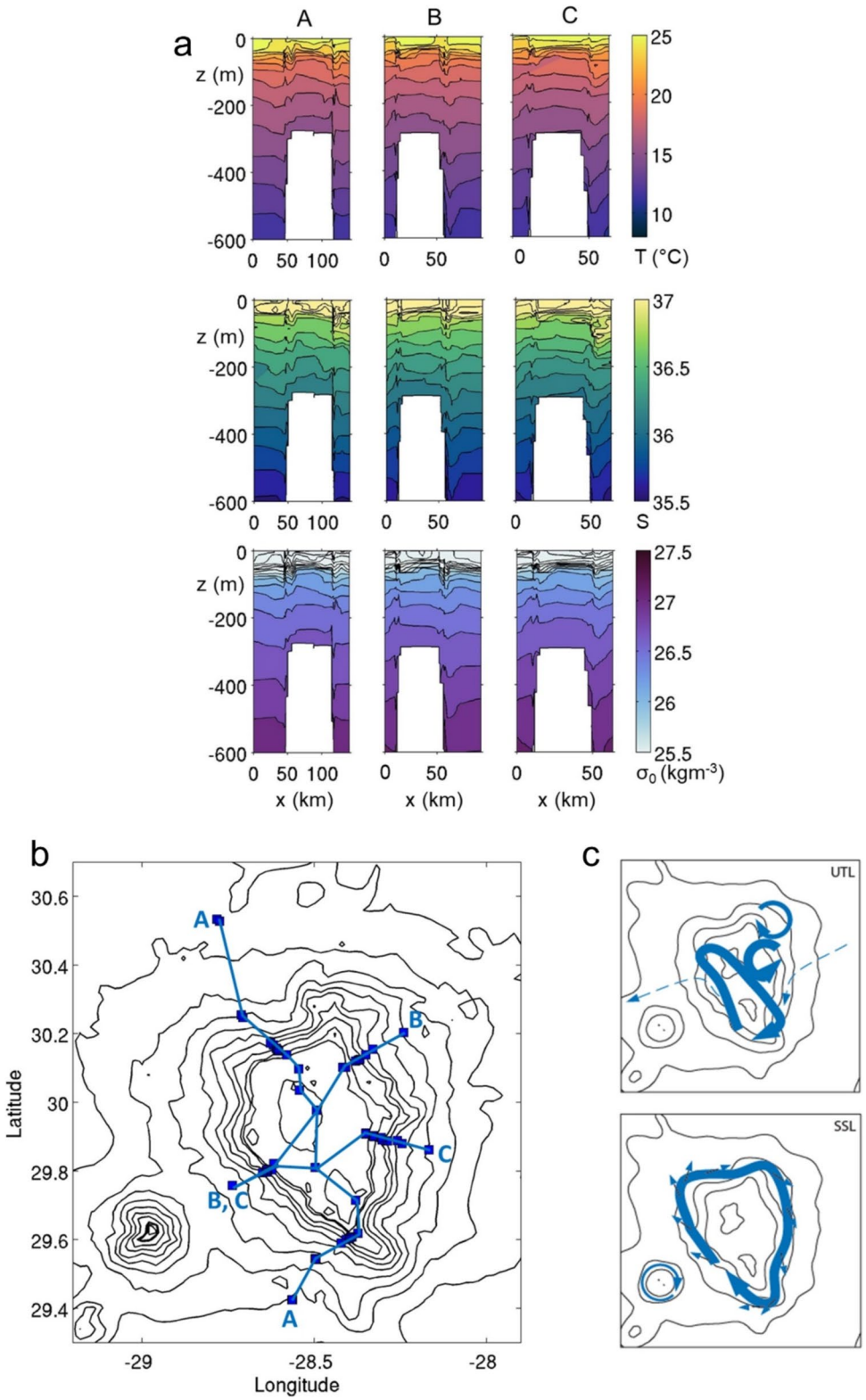

Fig. 4 Water mass properties above Great Meteor Seamount (GMS). **a** Vertical distribution of temperature (T), salinity (S), and potential density (σ_0) in the upper 600 m along three transects (A, B, and C) from CTD measurements obtained during the RV "Meteor" cruise M42/3 in 1998 shown in **b**; **c** schematic view of the time-mean circulation at GMS in the upper thermocline layer (UTL) and seamount summit layer (SSL) from simulations with a hydrodynamic model (Mohn and Beckmann 2002; Mohn 2010)

shown in Fig. 4 b; Mouriño et al. 2001a, b; Mohn and Beckmann 2002). In the hydrodynamic model by Mohn and Beckmann (2002), the time-mean circulation is described as a two-layer system consisting of a stable anti-cyclonic vortex inside the seamount summit layer (100–270 m) and a more variable aggregation of smaller counter-rotating eddies in the upper thermocline layer (< 100 m) (Fig. 4c; Mohn and Beckmann 2002; Mohn 2010). Both layers appeared

to be connected by a secondary circulation in the vertical, featuring downwelling in the center and upwelling above the steep slopes, superimposed on energetic, and high frequency tidally dominated currents (Beckmann and Mohn 2002). However, these results can at best be considered as a snapshot. Field observations by Mouriño et al. (2001a, b), described in more detail in the next section, showed high levels of temporal and spatial variability of the seamount circulation and only short and intermittent trapping of subtidal oceanic motions.

Near-bottom currents close to GMS at water depths are greater than 3000-m transport cold Antarctic Bottom Water (AABW) toward the Northeast. When these currents encounter the seamount, they are deflected, leading to intensified flow along the western side and weaker flow on the eastern side (von Stackelberg et al. 1979). Consequently, sedimentation patterns around GMS exhibit asymmetry, with the eastern side showing the greatest accumulation of displaced material, highest sedimentation rates, and minimal bioturbation (von Stackelberg et al. 1979; Kuijpers et al. 1984).

The existence of a closed time-mean and near-summit vortex does not imply that the seamount is physically isolated. Substantial tidal and internal wave activity leads to strong sub-mesoscale variability in the seamount surroundings, including the bottom boundary layer (van Haren 2005). The conversion of barotropic to internal tidal energy around GMS was estimated at 0.3 GW for the principal lunar semidiurnal constituent, M_2. This value is approximately 60 times lower than that of the Hawaiian Ridge. However, since the Hawaiian Ridge comprises around 80 seamounts, the energy conversion per seamount is comparable (Gerkema and van Haren 2007). The complex interplay of tidal currents and seamount bathymetry generates a number of energetic physical processes: non-linear rectification of amplified K_1 tidal currents, semidiurnal internal tide generation, Kelvin–Helmholtz overturning billows created by internal wave shear and wave breaking via turbulent upslope moving internal bores (Gerkema and van Haren 2007; van Haren and Gostiaux 2010, 2012). Upslope moving bores resuspend matter from the seafloor up to (at least) 50 m was observed (van Haren and Gostiaux 2012). Once resuspended, matter may be transported further up. These processes may support enhanced upwelling of nutrients into the photic zone leading to higher primary production above the seamount, compared to an otherwise less productive oceanic far field (White et al. 2007). On the other hand, circumstantial evidence from early expeditions describing a "deep blue-colored" ocean at GMS indicates at least episodically diminished or scattered food availability for the seamount fauna (Nellen and Meincke 1999). Studies indicate that while upwelling and enhanced primary production over seamounts do occur, they are rarely observed (Rogers 1994; Genin 2004) or are often transient or short-lived when they occur (e.g., Mendonça et al. 2012). More consistent primary production enhancement over seamounts has been observed in cases when unique circulation patterns, such as Taylor caps, trap nutrients, and organic matter (Mendonça et al. 2012; Bashmachnikov et al. 2013). Internal waves have also been reported as a mechanism for downward transport and aggregation of organic matter over seamounts (Read and Pollard 2017).

Biophysical coupling and plankton distribution

The myriad of physical processes happening on seamounts on different temporal and spatial scales impacts plankton composition and dynamics in two main ways. First, physical dynamics at seamounts alter turbulence and stratification conditions in the water column. Both properties determine the intensity of vertical mixing (Moum 2021), which is crucial for phytoplankton growth and composition as it controls the availability of two main resources, light and nutrients (Margalef 1978; Villamaña et al. 2019). Mixing in oligotrophic waters plays a crucial role in promoting phytoplankton growth by facilitating the upward transport of nutrients from deeper layers to the nutrient-limited surface waters (Mouriño-Carballido et al. 2021). Secondly, physical processes may increase retention of matter and organisms produced over, or entrained into seamounts, but they can also promote the downstream advective loss and patchiness (Mohn and White 2010). A detailed overview of potential biological responses to physical disturbances at seamounts can be found in White et al. (2007).

It is a widely held view that physical processes at seamounts stimulate phytoplankton production and retention, which in turn fuel higher trophic levels. Nervertheless, phytoplankton biomass enhancement over seamounts is only occasionally observed due to the generally complex nature of the coupling between the physical field and plankton acting over a wide range of temporal and spatial scales (Steinbuck et al. 2010). On the other hand, the effect of the physical forcing on phytoplankton production at a seamount may be masked by the background variability of the surrounding ocean, as the horizontal spatial scales of seamounts and patchiness of plankton distribution typically match (Kaiser et al. 2007). For zooplankton, it has been observed that groups which are performing diurnal vertical migrations, like euphausiids and several copepod species, can get trapped by the summit of a seamount during downward migration in the morning, if the summit is shallower than the migration depth of these species (Genin et al 1988, 1994). The accumulated organisms that are stranded on the peak can be easily preyed upon by seamount inhabiting fishes. This mechanism is referred to as the "trapping effect" of seamounts (Genin and Dower 2007), leading to enhanced

production of predator populations. When the zooplankton migrates upward the following evening the stocks are reduced compared to the surrounding open ocean which causes increased patchiness leeward of the summit (Fig. 5).

During a major multidisciplinary research programme conducted at GMS on 5 research cruises between 1992 and 1999, bio-physical connections and their temporal and spatial variability patterns were investigated with a focus on phytoplankton distribution (Mouriño et al. 2001a, b; Fig. 6). Only in March 1992, trajectories of two drogued buoys showed some trapping of the flow at the seamount with a mean particle residence time of 21 days. This is equivalent to a mean advective velocity of 2.9 km day^{-1}, a value 2.5 times less than the mean displacement velocity estimated for the surrounding oceanic region. Short records (4 days) from current meter moorings deployed in March 1992 indicated the presence of a clockwise flow associated with GMS (Mouriño et al. 2001a, b). In March 1992, evidence for enhanced phytoplankton biomass and primary production was observed alongside vertical dome-like displacements of isotherms and isohalines within the upper 100 m over the seamount (Fig. 6a). Enhanced phytoplankton biomass was measured over the GMS slope and summit, whereas increased primary production was only observed over the seamount center. Clear differences were detected in the relative contribution of various taxonomic groups to total microplankton biomass between GMS and nearby waters. Large diatoms typical of shallow coastal areas were more abundant at GMS. In contrast, doming of isotherms did not occur over the seamount summit with the development of stratification in the upper water column in April 1999 (Fig. 6b). Maximum Chl-a values were observed associated with the shallower thermocline over the seamount slope, whereas primary production was higher above the summit. No clear differences in phytoplankton composition were observed at this time inside and outside GMS.

Phytoplankton biomass and production averaged for the five cruises did not show significant differences between stations located over GMS, slope or deep waters though seasonality was evident. Mixing and stratification of the water column showed a gradual shallowing of the mixed layer as the seasonal thermocline becomes established during the summer. This pattern translated into 2 to threefold changes in depth-integrated Chl-a and primary production rates, which on average decreased in the period December to April. However, vertical displacements up

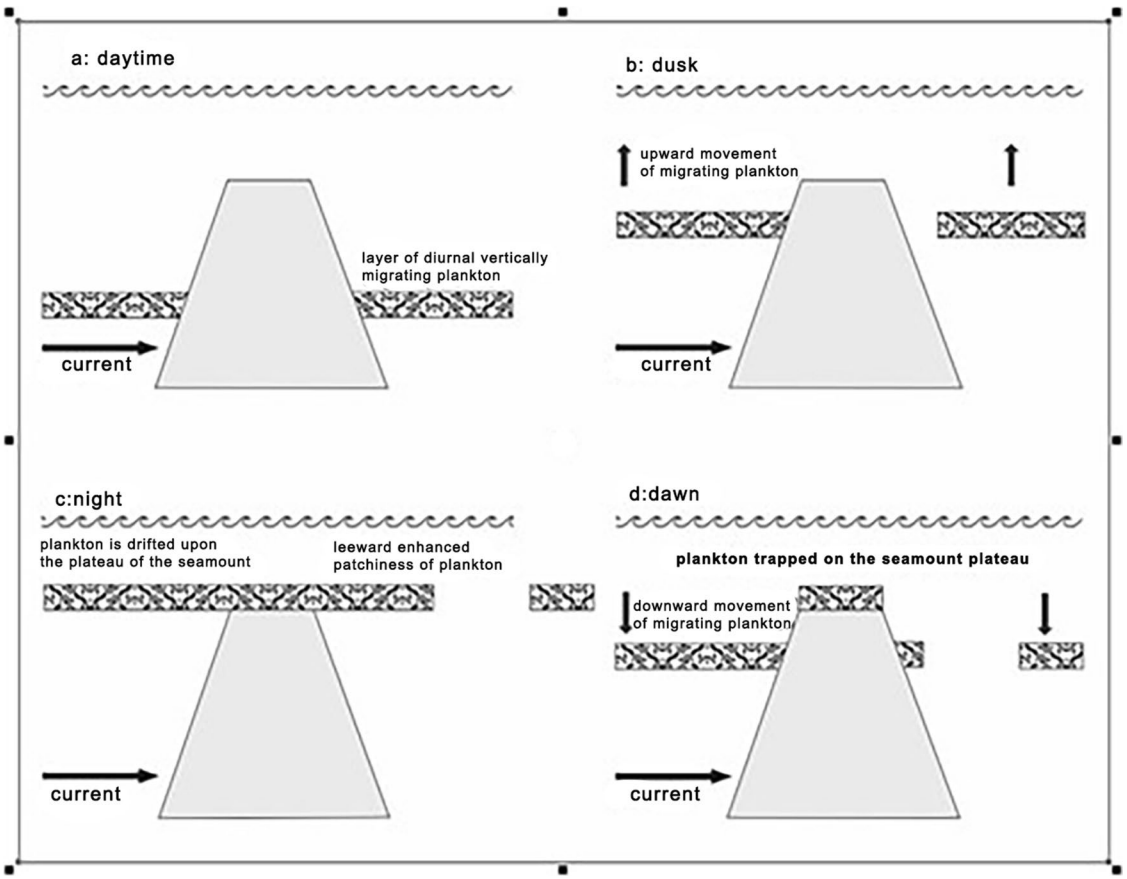

Fig. 5 Trapping effect of a seamount summit during diurnal migration of zooplankton. Modified from Genin and Dower (2007)

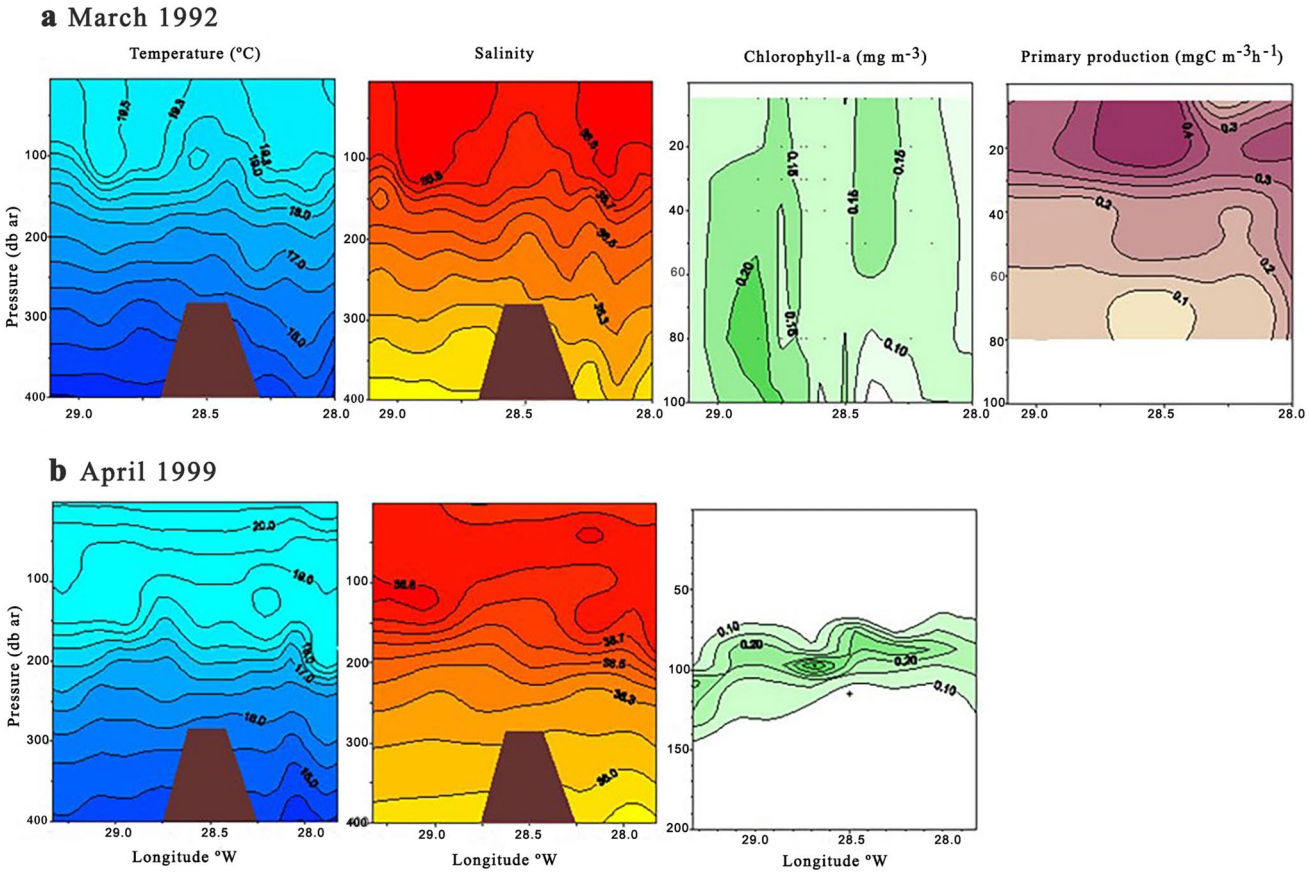

Fig. 6 Biophysical connections at Great Meteor Seamount (GMS); **a** vertical distribution of temperature, salinity, chlorophyll-a (Chl-a) and primary production across GMS in March 1992; **b** temperature, salinity and Chl-a in April 1999. Note the different vertical axes for physical and vertical variables. Extracted from Mouriño-Carballido (2002)

to 40 m observed over a few hours in isotherms and the Chl-a maximum clearly indicated that the seasonal scale was undersampled.

In summary, the study by Mouriño et al. (2001a, b) clearly highlighted that the physical-biological coupling at GMS exhibit significant temporal and spatial variability, across both seasonal and shorter time scales but did not show persistent increases in phytoplankton biomass and production over GMS. These results are consistent with those reported by White et al. (2007), who analyzed Chl-a values from 7 years of remote sensing data (1998–2004), averaged between the latitude range 29.4–30.4° N along a transect from 35° W to 22° W (Fig. 7). The 7-year mean summer values showed a small peak, relative to mean background values, within the vicinity of GMS (29–28° W). However, Chl-a distributions in individual years revealed significant mesoscale and interannual variability with individual peaks over the seamount, which were of similar magnitude than background values close to GMS. White et al. (2007) conclude that GMS is an important source of variability in surface Chl-a in the region.

This is also confirmed by previously unpublished data collected in September 1998, which revealed a distinct seamount effect on nutrients and phytoplankton distribution in comparison with the surrounding open ocean (Kaufmann 2004). A pronounced deep Chl-a maximum between 75 and 100 m depth was observed above the summit plateau and directly below the pycnocline along a North–South transect across the GMS (transect A in Figs. 4b and 8). This maximum layer was separated from deep off-seamount Chl-a maxima by very low concentrations above the seamount slopes. Above the plateau, a slight elevation of Chl-a and nutrient isopleths was also observed compared to stations located over deeper waters. Chl-a concentrations above the summit plateau were three to four times higher (maximum value 0.23 µg/l) than highest values towards the steep slopes (0.05 µg/l). Only very low Chl-a levels (< < 0.05 µg/l) were detected in the surface layers above 30 m depth. Elevated nutrient concentrations above the summit were also observed indicating a slight upward movement of water masses near the base of the plateau, but not reaching the surface (Mohn and Beckmann 2002). However, a comparison with

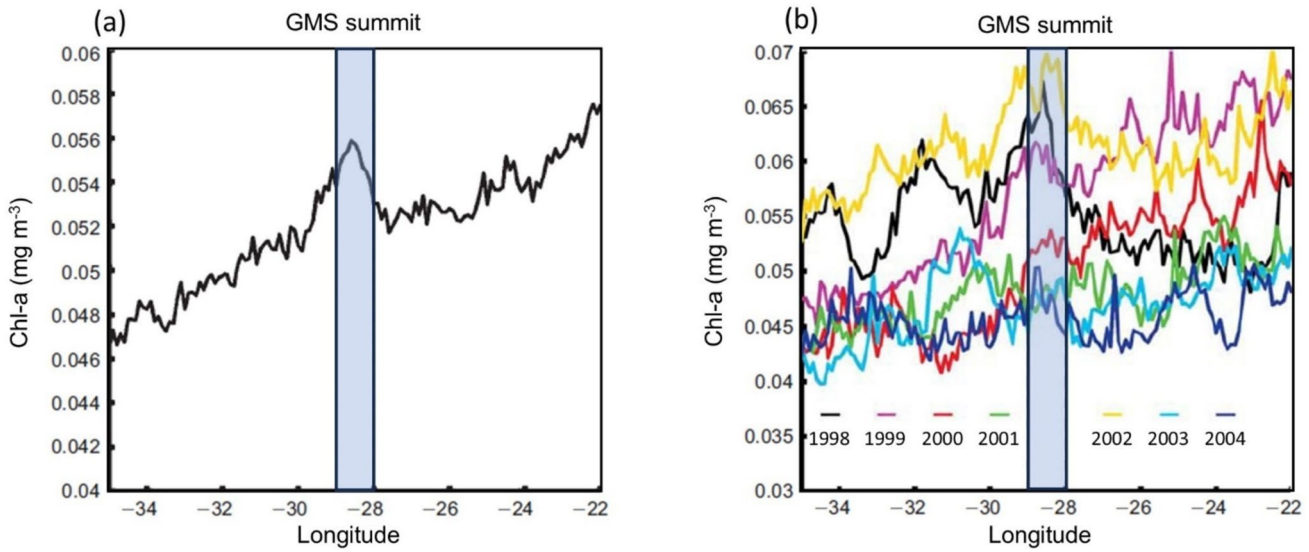

Fig. 7 Surface chlorophyll-a (Chl-a) distribution from 35° W to 22° W, averaged between 29.4° N and 30.4° N; **a** 7-year mean (1996–2004) for months June–August; **b** 7-individual years of August Chl-a values. Modified from White et al. (2007)

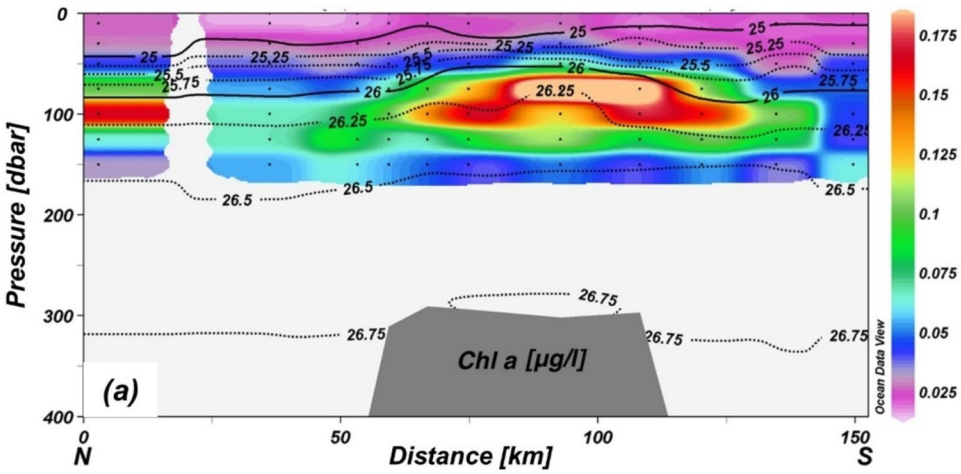

Fig. 8 Chlorophyll-a (Chl-a) distribution along the North–South transect across the Great Meteor Seamount (see Fig. 4 b). The dotted lines represent σ_θ isopycnals with highlighting (solid lines) of the 25.0 and 26.0 kg m.^{3} isopycnals. Modified from Kaufmann (2004)

biological parameters showed that the enhanced nutrient concentrations above the seamount did not cause a significant increase in biomass (Fig. 9), which is in line with the results of Mouriño et al. (2001a, b).

The increase of nutrients is limited to water depths below the 0.1% light depth. Only organisms adapted to low light intensities, such as Prymnesiophyceae (Winter and Siesser 1994) or Cyanobacteria (*Synechococcus* and Prochlorophyceae) (Moore and Chisholm 1999) could benefit from the slightly increased nutrient levels at these depths. A nitrite maximum was observed below the density thermocline and roughly coinciding with the Chl-a maximum (Fig. 9). This could be due to a reduction of nitrate to nitrite by phytoplankton (Hattori and Wada 1971). The existence of this maximum suggests a relative excess of nitrogen nutrient salts and a simultaneous lack of light for phytoplankton growth. Due to the lack of light, the rate of carbon assimilation decreases, and the rate of reduction of nitrate to nitrite increases, so that phytoplankton releases nitrite into the surrounding water (Carlucci et al. 1970; Vaccaro and Ryther 1960). Otherwise, the excretion of nitrogen products from zooplankton feeding at depths of the Chl-a maximum could be another explanation for the nitrite maximum (Haury et al. 1995).

In September 1998, the phytoplankton populations were numerically dominated by pico- and nanophytoplankton (< 20 µm). In particular, the prokaryotic picoplankton (*Synechococcus* and *Prochlorococcus*) made up the majority in terms of Chl-a equivalents (Kaufmann 2004). This distribution largely corresponded to the conditions expected for subtropical, oligotrophic marine areas, as found in open waters (Campbell and Vaulot 1993; Partensky et al.

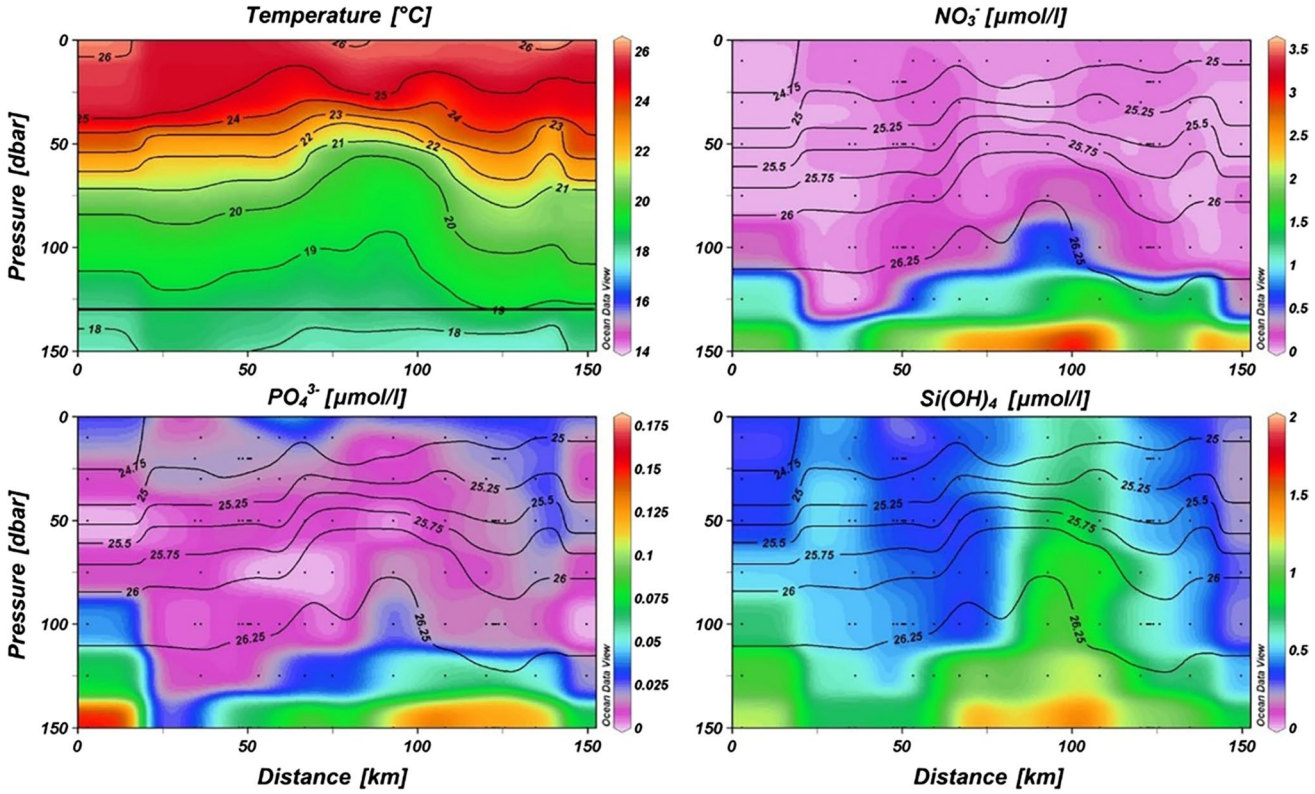

Fig. 9 Relationship between temperature and nutrients, shown in a north–south section over the Great Meteor Seamount from 0 to 150 m depth. In the top left, the mean depth of the 0.1% light depth at 130 m is drawn as a thick line. In the figures of the nutrient salts, the distributions of the potential density σ_θ are drawn as isolines. Modified from Kaufmann (2004)

1996). The measurements also revealed that *Synechococcus* reached larger cell numbers in the surface layer above the deep chlorophyll maximum and was then replaced by *Prochlorococcus*.

The analysis of the zooplankton sampled using a LHPR during the September 1998 RV "Meteor" showed accumulation of zooplankton during daytime above the summit compared to deeper stations (Fig. 10 a, b) and higher biomass on the upstream side of the seamount in the northeast compared to its downstream side in northwest (Fig. 10c; Martin and Nellen 2004). Furthermore, strongly vertically migrating groups like euphausiids and Copepoda of the genus *Pleuromamma* were found in high abundances at daytime close to the bottom at the northeastern part of the plateau) and constituted the main component of the relatively high biomass.

The observations with the echosounder showed an upper scattering layer at 100 m and another layer close to the bottom during the daytime above the plateau. At night one scattering layer extended from the surface down to 130 m depth. All these layers seem to correspond to the biomass found in the zooplankton samples (Fig. 11). Even though frequencies of 33 or 38 kHz are not routinely used for studying biological processes because of their relatively low resolution, these frequencies do reflect euphausiids as well as smaller organisms if they occur in dense layers down to 1000 m (Kaltenberg et al. 2007, Krause 1971, Krause M. 1978, Mair et al. 2005) and even deeper (Burd et al. 1992). For example, deep scattering layers, such as those observed with diel vertical migration of zooplankton, can only be detected with low frequencies due to the low penetration depth of higher frequencies.

Both survey methods suggest that the summit plateau of the GMS exerts a trapping effect on the vertically migrating plankton (Fig. 11). The distribution of zooplankton in the vicinity of the seamount was probably influenced by both predation and the flow regime initiated by the irregular bottom topography.

Meiofauna

The first benthic surveys of the GMS, which included the processing of the meiofauna, were conducted as part of early Atlantic Seamount cruises (Closs et al. 1969; Hempel 1968, 1970a; Thiel 1970) and their 1970 supplement ("Roßbreiten-Expedition"; Hempel 1970b; Hempel and Nellen 1972). However, these meiobenthic studies were limited to taxonomic aspects such as the description of

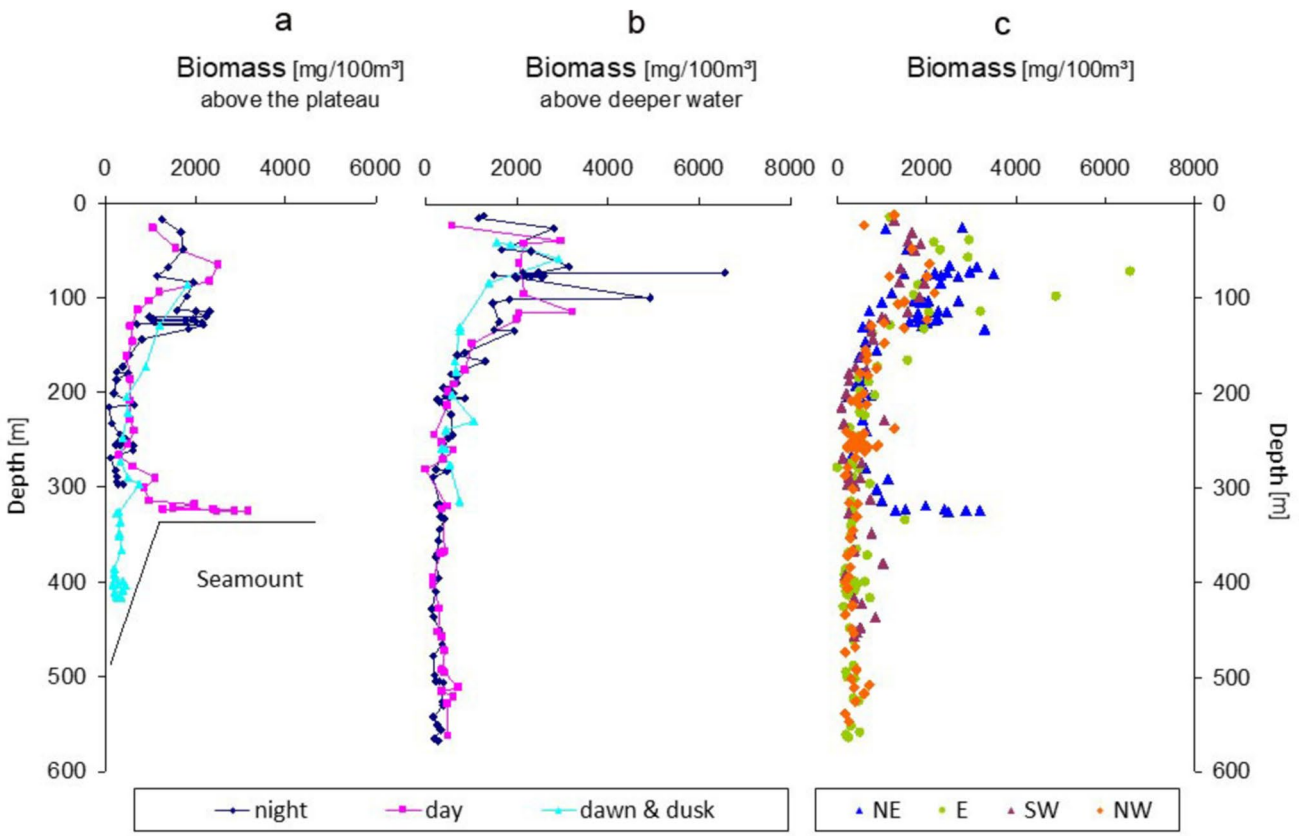

Fig. 10 Distribution of zooplankton biomass: **a** above the plateau, **b** above bottom depth > 1500 m and **c** in different regions of the seamount, independent of bottom depth. Modified from Martin and Nellen (2004)

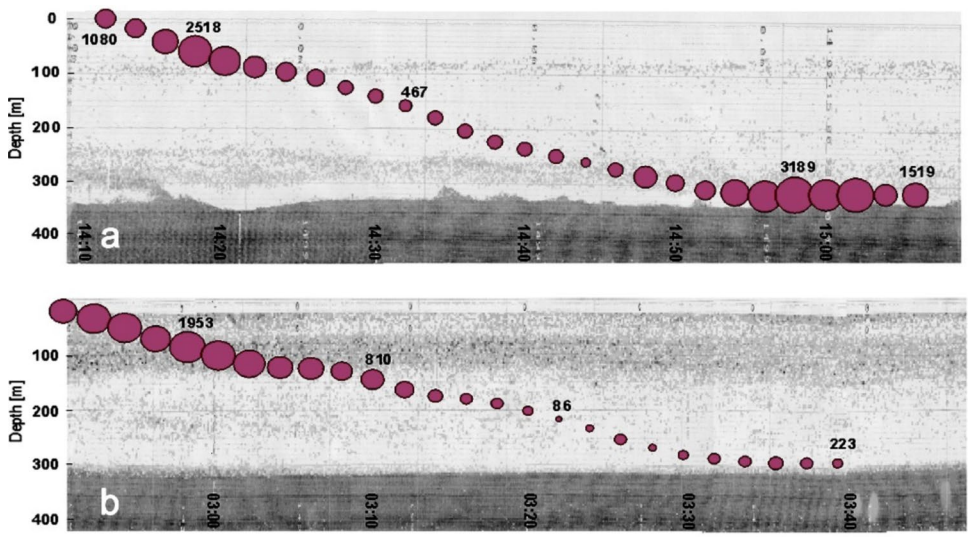

Fig. 11 Biomass (mg/100 m.^{3}) vs. echo sounder recordings (33 kHz); **a** NE Great Meteor Seamount (GMS) above the plateau at daytime; **b** SW GMS above the plateau at night-time Bubble size corresponds to the biomass of the discrete samples. Some values are shown in the graph. Extracted from Martin and Nellen (2004)

species found on the plateau (e.g., Emschermann 1971; Bartsch 1973a, b, c). Thiel (1972) was the first to use results of meiofauna studies at the GMS for an interregional comparison of meio- and macrofauna of marine areas far from the coast.

In an extensive revision of benthic research at the GMS, Mironov and Krylova (2006) included first meiofaunal data, and George (2013) provided a comprehensive summary of meiofauna research at the GMS (among other seamounts) from the abovementioned expeditions until 2011. By then,

25 meiobenthic major taxa had been recorded on the seamount (Table S2 in the Online Resource 2). At the time, 63 species were described from six of the major taxa: Amphipoda (1 species), Entoprocta (1 species), Halacarida (22 species), Harpacticoida (8 species), Loricifera (10 species), and Nematoda (21 species) (see Fig. 12, Table S2 in the Online Resource 2). In addition to taxonomic studies, the meiofaunal material collected on the RV "Meteor" M42/3 cruise (1998) allowed a first assessment of the question of origin and dispersal of species recorded on the seamount. These studies focused on Nematoda (Gad 2002, 2004a, 2009) and Loricifera (Gad 2004b) but particularly on the benthic Copepoda (Harpacticoida and Canuelloida) (George and Schminke 2002; George 2004a, b; Plum and George 2009; Koller and George 2011). These first analyses led to initial hypotheses about the role of seamounts in the dispersal of

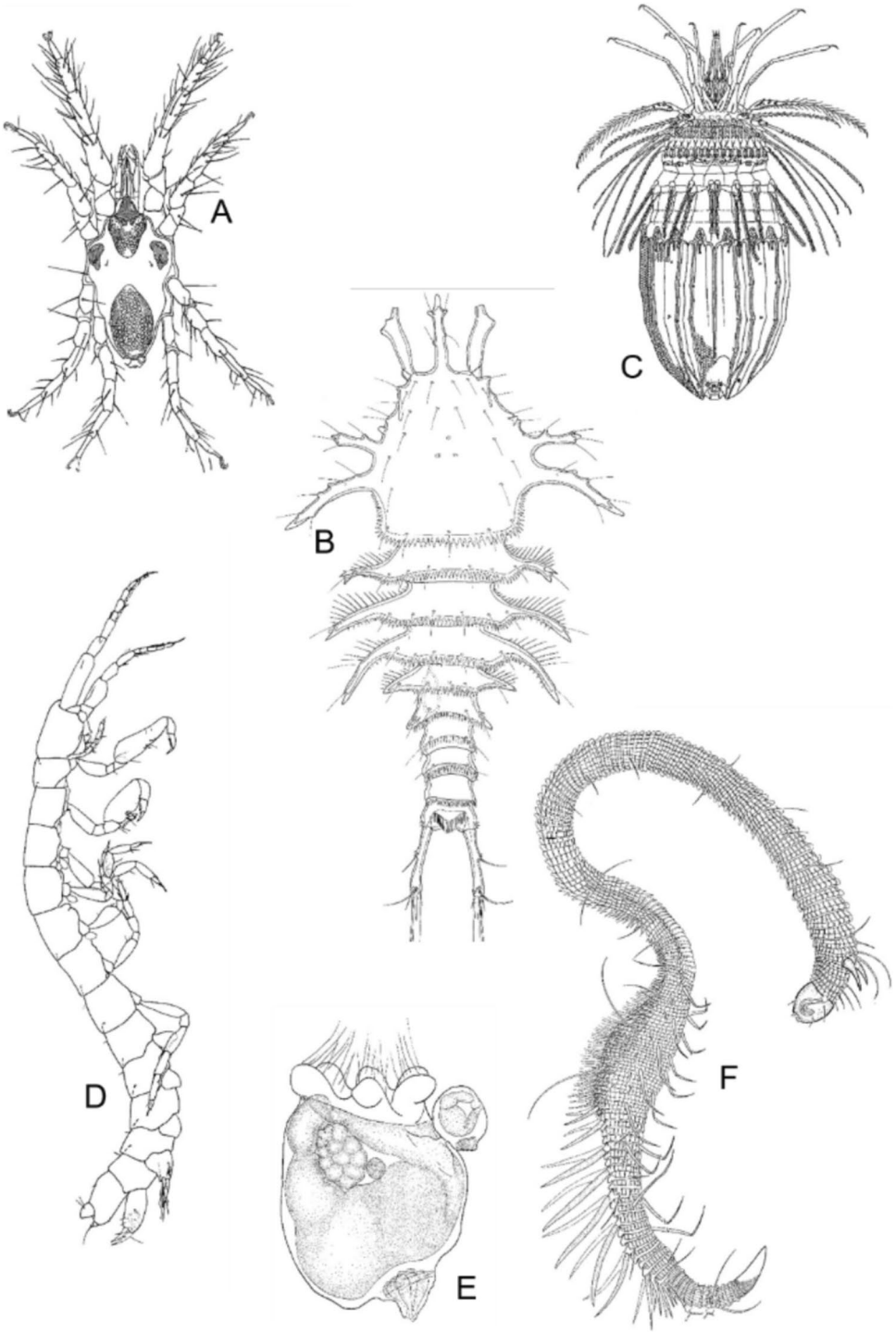

Fig. 12 Examples of meiobenthic species collected at Great Meteor Seamount; **a** *Halacarus ctenopus* Gosse, 1855 (Halacarida; the shown species has not been found on seamounts, but is a close relative of, e.g., *H. leptopus* Bartsch, 2002a, found on GMS); **b** *Meteorina magnifica* George, 2004b (Harpacticoida); **c** Nanaloricidae gen. et sp. II (Loricifera); **d** *Ingolfiella sandroruffoi* Andres, 2004 (Amphipoda); **e** *Loxomespilon* cf. *perezi* var. *meteoris* Emschermann, 1971 (Entoprocta); and **f** *Glochinema kentrosauroides* Gad, 2002 (Nematoda). Modified from George (2013); not to scale

meiofauna in the oceans (George and Schminke 2002; Gad and Schminke 2004; George 2004a, b; Plum and George 2009; Koller and George 2011), especially in relation to the so-called "meiofauna paradox," which expresses the often wide to worldwide distribution of meiobenthic species despite severely limited dispersal capabilities (see also Giere 2009). The null hypothesis underlying these analyses assumes that seamounts act as stepping stones also for meiofauna and can thus contribute to the geographical dispersal of these organisms. The alternative hypothesis, on the other hand, states that seamounts act as a trap for meiofauna ("trapping stones"). Species stranded by chance can no longer leave a seamount. As a result, new endemic species emerge on a seamount over time and due to isolation.

By 2011, 70 species of two orders of the benthic Copepoda (Harpacticoida and Canuelloida) were recorded (see George 2013). However, *Dorsiceratus ursulae* (George 2006) was mistakenly omitted and thus 69 species only were listed. Three species—*Retrocalcar brattstroemi* (Geddes 1981), *Wellsopsyllus (Intermediopsyllus) intermedius* (Scott, T. & A. Scott 1895) and *Zosime bergensis* (Drzycimski 1967)—were already known from other marine areas, whereas the others are scientifically new. Eight species were newly described by 2011 (see Table S2 in the Online Resource 2 and Table S3 in the Online Resource 3—species set in bold and marked with one asterisk *). Since then, the total number of species recorded has almost quintupled (334 species; Table S3 in the Online Resource 3). The number of species already described from other regions has also increased considerably (33 species), and the number of newly described species has more than doubled (17 species; see Pointner et al. 2013; Pointner 2015, 2017; George 2018; and Richter 2019) (Table S3 in the Online Resource 3, species set in bold and marked with two asterisks **). Nevertheless, the taxonomic description of new species has taken a back seat to synecological studies. Already George and Schminke (2002) concluded that due to the overwhelmingly high proportion of scientifically new species the harpacticoid fauna of the GMS represents an isolated community with an exceptionally high proportion of endemic species. Subsequent studies seem to confirm this hypothesis; for example, the assumed close relationship within Argestidae and Zosimeidae, whose respective species seem to be restricted to the GMS, is an indication of a species radiation on the seamount (George 2004a; Pointner 2017).

Another aspect concerns the bathymetric migration behavior of different species. George and Schminke (2002) recorded a remarkably large number of species of the Argestidae, a typical deep-sea family, on the GMS plateau. Nevertheless, the number of species found both on the plateau and in the surrounding deep-sea was surprisingly low (George 2004a; Fig. 13). In contrast to Emschermann's (1971) assumption that there should be a gradual increase

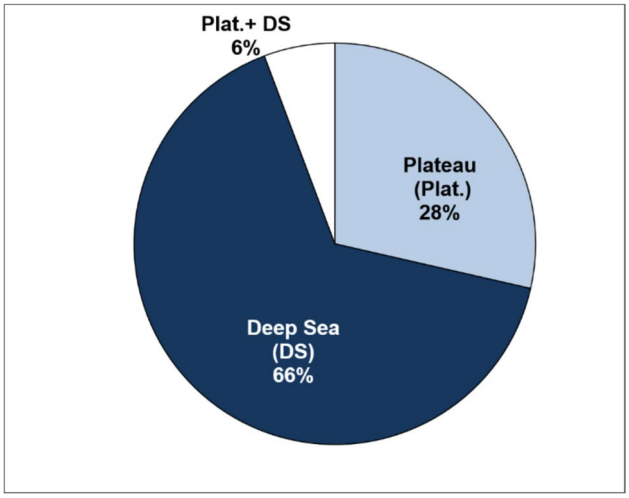

Fig. 13 Distribution (% of species) of Argestidae Por, 1986 on the Great Meteor Seamount and in its immediate deep-sea vicinity. Modified from George 2004a

of deep-sea meiofauna species on the shallow plateau of the GMS over time, George and Schminke (2002) speculated (further elaborated by George (2004a) afterwards): the Argestidae of the plateau had originally emerged from the deep-sea with the seamount, adapted to shallow water conditions, established new niches, and underwent strong radiation, as indicated by the kinship proximity of the plateau species among themselves. However, there is also evidence of bathymetric emergence: 6% of the Argestidae were recorded both on the plateau and in the surrounding deep-sea (George 2004a; Fig. 13). Similar results were obtained later for single species of Zosimeidae (Koller and George 2011; Pointner 2017), Paramesochridae (Plum and George 2009; Pointner et al. 2013), and Cylindropsyllidae (Richter 2019).

The first quantitative collection of meiofauna samples was conducted in March 2010 on board FS Poseidon (George 2011). Earlier seamount expeditions showed that the multiple corer (MUC), normally used for sampling meiofauna, on the crests and slopes of seamounts only provided very unsatisfactory samples. This is mainly due to the sandy sediment, which cannot be sufficiently held by the MUC's acrylic tubes, so that significant amounts of sediment are lost during heaving. For this reason, the van Veen grab was used during the 2010 survey. An array of 21 stations was evenly distributed across the entire plateau of the GMS (Richter and George 2019), and all stations were sampled repeatedly. This allowed the meiofaunal community of the plateau to be recorded and documented in detail for the first time. As a result, four additional meiobenthic large taxa could be added to the known number of taxa: Brachiopoda, Chaetognatha, Holothuria, and Priapulida (Table S2 in the Online Resource 2, grey rows). The comparison of all stations revealed a homogeneous distribution of meiobenthic

major taxa across the entire plateau (Fig. 14), with a clear general dominance of the Nematoda (72.49%), followed by the Copepoda (18.64%) and the Annelida (6.55%). All other taxa were much rarer with relative abundances of > 1%, although also present at all stations (Richter and George 2019). The significant increase in the number of benthic copepod species recorded (Table S3 in the Online Resource 3) is also almost exclusively due to the quantitative evaluation by Richter and George (2019).

The initial assumption that the GMS harbors different communities of benthic copepods, each established in the northern, central, and southern areas of the plateau, was rejected on the basis of the data collected (Richter and George 2019). Instead, community analyses could prove that Harpacticoida and Canuelloida found are heterogeneously distributed over the entire plateau both at family and at species level. Species diversity on the plateau seemed to be essentially uniform but increased slightly from north to south (Richter and George 2019). This increase can be explained by an increment in species number (while the evenness remains rather constant), which was 1.6 times higher in the south than in the north (Richter and George 2019). However, the diversity at the individual stations was very different, regardless of their location in the north, center, or south of the plateau (Richter and George 2019). This may be due to the existence of microhabitats, which lead to the observed heterogeneous distribution of species on the plateau. Therefore, Richter and George (2019) concluded that there is one heterogeneous copepod community that extends across the entire plateau.

At the species level, the data confirmed clear differences to other seamounts and a very high proportion of presumably endemic species, which, according to Richter and George (2019), proves the isolated position of the GMS, which is thus only likely to act as a stepping stone to a very limited extent. However, this isolation may have occurred only in the course of the spreading of the Atlantic, which can be concluded from the comparatively high number of known, characteristically shallow-water genera that may have migrated from adjacent coastal regions in earlier times. Nevertheless, the presence of single species known to other marine regions indicates that the GMS can provide a habitat for accidentally stranded meiofauna organisms and, in a weakened form, possibly take on a stepping-stone function.

The benthic communities of Great Meteor Seamount

Typically, seamount communities are dominated by slow-growing sessile suspension feeders, dense aggregations of demersal and benthopelagic fishes, and elevated abundances of zooplankton and micronekton (Boehlert & Genin 1987; Clark et al. 2010; Genin et al. 1986). This biodiversity is, in part, a reflection of the hydrodynamic regime in the seamount: the ocean currents, along with the breaking internal waves and Taylor columns, bring up nutrients and re-suspend organic matter from the deep ocean floor enhancing food supply, exposing rocky substrata, removing waste products and, simultaneously, preventing smothering the colonies due to sediment deposition (Grigg 1984; Rogers 1994, 2018).

The seamount benthic fauna differs across multiple spatial scales resulting in differences in the composition among habitat patches on a single seamount to totally different faunal assemblages between seamounts on different ridges and ocean basins (Clark et al. 2010). At the scale of the seamount, the most obvious changes in the composition of benthic assemblages are related to depth (Boehlert & Genin 1987; Clark et al. 2010) but also reflect other environmental

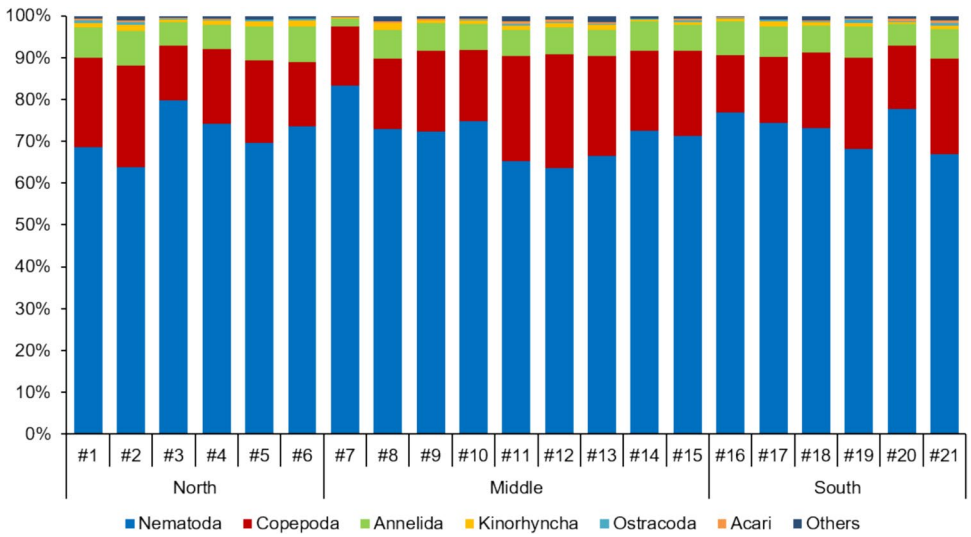

Fig. 14 Relative abundance of the meiobenthic major taxa collected during the 2010 RV "Poseidon" benthic survey at single stations on the Great Meteor Seamount. The group "others" unites Amphipoda, Bivalvia, Brachiopoda, Chaethognata, Cnidaria, Cumacea, Gastrotricha, Gastropoda, Holothuria, Isopoda, Loricifera, Pantopoda, Priapulida, Rotifera, Sipuncula, Tanaidacea, Tantulocarida, and Tardigrada. Extracted from Richter and George (2019)

gradients such as temperature, oxygen concentration, food availability, and pressure, which are responsible for shaping the distribution and abundance of benthic fauna (see Fig. 15; Thistle 2003).

At GMS, the meso-scale distribution (10 km) of megabenthic assemblages reflects a difference between the slope and the plateau, and, though less evident, between the northern and southern plateau, which corresponds with the hydrography patterns observed above the seamount (Piepenburg & Müller 2004). According to Piepenburg & Müller (2004), the megabenthic epifauna at GMS is dominated by sessile suspension-feeding species, such as sponges (e.g., *Haliclona* sp.) and corals (e.g., *Dendrophyllia cf. cornigera*), and presents both low abundance and diversity when compared to communities reported from continental shelves or shallower seamounts. The same study highlights the pronounced patchiness of small-scale (10 m) distribution of dominant species and relates those patterns with topographically induced flow currents that affected sedimentation rates, food supply, retention/accumulation of planktonic larvae, and seabed composition.

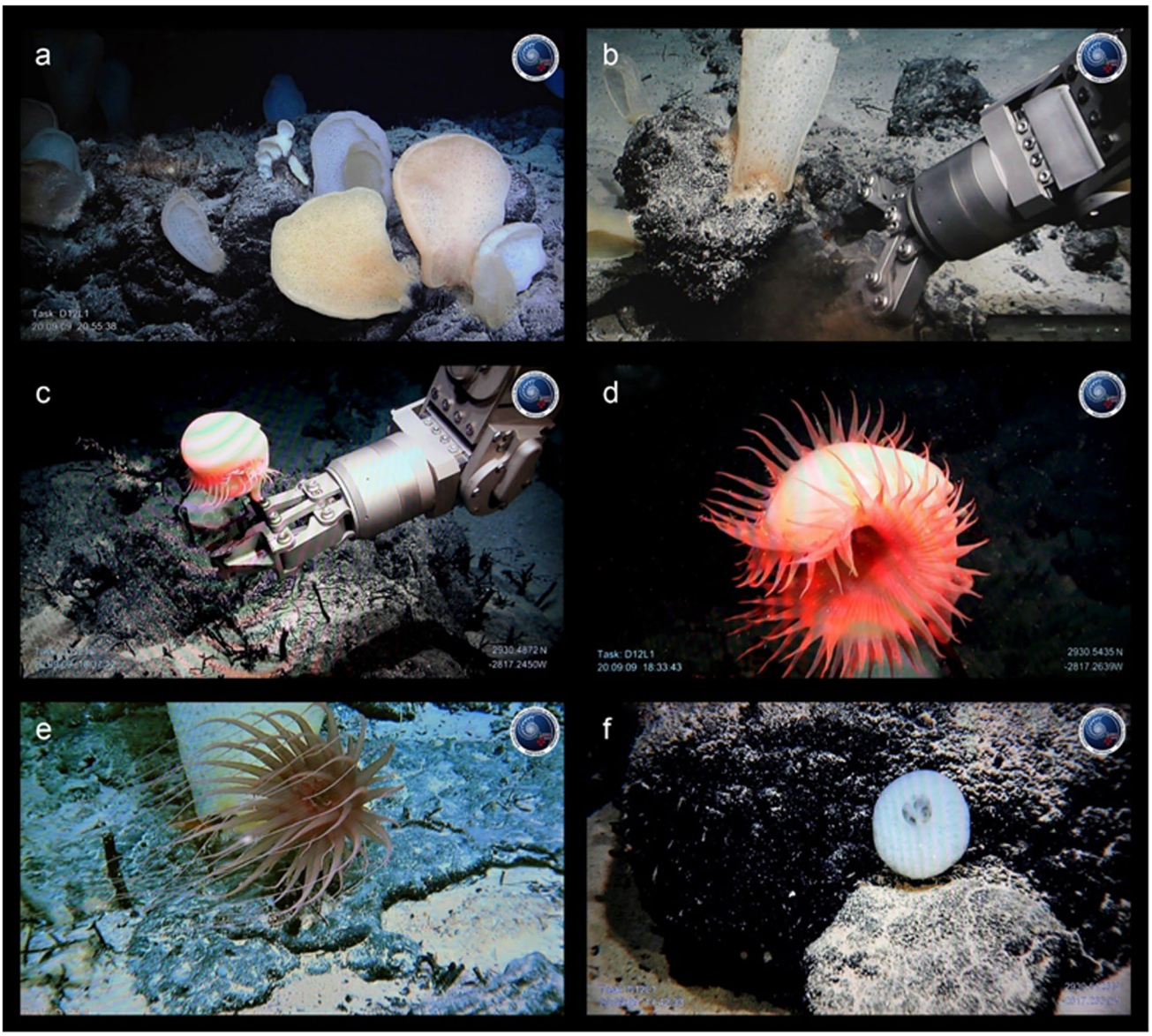

Fig. 15 Benthic communities of Great Meteor Seamount collected with the LUSO remotely operated vehicle (ROV) (EMEPC) **a** aggregation of the hexactinellid sponge *Poliopogon amadou* Thomson, 1878 at ~ 2700 m depth; **b** the Luso ROV sampling a rock with a *P. amadou* specimen attached; **c** and **d** show a venus flytrap anemone (*Actinocyphia* cf. *aurelia*), an example of epifauna on a high relief feature: a dead coral skeleton; **e** detail on an unidentified Actiniaria specimen next to a glass sponge; and **f** unidentified Hexactinellid possibly family Leucopsacidae, on a basalt outcrop

The first known expedition dedicated to exploring the seamount's benthic fauna took place in 1967 (see Fig. 2) on bard RV "Meteor" as part of the early Atlantic Seamount cruises ("Atlantische Kuppenfahrten"; Hempel 1968, 1970a; Thiel 1970). During this cruise, 103 samples were collected at depths from 268 to 1280 m (Mironov & Krylova 2006). Several expeditions followed dedicated to studying the benthic fauna of this area (see Fig. 2).

Most studies were qualitative and focused on specific taxonomic groups, such as Mollusca, Gastropoda (Oliverio and Gofas 2006; Gofas 2005; Gofas 2007), Bivalvia (Krylova 2006), Echinodermata, Crinoidea (Clark 1980, Moskalev et al. 1983), Echinoidea (Mironov and Sagaidachny 1984, Mironov 1985, Mironov and Krylova 2006), Ophiuroidea (Litvinova 2001), Porifera (Tabachnick, 2002) (Tabachnick and Menshenina 2007; Tabachnick and Collins 2008) (Tabachnick 2014) and Cnidaria, Gorgonaria and Pennatulacea (Grasshoff 1981; Grasshoff, 1985) Antipatharia (Molodtsova 2006; Molodtsova 2011) Scleractinia (Squires 1959), and Stylasteridae (Zibrowius 1992). These last two groups (Porifera and Cnidaria) are considered vulnerable marine ecosystem (VMEs) indicators. Both groups have particular life history characteristics being fragile species, long-lived, and their larvae and reproductive habits are unknown or poorly understood (Watling & Auster 2021). These characteristics along with their ecosystem function meet the criteria for the identification of VMEs. Although the identification of VMEs has been based on the occurrence of such species, determination whether a VMEs is present is a matter of expert judgment in the absence of explicit thresholds given by the Food and Agriculture Organization of the United Nations (FAO) guidance (Auster et al. 2010; Fuller et al. 2008; Long et al. 2020; FAO 2009).

Knowledge on the taxonomic diversity of cold-water corals on GMS were mainly provided by 9 oceanographic expeditions during the 2nd half of the 20th and beginning of the 21th centuries (onboard, e.g., RVs "Atlantis," "Chain," "Calypso," "Vityaz," "Ikhtiandr," "Le Suroit," "Meteor," and "Poseidon"). These campaigns have reported a total of 40 species of cnidarians, corresponding to 150 records from nearly 70 stations in the depth range from 275 to 2160 m (Squires 1959; Zibrowius 1980; Grasshoff 1985; Pasternak 1985; Zibrowius and Cairns 1992; Gofas 1993; Keller and Oskina 2009; Mironov and Krylova 2006; Molodtsova et al. 2006, 2011). The most speciose group of cold-water corals was the Order Scleractinia (23 species), followed by subclass Octocorallia (9 species), order Antipatharia (6 species) and family Stylasteridae (Class Hydrozoa) (2 putative species) (Fig. 16, Table S4 in the Online Resource 4). The most common species by number of records were the octocorals *Viminella flagellum* (Thomson & Russell, 1910), *Dentomuricea meteor* Grasshoff, 1977, *Callogorgia verticillata* (Pallas, 1766), and the antipatharians *Leiopathes montana* Molodtsova, 2011 and *Parantipathes hirondelle* Molodtsova, 2006.

Three species were described with type specimens collected at the GMS. The species *Dentomuricea meteor* described by Grassoff (1977), initially thought to be endemic of the GMS, may also occur at seamounts in the Azores (Braga-Henriques et al. 2013), which still requires taxonomic confirmation. The sub-species *Stylaster erubescens meterorensis* has been recorded on the GMS and in the Azores region (Zibrowius and Cairns 1992) and *Leiopathes montana* described by Molodtsova (2011).

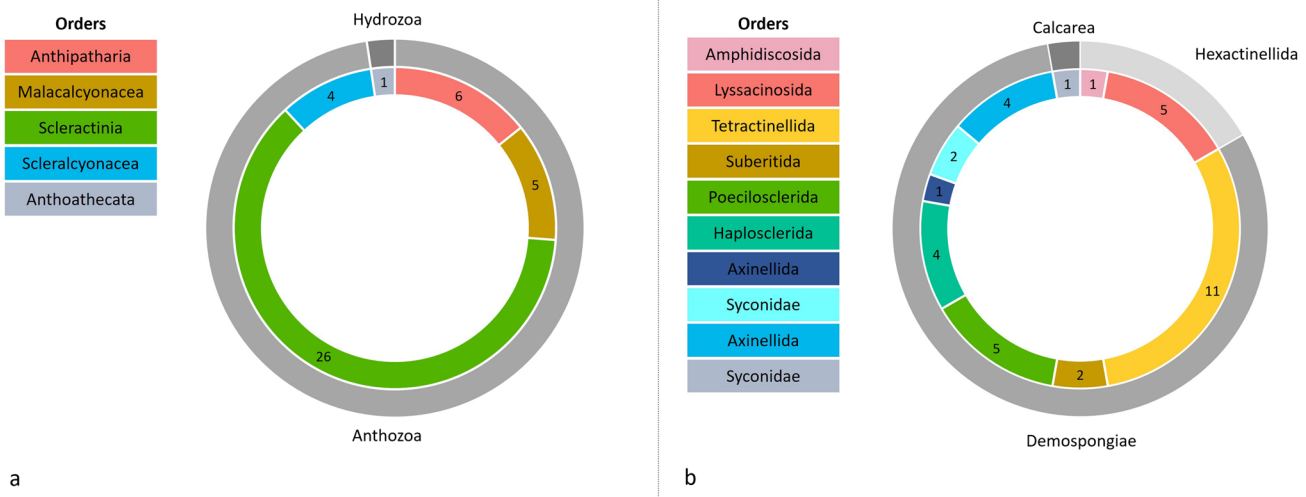

Fig. 16 Taxonomic diversity of the **a** corals—phylum Cnidaria, and **b** sponges—phylum Porifera, reported for the Great Meteor Seamount. Species distribution per class is represented in the outer ring, whereas species distributions per order are represented in the inner ring. Number of species per order is indicated and orders color-coded

Species assemblages presented a strong zonation pattern with depth. Characteristic species recorded at the summit of the GMS comprised large aggregations of free-living scleractinians on soft-bottom sediment areas between 270 and 400 m depth, including the solitary *Flabellum chunii* and mixed associations of the colonial *Anomocora fecunda* and *Eguchipasammia gaditana* (Squires 1959; von Rad 1974; Zibrowius 1980; Gofas 1993; Keller and Oskina 2009). Although these colonial species are typically of sedimentary areas, they were also found at deeper areas of the GMS, laying under more consolidated sediments (Zibrowius 1980). Moreover, in hard substrate areas of the GMS summit (310–328 m), the scleractinian *Caryophyllia calvery* was documented forming mass accumulations by Keller (2012) (noticed from a catch of more than 2000 specimens in a trawl during R/V "Vityaz 2" Expedition) and by records gathered with R/V "Meteor", "Calypso," and "Atlantis" (Zibrowius 1980).

At the upper slopes (300–450 m depth), the most frequent recorded taxa were the octocorals *Viminella flagellum*, followed by *Dentomuricea meteor*, *Callogorgia verticillata*, *Paracalyptrophora josephinae*, and the antipatharian *Antipathella subpinnata* (Grasshoff 1985; Gofas 1993; Mironov and Krylova 2006). At this depth strata, other smaller octocoral species occurred, such as *Nicella granifera*, *Acanthogorgia aspera*, and *A. armata*, and *Bebryce mollis*. Small scleractinians were reported to occur at outcropping rocks of the GMS slopes, e.g., *Madracis profunda*, *Paracyathus arcuatus*, *Deltocyathoides stimpsonii*, *Caryophyllia smithii*, *C. arcuata*, and *Leptopsammia formosa*. The stylasterid (Filifera) *Stylaster erubescens meterorensis* makes part of this upper slope assemblage, with small bushy colonies documented in R/V "Meteor" and "Chain" expeditions during the 1970s (Zibrowius and Cairns 1992). Several antipatharian species were also documented at the upper slope (310–335 m), including *Leiopathes glaberrima* and *L. montana* (Grasshoff 1985; Molodtsova et al. 2011), *Elatopathes abietina* (Grasshoff 1985; Mironov and Krylova 2006), and *Parantipathes larix* (Grasshoff 1985). Instead, *Parantipathes hirondelle* occurred in lower slope areas, from 510 to 680 m (Molodtsova et al. 2006), with additional records of the dendrophyllids *Enallopsammia pusilla* and *E. rostrata* at 480 to 660 m depth (Zibrowius 1980; Keller and Oskina 2009).

Deeper than 1000 m depth, scleractinians were the most common taxa (Squires 1959; Zibrowius 1980; Gofas 1993; Keller and Oskina 2009) with 10 species reported. Reef building scleractinians, *Lophelia pertusa* (recently synonymized to *Desmophyllum pertusum* (Addamo et al. 2016; 1070–1685 m), *Madrepora oculata* (1070–1760 m) and *Solenosmilia variabilis* (1750–1760 m) were found at deep bathyal areas. Smaller size species, such as *Javania pseudoalabastra*, *Delthocyathus italicus*, *Fungiacyathus (Bathyactis) crispus* and *Vaughanella concinna*, are also characteristic of deep areas below 1000 m. A deep record of an alcyoniid *Tubigorgia cylindrica* (*uncertain sedis*), found once at around 1750 m depth, was described as a new species for the area by Pasternak (1985); however, this record remains doubtful.

The recorded number of cold-water coral species at GMS is lower than other areas within the Macaronesia region (e.g., Azores, Madeira, and Canary Islands) suggesting a low diversity for this specific seamount (Braga-Henriques 2013). However, diversity and bathymetric ranges of the recorded species might be biased by data scarcity due to the sampling gear methods (dredges, box corers, and trawl hauls). For example, several octocoral species commonly recorded of the bathyal areas are missing from this large historical records collection (e.g., bamboo corals, chrysogorgiids, and soft corals species).

The sponge diversity known to occur on the GMS is similar to that of corals, with 36 species reported to date, representing three (out of the four) poriferan classes, i.e. Demospongiae, Hexactinellida, and Calcarea. The most diverse class is Demospongiae with 29 species representing 22 genera and families, and seven orders. Within this class, the order Tetractinellida comprises nearly one-third of the species (11 species), including seven lithistid species (a.k.a. rock sponges) in the genera *Discodermia*, *Leiodermatium*, *Macandrewia*, and *Neophrissospongia*. The class Hexactinellida is represented on the seamount with six species, representing four genera and three families across two orders. The genus *Asconema* is particularly prominent with three species—viz., *A. fristedti*, *A. megaatrialia*, and *A. topsenti* Tabachnick & Menshenina, 2007 occurring on the GMS, which represents 3/5 of the known global diversity of the genus. In contrast, only one calcareous species has been reported to date for this seamount (*Sycon* sp.) (Fig. 16, Table S5 in the Online Resource 5).

Despite similar diversity in terms of species richness, the number of sponge records ($N = 50$) is considerably lower than those of cnidaria, and result from just a few expeditions, for instance the Seamount 2 campaign (RV "Le Suroit"), the M42/3 expedition (RV "Le Suroit Meteor"), campaigns of the Institute of Oceanology of the Russian Academy of Sciences (RV "Vityaz 2"), and the EMEPC/LUSO/2009 (RV "Almirante Gago Coutinho") (Brenke 2002, Carvalho et al. 2020, Tabachnick 2002, Tabachnick and Menshenina 2007, Xavier et al. 2015).

For three rock sponge species (*Discodermia arbor* Carvalho & Xavier, 2020, *Macandrewia minima* Carvalho & Xavier, 2020, *Leiodermatium tuba* Carvalho & Xavier, 2020), and one glass sponge species (*Asconema topsenti* Tabachnick & Menshenina, 2007) the GMS constitutes the type-locality (Carvalho et al. 2020, Tabachnick and Menshenina, 2007). Of these, *D. arbor* and *M. minima* are only reported for this seamount, whereas *L. tuba* and *A.*

topsenti are also known to occur in the Azores archipelago (Tabachnick and Menshenina, 2007, Xavier et al. 2021).

Notwithstanding the relatively low number of species reported to date for the GMS, the sponge fauna seems to be quite diverse at higher taxonomic levels, from genera up to orders, which suggests that the known diversity is an underestimation and that additional species are likely to be found with increasing surveying and research efforts.

It is also important to note that taxonomic descriptions were only provided in the studies by Tabachnick (2002), Tabachnick and Menshenina (2002), Tabachnick and Menshenina (2007), and Xavier et al. (2015) on hexactinellids, and Carvalho et al. (2020) on lithistid tetractinellids, with the remaining records corresponding to checklists presented in studies focusing on the ecology of the seamount's epibenthic communities (e.g., Brenke 2002, Piepenburg and Müller 2004). This is reflected in a poor taxonomic resolution (e.g., Porifera type I-X in Piepenburg and Müller 2004) and dubious accuracy of several of the records reported (e.g., *Petrosia ficiformis* which is a typical shallow-water sponge). A significant proportion of records were only identified at higher (supraspecific) taxonomic levels highlighting the need for more detailed taxonomic effort in studying the sponge fauna in the region.

Unlike what is observed for coral records, very few sponge records comprise information on the depth at which they were collected (see Table S5 in the Online Resource 5) which further hampers assessing patterns of bathymetric distributions of these species and the communities they form. Notably, a patchy aggregation of a glass sponge species, *Poliopogon amadou* Thomson, 1878 was found on rocky outcrops on the Southeast slope of the GMS at 2765 m depth, with local densities attaining up to 5 ind./m^2 (Xavier et al. 2015). This species, originally described from a specimen collected southwest of the Canary Islands during the HMS Challenger expedition, and with a depth distribution apparently constrained to the lower bathyal, was later found to form a similar habitat on the Tropic seamount (Ramiro-Sanchez et al. 2019).

Future studies using video platforms (e.g., ROVs, towed and drift cams) may reveal a greater diversity of epibenthic megafauna species than what has been reported until now.

Fishes from Great Meteor Seamount

Assemblages of seamount fishes are generally highly diverse at depths shallower than 500 m (Parin et al. 1997). GMS bottom trawl surveys have been conducted on the seamount plateau at depth ranges from 285 to 505 m, while longlines have been deployed over the flanks down to 1099 m (Ehrich 1977; Uiblein et al. 1999; Fock et al. 2002a). With regard to habitat affiliation, fishes can be assigned to eco-types of benthic, near-bottom, off-bottom, benthopelagic. and mesopelagic species. There has been exploratory Russian fishing on the GMS Archipelago (GMSA, from Atlantis seamount to GMS) with evidence of catches of benthopelagic species such as horse mackerel, *Trachurus picturatus* and mackerel, *Scomber japonicus* in total of 18,800 t and off-bottom dwelling alfonsino, *Beryx splendens*, of 5400 t. However, the status of the fisheries on GMS directly remains unclear (Shcherbachev et al. 1985; Vinnichenko and Kakora 2008).

A total of 115 fish species were collected on GMS (Gebruk and Mironov 2006), of which one species is endemic to GMS, *Protogrammus sousai* (Maul 1972), while 3 more species are confined to the South Azores seamount area, i.e., GMSA. For some species, e.g., *Phycis phycis*, GMS subspecies may have developed (Uiblein et al. 1999). The similarity of fish assemblages is 81.1%, as compared to Madeira and Canary Islands' faunas, while only 32.1%, as compared to Cabo Verde (Uiblein et al. 1999). This indicates the separation of faunas through the Cape Verde Frontal Zone between tropical and subtropical waters while the fauna in general can be of the eastern panthalassic pattern, i.e., open ocean fauna with a resemblance to faunas of the subcontinental slopes of the Eastern Atlantic. Table S6 in the Online Resource 6 provides an overview of fish species reported for GMS between 1970 and 1998.

Fish recruitment to seamount populations and thus persistence depends on the modes of reproduction in relation to local hydrographic conditions. For species with planktonic larvae, employing the Taylor column for larval retention would enhance sustaining seamount populations. This was shown for *Zenopsis conchifer* on GMS (Fock and Zidowitz 2004), adapted to variable environmental spawning conditions and thus episodic recruitment through enhanced longevity of up to 14 years and an iteroparous spawning mode. Youngest *Z. conchifer* in 1998 were observed to be 4 years old and accordingly recruitment events could be identified in 1994, 1992, and 1984 related to lower SST and weakened westerly winds. SW winds weaken the recirculation cell over the seamount top (Taylor column) (Beckmann and Mohn 2002), and planktonic life stages are then subject to off-seamount dispersal. In turn, Rogers (1994) discussed the frequent failure to recover from stock collapse in semelparous seamount fishes dependent on their lowered capacity to sustain periods of unfavorable recruitment conditions.

It can be expected that seamount faunas undergo similar changes as open ocean mesopelagic faunas dependent on changes in ocean productivity, as has been observed for mesopelagic communities of the tropical and subtropical North Atlantic in relation to NAO dependent changes in the wind regime (Fock and Czudaj 2019). Accordingly, the German GMS trawl surveys 1967–1970 and 1998 at GMS revealed a change in composition in favor of off-bottom fishes *Capros aper*, *Macroramphosus scolopax/gracilis*, *Chlorophthalmus*

agassizii, and *Heptranchias perlo*, while no increase was indicated for benthic dwellers (Fock et al. 2002a). Fock et al. (2002a) employed a trophic-reproductive hypothesis to explain these long-term changes. *M. scolopax/gracilis* and *Capros aper* can be described as planktivorous species with about 93% of diet belonging to planktonic prey in terms of relative importance, while *Capros aper* further appears to be feeding to a minor degree on small mesopelagics and fish fry (Fock et al. 2002b). Increased planktonic prey would sustain a larger population of planktivores, and *H. perlo* with its ovoviviparous reproduction mode would not depend on Taylor column stability for sustaining its population while benefiting from increased prey availability in terms of small planktivores.

Conservation efforts

A marine protected area (MPA) can be defined as a clearly defined geographical space, recognized, dedicated, and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values (Dudley 2008).

In Portugal, designation of MPAs started in the 1970s with the Selvagens Natural Reserve (Batista and Cabral 2016). Currently, the area covered by MPAs equals 7% (DGPM 2018; Statistics Portugal 2023), being the result of several regional, national, and international initiatives and commitments assumed by Portugal. Recently, on 17 October 2024, the Azores Regional Government approved an amendment to legislation for establishing a regional MPA network that will contribute to practically double the national marine protected area coverage. However, this value is far below the target of 30% under protection by 2030, including 10% of exclusion zones, which was recently established in the National Strategy for the Sea 2021–2030 (RCM no. 68/2021) and under the international commitments assumed by Portugal (CBD 2022).

In 2014, the Programme of measures, executed under the Marine Strategy Framework Directive (MSFD), included spatial protection measures as determined pursuant to Article 13(4) of the Directive 2008/56/EC. In this context, two new oceanic MPAs were proposed: Madeira-Tore MPA between mainland Portugal and Madeira Archipelago and the GMSA, located south of Azores Archipelago (MAM, SRMCT, SRA, 2014). Both proposals will contribute to establishing a national network of MPAs. GMSA encompasses ten submarine seamounts being Pico-do-Sul, the only seamount inside the Exclusive Economic Zone (EEZ), and the other nine (Atlantis, Tyro, Plato, Cruiser, Irving, Hyeres, Great Meteor, Small Meteor, and Closs) located on the Extended Continental Shelf of Portugal (Fig. 17). This area was included under the Regional Protection by specific legislation of the Azores Archipelago. In 2016, six new areas were added to the Azores Marine Park, including GMSA (Regional Legislative Decree no. 28/2011/A, 11 November of 2011, in its updated version). GMSA was also recognized as ecologically or biologically significant marine area (EBSA Great Meteor) presented by Portugal under the Convention on Biological Diversity (CBD) (CBD/EBSA/WS/2019/1/4 2019). The importance of this area for biodiversity conservation was once again reinforced by the recent approval of the aforementioned legislation, as it is part of the biggest MPA network of the Atlantic North that contributes to the biological connectivity between deep sea communities (Blue Azores 2024).

Complementary to these initiatives, Portugal developed other spatial protection measures, such as the large potential areas of exclusion for submarine cables and ducts. These areas were designated under the development of the Portuguese Maritime Spatial Planning (PMSP), in 2019, to protect the VMEs (MM 2019). GMSA was included in this proposal (Fig. 17). Prior, in 2014, in addition to the recommendations of the North East Atlantic Fisheries Commission (NEAFC) to protect VME, Portugal endorsed a new fishing management measure which interdicted the use of bottom fishing gears, except for longlines, to the entire Portuguese fleet (Order no. 114/2014, 28 of May) (Fig. 17). This initiative is in line with the following UN General Assembly Resolutions, since 2004 (UNGA Resolution 59/25 2005), until the present days (76/1 2021), where all coastal states and Regional Fisheries Organizations were encouraged to take specific measures to reduce the impact of bottom-fisheries on VMEs, including seamounts. In addition, the Resolution (EU) 2016/2336 established a depth limit of 800 m for fishing with bottom trawls which covered the international waters where GMS is located and created measures to prevent significant adverse impacts in VMEs.

However, an effective protection of VMEs will only be achieved if these measures will be monitored and enforced. According to the Directorate-General for Natural Resources, Safety and Maritime Services (DGRM), the Portuguese entity that ensures the control and regulation of fisheries activity, there are no reports neither about sponges or corals encounters nor administrative offenses in the GMS area (C. Rosa, personal communication, February 2, 2023).

Finally, it is important to mention the new agreement on the conservation and sustainable use of marine biological diversity of areas beyond national jurisdiction (UN-GA, 2023) which reinforced the importance of cooperation and coordination in the use of area-based management tools, including MPAs, to preserve the marine environment.

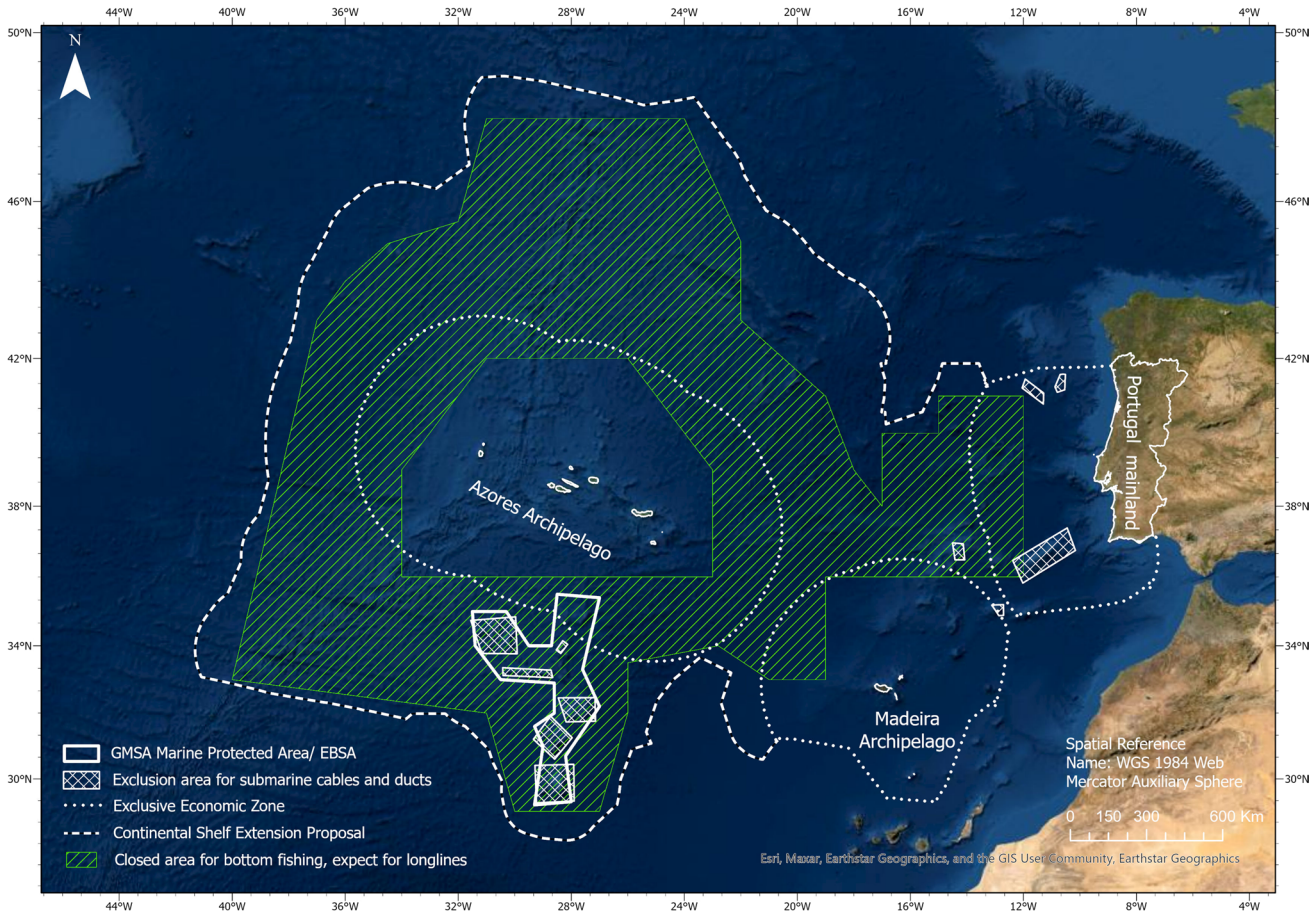

Fig. 17 Conservation efforts in the Great Meteor Seamount. The figure highlights the GMSA MPA established under the Regional Legislative Decree no. 28/2011/A, 11 November of 2011, in its updated version; the ecologically or biologically significant marine area purposed under Convention on Biological Diversity (CBD/EBSA/WS/2019/1/4) which area is coincident with GMSA MPA; the exclusion areas for installation of submarine cables and ducts (MAM, SRMCT, SRA, 2014) and the closed area for bottom fishing, except longlines, for the Portuguese fleet according to the legal act Order no. 114/2014, 28 of May

A brief outlook

GMS is one of the largest and best studied seamounts in the world. It also combines a set of environmental and topographic characteristics that makes this seamount a unique ecosystem. It is located in a region dominated by complex tidal motions and processes (Gerkema and van Haren 2007; van Haren and Gostiaux 2010), which strongly affect the plankton production and distribution and have great importance for shaping biological distribution patterns. These processes, however, are subject to a large variability, and accurately measuring their effects across coherent temporal and spatial scales remains a challenge.

To better understand these processes and their biological implications, future research must prioritize strategic long-term, high-resolution monitoring through the deployment of current meters and temperature moorings. These moored instruments are uniquely suited to capture critical time-series data, providing continuous, in situ insights that are essential to fully characterize the variability of physical processes at seamounts and their influence on biological distributions. By conducting consistent, targeted measurements over extended periods, these instruments can reveal patterns and interactions that are otherwise obscured by seamounts' variable dynamics.

Although the biology and ecology at GMS has been studied over the last decades, the seamount geomorphology with its steep slopes and deep plateau makes the sampling a challenging endeavor. Moreover, working below 2000-m water depth has technical limitations and requires specialized gear, such as towed and drift cams and ROVs. This type of equipment not only allows us to strategically target areas that were never sampled before, such as deep slopes and bases, but also enables the collection of high-resolution footage of the deep-sea communities alongside a combination of environmental data and samples. By producing integrated datasets for investigating seamount ecology, this equipment helps fill existing knowledge gaps

in this and other deep seamount areas that have remained unexplored until now. However, even with an outstanding sampling effort, it will be impossible to cover seamount habitats in their entirety. Hence, predictive modeling including hydrodynamic and species distribution models could be a useful tool to extrapolate and expand the spatial coverage for an unknown area and redirect our future sampling. The opportunities that lie ahead are considerable. Future seamount research should involve a combination of multidisciplinary tools and teams to produce high-quality datasets, covering unexplored and undersampled habitats in geographic areas where scientific gaps have been identified.

Following increasing research interest on seamounts in combination with growing management concerns, the Global Census of Marine Life on Seamounts (CenSeam) was established in 2005 as part of the Census of Marine Life program (Clark et al. 2012; Stocks et al. 2012). The long-term mission of CenSeam was to "determine the role of seamounts in the biogeography, biodiversity, productivity, and evolution of marine organisms, and to evaluate the effects of human impacts on seamounts" (Stocks et al. 2012). Along with the CenSeam project, the seamount and deep-sea research community engaged in different follow-on initiatives and networks including SBN (Seamount Biogeosciences Network), INDEEP (International Network for Scientific Investigations of Deep-Sea Ecosystems), DOSI (Deep-Ocean Stewardship Initiative), and DSBS (Deep-Sea Biology Society). These efforts demonstrate the high value and benefit of collaborative research that can result in new data and knowledge and lead to effective management action and plans in highly complex deep-sea environments both inside and outside of areas of national jurisdiction.

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Declarations

Conflict of interest The authors declare no competing interests.

Ethics approval No animal testing was performed during this study.

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Author contribution Conceptualization: IT, CM, MK, and MS; original draft design: CM; methodology: CM, IT, and JRX; writing—sections: IT and CM (timeline of exploration); IT and MS (geographic setting); MK, TG, HvH, BM, MW, and CM (physical oceanography); MK, BM, BM, and CM (biophysical coupling); KG (meiofauna); IT, JRX, MR, and MCS (benthic communities); HF (fish); IT, TR, and MS (conservation efforts); writing—review: TM, HC, JC, and JRX; writing—review and editing: IT and CM. All the authors have read and approved the manuscript.

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