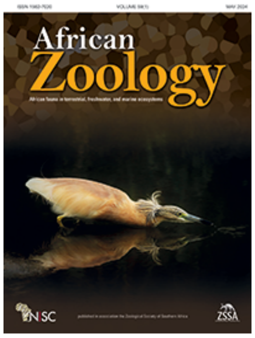

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Diversity, distribution and knowledge gaps of Polychaeta on the continental shelf of southern Namibia

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This study investigated the diversity, composition and distribution patterns of polychaete macrofauna inhabiting unconsolidated sediments on the continental shelf of southern Namibia. During the austral summer of 2021, 910 Van Veen grab samples were collected from 91 sites in water depths ranging between 43 and 146 m. All benthic macrofauna (> 1 mm) were extracted, identified, enumerated and weighed. Polychaetes were the most abundant taxon, equating to 66% of total abundance and 37% of total biomass. A total of 83 712 polychaete specimens comprising 112 species, 80 genera and 33 families were collected. Several taxa identified were listed as putative cosmopolitans (19 taxa) or have known wide local distributions (10 taxa). Voucher specimens were collected for DNA barcoding to improve reference sequence libraries for the region. Hierarchical cluster analyses using both abundance and biomass data were undertaken to determine spatial distribution patterns in polychaete communities. Both datasets yielded similar results with polychaete assemblages divided into inshore and offshore communities, that were further subdivided at a local scale. Investigation of physical and chemical drivers suggested that polychaete communities in southern Namibia are structured to varying degrees by water depth, latitude, sediment composition, redox potential and organic content. Deeper stations comprised the highest diversity of polychaeta fauna. Species adapted to hypoxic conditions (e.g. *Sigambra parva, Pararionospio pinnata, Diopatra cf. monroi* and *Nepthys* cf. *hombergii*) dominated an area known as the mudbelt, where organically enriched silts and clays originating from the Orange River are deposited on the mid-shelf between the 40 and 120 m isobaths.

Keywords: Benguela Upwelling System, benthos, cosmopolitan, DNA barcoding, hypoxic, latitude, sediment composition, water depth

Supplementary material: available at https://doi.org/10.1080/15627020.2024.2349648

Introduction

Despite over two centuries of studying the ocean, our knowledge of its organisms and processes remains poor (Briggs 1994; Costello et al. 2010, 2012; Mora et al. 2011). In southern Africa, the generation of knowledge on local benthic taxa, particularly those on the continental shelf, started in the late 1800s but was greatly enhanced over the 1900s through work undertaken by researchers at the University of Cape Town (Griffiths et al. 2010) and elsewhere (Barnard 1916, 1924, 1946, 1951, 1957, 1974; Millard 1975, 1978; Kensley 1981; Gosliner and Ghiselin 1987; Thandar 1989; Williams 1992). This is reflected in the surge of taxonomic descriptions during these years, including the publication of “A Monograph on the Polychaeta of Southern Africa” (Day 1967).

Among benthic communities, polychaetes consistently rank among the most dominant taxonomic groups in terms of densities, species richness and biomass (Pabis et al. 2011; Shields and Blanco-Perez 2013; Steffani et al. 2015; Eisenbarth and Zettler 2016; Aliakbarian et al. 2020; Capa and Hutchings 2021; Kim et al. 2021; Pamungkas et al. 2021, Sobczyk et al. 2021; Naser 2022; Saeedi et al. 2022). They are also considerably diverse (Hutchings 1998), with over 12 000 documented species according to The World Polychaete Database (WPD, http://www.marinespecies.org/polychaeta). However, ongoing discoveries and descriptions of new polychaete species indicate that a substantial number of species remain undiscovered (Clarke et al. 2010; Fiege et al. 2010; Saeedi et al. 2022; Simon et al. 2022; Sedick et al. 2023). Recent models predict that 5 200 additional species will be discovered by 2100 (Pamungkas et al. 2019). This number can further be increased by implementing molecular techniques, including environmental DNA (eDNA) and voucher specimen barcoding (Fleming 2023).

The importance of documenting polychaete distributions and diversity in the marine environment is emphasised by experimental studies, which have identified certain taxa as ecosystem engineers (Herringshaw et al. 2010; Jones

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et al. 2018; Bruschetti 2019 and references therein). These taxa play an important role in the functioning of an ecosystem (Hooper et al. 2005) via bioturbation, biogenic habitat formation, detritus degradation, and burial of organic material and sequestration of harmful substances (Hutchings 1998; Snelgrove 1998). Benthic marine polychaetes have evolved certain biological characteristics or traits in response to the environmental conditions present on the seafloor. It is important to understand how these environmental drivers influence infaunal community structure and, in turn, ecosystem function (Lam-Gordillo et al. 2021; Shojaei et al. 2021; Beauchard et al. 2023).

Depth has been identified as a major factor influencing faunal zonation and diversity of benthic species, including polychaetes (Ellingsen et al. 2007; Saeedi et al. 2022; Kohlenbach et al. 2023; Sobczyk et al. 2023). Indeed, studies have demonstrated a positive correlation between species richness and depth, with an increase in diversity from the shelf to around 3 000 m depth (Rex et al. 1997; Hilbig and Blake 2006; Brandt et al. 2007; Rex and Etter 2010), while others report a peak in species richness and abundance on the shallow (25−50 m) (Sobczyk et al. 2023) and deep (100−400 m) continental shelf (McCallum et al. 2015). Such differences have been attributed to limited sampling effort (McCallum et al. 2015). It is expected that expanding the (spatial) sampling effort across the entire continental margin, ranging from shallow to abyssal depths, would reveal broader trends distinct from those observed within narrower depth ranges, such as between 100 and 1 000 meters (McCallum et al. 2015). Other abiotic factors known to influence polychaete community structure include dissolved oxygen, temperature, sediment composition, sedimentation rates, salinity and organic matter (Benedetti-Cecchi et al. 2010; Chouikh et al. 2020; Kim et al. 2021; Sobczyk et al. 2021; Kohlenbach et al. 2023; Sobczyk et al. 2023) — factors which have also been shown to influence the broader macrozoobenthic community (Chou et al. 2004; Wlodarska-Kowalczuk et al. 2004; Steffani et al. 2015; Eisenbarth and Zettler 2016; Donnarumma et al. 2019; Aliakbarian et al. 2020; Lamarque et al. 2022; Saeedi et al. 2022; Amorim and Zettler 2023).

The continental shelf off Namibia falls within the Benguela Current Large Marine Ecosystem (BCLME) and is a highly dynamic marine environment (Crawford et al. 1989; O'Toole et al. 2001). The area constitutes one of the world's most productive perennial upwelling systems, which brings nutrient-rich waters to the surface, promoting phytoplankton growth (Mohrholz et al. 2014; Verheye et al. 2016). Such high primary production often results in high microbial oxygen demand in deeper waters due to the bacterial breakdown of organic matter ultimately leading to oxygen depletion (Brüchert et al. 2006). The prevailing oceanography in the BCLME therefore includes numerous strong and dynamic environmental drivers that may structure benthic communities. Indeed, previous studies have identified water depth, hydrogen sulphide flux, dissolved oxygen, latitude and distance from the Orange River as significant drivers structuring benthic communities on the Namibian shelf (Steffani et al. 2015; Amorim and Zettler 2023).

Despite the importance of studying marine biodiversity, it has largely been undocumented in benthic habitats on the continental shelf of Namibia, an area that is also increasingly exploited anthropogenically (Rogers and Li 2002; Clarke et al. 2010; Steffani et al. 2015; Eisenbarth and Zettler 2016; Amorim and Zettler 2023). This is especially true for the southern continental margins of Namibia (Rogers and Li 2002; Clarke et al. 2010; Steffani et al. 2015; Sedick et al. 2023), as most studies of macrozoobenthic communities have been conducted in the continental margin off northern Namibia and at the northern boundary with Angola (Zettler et al. 2009, 2013; Eisenbarth and Zettler 2016; Amorim and Zettler 2023). Insights into the polychaete community of southern Namibia could aid in monitoring anthropogenic impacts, as polychaetes act as sensitive indicators to environmental changes due to their relatively short life span and high dispersal ability (Rouse and Pleijel 2001). However, documenting polychaete diversity in Namibia is challenging because most Polychaeta in southern Africa were described in a monograph compiled by John H. Day in 1967, and continuing taxonomic revisions have detected several taxa that are putative cosmopolitan or composed of species complexes (Simon et al. 2022 and references therein). According to Simon et al. (2022), half of the 609 polychaete species recorded locally in southern Africa are unresolved cosmopolitan complexes, and it was estimated that at least 500 polychaete taxa remain undescribed in the region. It is, therefore, likely that several Namibian polychaete species inhabiting the continental margins are undescribed and need to be accounted for when investigating Polychaeta within this region. Voucher specimens for barcoding can improve taxonomic classifications of Namibian Polychaeta by blasting barcodes against genetic databases, such as GenBank and BOLD (Fleming 2023).

The goal of this research was to provide insights into the distribution and diversity of polychaetes inhabiting the southern parts of the continental shelf of Namibia and to address knowledge gaps in the taxonomy and nomenclature of polychaete fauna in the region. To achieve this, research was undertaken to address four objectives:

1. Determine the spatial patterns in diversity, abundance, and biomass of Polychaeta on the southern Namibian (26°S to 28°S) inner shelf (40 m to 150 m).
2. Determine the environmental factors contributing to this distribution, including depth, latitude, total organic carbon, total organic nitrogen, redox potential (mV) and sediment composition.
3. Update the known biogeographic records of polychaetes within southern Namibia using the results of Simon et al. (2022).
4. Collect voucher specimens of taxa that are putative cosmopolitans or have a wide local distribution for DNA barcoding to blast against GenBank and BOLD databases for improved taxonomic classification.

Materials and methods

Study area

The study is located across the continental shelf and is situated north of the Orange River Mouth, which marks the border between Namibia and South Africa (Figure 1). It falls within the BCLME, one of the largest upwelling areas

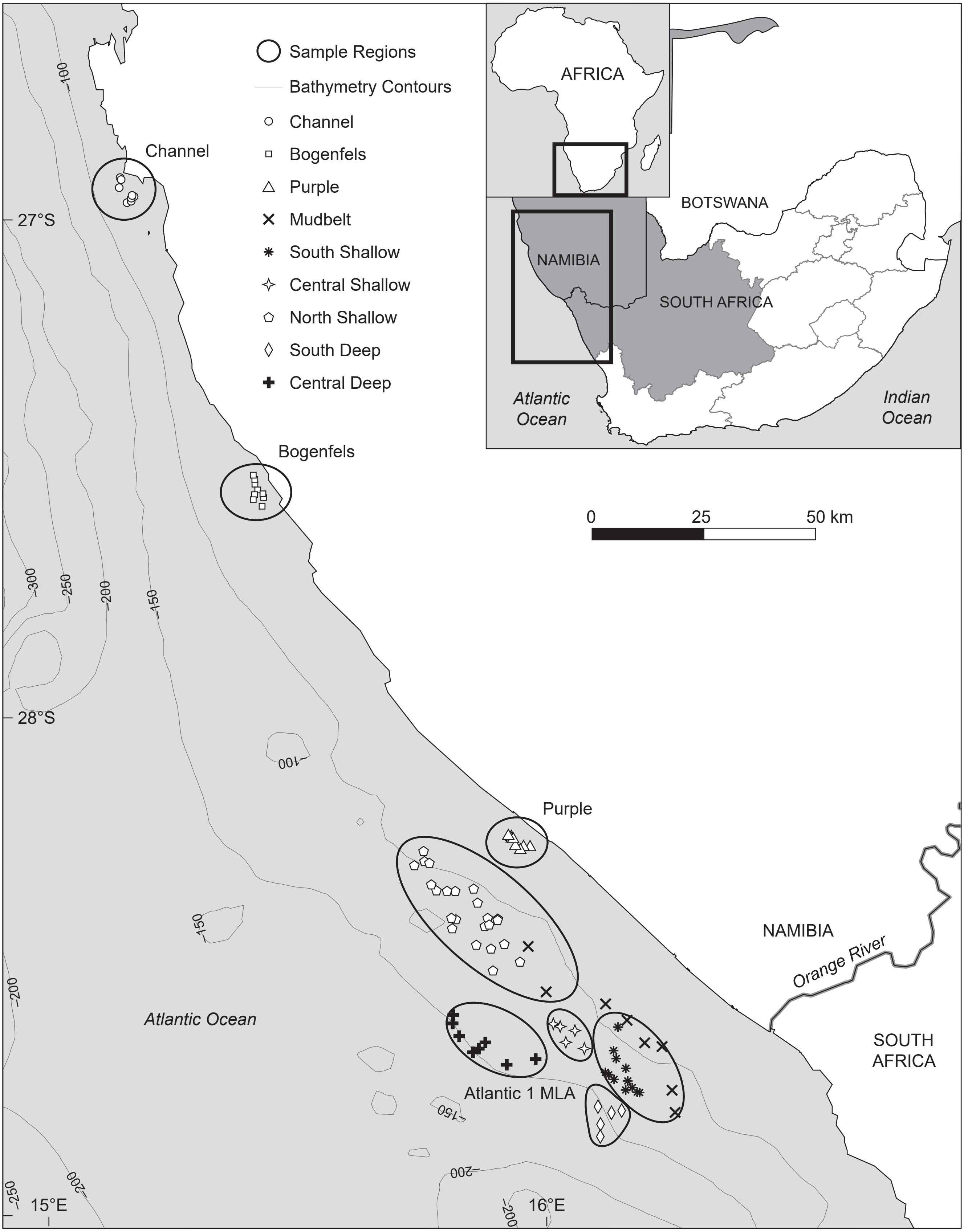

Figure 1: Locations of the 91 sampling stations, including 66 offshore and 25 inshore stations on the continental shelf off southern Namibia

in the world. The shelf extending off the Orange River is broad, reaching approximately 180 km in width (Shannon 1985). Muddy sediment on the inner shelf, known as the mudbelt, comprises high organic content of terrigenous origin, predominantly attributed to fluvial input, whereas sand-dominated sediment in the north is predominantly influenced by aeolian transport of terrigenous material from the Namib Desert (Bremner 1981; Rogers and Bremner 1991). The production of phytoplankton growth in the area is promoted by nutrient-rich deep water that is upwelled by strong winds (Verheye et al. 2016). The decomposition of sinking detritus by bacteria results in hypoxic (0.5 ml $l^{-1)}$ and periodically anoxic (complete absence of dissolved oxygen) areas on the seafloor (Diaz and Rosenberg 1995; Levin 2003; Helly and Levin 2004). In times of oxygen deficiency, hydrogen sulphide can be produced in the sediments and accumulate in the bottom water of the shelf regions (Van der Plas et al. 2007; Mohrholz et al. 2008; Ohde and Mohrholz 2011).

Four main areas were sampled in the study location, including the Atlantic 1 Mining License Area (Atlantic 1 MLA) and three “midwater” mining concessions ML 43 (Purple; PPL), ML 44 (Bogenfels; BOG), and ML 45 (Channel; CHL) that fall under diamond-mining-license areas held by De Beers Marine Namibia and the Namdeb Diamond Corporation, respectively. The latter sites are in shallower waters (44 m to 67 m) and are collectively referred to as inshore sites, whereas Atlantic 1 MLA occurs in deeper waters (87 m to 146 m), and sites sampled here are referred to as offshore sites. For the purposes of this study, samples collected in Atlantic 1 MLA were further categorised according to position and depth and are named accordingly (NS – North Shallow, CS – Central Shallow, CD – Central Deep, SS – South Shallow, and SD – South Deep). Samples close to the Orange River mouth (< 40 km away) in Atlantic 1 MLA are referred to as “mudbelt” (MB). The sites chosen for this study were specifically selected because they have not been affected (are undisturbed) by diamond recovery operations.

Sampling

Sample collection took place from 11 November to 4 December 2021 aboard the vessel DP Star (Supplementary Table S1). At each station, 10 replicate samples were collected using a Van Veen grab. The grab samples an area of 0.2 m^2 and penetrates the sediment to a maximum depth of ~20 cm. Each grab sample was emptied into a receiving bin and a sediment sample was collected for granulometry, total organic nitrogen (TON) and total organic carbon (TOC) analyses, all of which were immediately transferred to cold storage at -20°C. The remaining material from each grab was transferred to a “processing tray” where the volume was recorded. The sample was then washed through a 1 mm sieve bag and retained fauna were fixed in formalin, diluted to 10% with seawater. In the laboratory, all animals were identified to the lowest taxonomic level possible using microscopy and available guides. Voucher specimens of 29 polychaete taxa were extracted from samples collected at Atlantic 1 MLA and were fixed in absolute molecular grade ethanol for DNA barcoding. Nomenclature was checked using the World Register of Marine Species (WoRMS: www.marinespecies.org). The abundance (no. of individuals) and biomass (blotted wet mass in grams to four decimal places) for each species was recorded. Redox potential measurements were recorded from each sediment sample using a handheld Hach LDO101 Rugged probe.

Biogeographic records

All taxa recorded in this study and their known distribution were tabulated (Supplementary Table S2) using biogeographic records from Day (1967) and the World Polychaete Database (WPD, http://www.marinespecies.org/polychaeta). This allowed us to distinguish taxa that occur locally from those that are widespread, cosmopolitan, or likely undescribed and potentially new to science (Simon et al. 2022).

DNA barcoding

Total genomic DNA from each voucher specimen was extracted using a commercial DNA extraction kit and the protocol was modified to increase DNA yields. DNA was amplified by Polymerase Chain Reaction (PCR) for a hypervariable region of the COI gene. Amplification success was determined by gel electrophoresis. PCR reactions for the DNA extractions were evaluated and the successful PCR products were purified, and Sanger sequenced. Raw sequences were trimmed and cleaned. Sequences were subsequently compared to the NCBI nt reference database (GenBank) using BLAST (Altschul et al. 1990; Sayers et al. 2022) and BOLD (Ratnasingham and Hebert 2007) to identify which of the sampled taxa represented novel additions to our identification pipeline. All generated sequences were compared against morphotaxonomic assignment.

Statistical analysis

To visualise polychaete community structure, non-metric multidimensional scaling plots (nMDS) were constructed based on a Bray–Curtis similarity measure using fourth root transformed species abundance and biomass data (Bray and Curtis 1957). Inshore and offshore sites were run separately at first and then together. These yielded similar results and only combined analyses are shown. Factors assigned to stations included location (offshore or inshore), region, latitude and four depth bins (40–70 m, 70–110 m, 110–140 m, and > 140 m). To further examine the structural variation of polychaete communities among inshore and offshore stations, a canonical analysis of principal coordinates (CAP; Anderson and Willis 2003) was performed. The similarity percentage (using a SIMPER analysis in PRIMER) was then calculated to identify species that contributed to the observed dissimilarity among sites. Only species that cumulatively contributed to 70% similarity were reported. Shannon diversity was calculated using the DIVERSE routine in PRIMER. Heat maps were produced in ArcGIS Pro 3.0.3. to illustrate the spatial distribution of the total number of taxa, abundance (no. of ind.), biomass (wet mass g), species richness and Shannon diversity index H’ (Shannon 1948).

Lastly, relationships between polychaete community composition and environmental variables were tested using a distance-based linear modelling analysis (distLM, Anderson 2004). For this, offshore and inshore assemblages were analysed separately, as it was confirmed these differed significantly (see results). The aim was to identify which variables influenced offshore and inshore assemblages. Subsequently, a distance-based redundancy analysis (dbRDA, Legendre and Anderson 1999) was used to visualise the influence of variables identified by distLM. All variables were normalised prior to analysis. Of the 910 samples collected, 133 lacked data on environmental parameters and were excluded from the distLM analyses. All multivariate analyses were undertaken using the PRIMER-PERMANOVA + v.6 software package (Anderson et al. 2008).

Results

Environmental variables

A summary of the recorded environmental variables is presented in Table 1. The sediment composition of inshore stations was characterised by a higher percentage of sand, compared to the offshore stations, whilst the opposite pattern was observed for mud content (Table 1). Stations within the mudbelt, in proximity to the Orange River, were characterised by a higher average percentage of mud (82%), compared to other offshore stations (Table 1).

In general, lower measurements of TOC were recorded inshore than offshore, whereas TON remained similar across all regions (Table 1). Negative redox values were observed across all regions, except at BOG (Table 1).

Community composition

A total of 127 915 benthic macrofaunal specimens belonging to 233 taxa within 16 classes were identified in 910 Van Veen grabs collected at 91 stations on the continental shelf of southern Namibia. Of these, polychaetes were the dominant group equating to 66% of the total abundance, 37% of the total biomass and 48% of total taxa (Figure 2 and Supplementary Figures S1 and S2). Across all stations, 83 712 polychaete individuals comprising 112 taxa belonging to 80 genera and 33 families were collected. The dominant families included Spionidae (28% of total abundance), followed by Capitellidae, Lumbrineridae, Nephtyidae, Cirratulidae, Orbiniidae and Onuphidae, each comprising ≥ 5% of total abundance. The most species-rich families included Spionidae (12), Cirratulidae (10), Lumbrineridae (10), Orbiniidae (7) and Terebellidae (7). However, all these families, except Lumbrineridae, comprised a low total biomass (≤ 48 g) (Figure 3). Dominant species (percentage total abundance ≥ 7%) included *Paraprionospio pinnata*, *Mediomastus capensis*, *Spiophanes* spp., *Lumbrineris meteorana*, *Micronephtys sphaerocirrata* and *Leitoscoloplos kerguelensis* (Supplementary Figure S3). Of the 112 polychaete taxa that were recorded, just under half (45%) could not be identified to species level. We suspect that many of these are likely new to science.

Biogeographic records

Most polychaete taxa identified in this study had wide biogeographical ranges (Day 1967, WPD, Supplementary Table S2). Of these, a total of 29 taxa were highlighted by Simon et al. (2022) as either unresolved cosmopolitan (19 taxa) or widespread indigenous polychaete species (10 taxa).

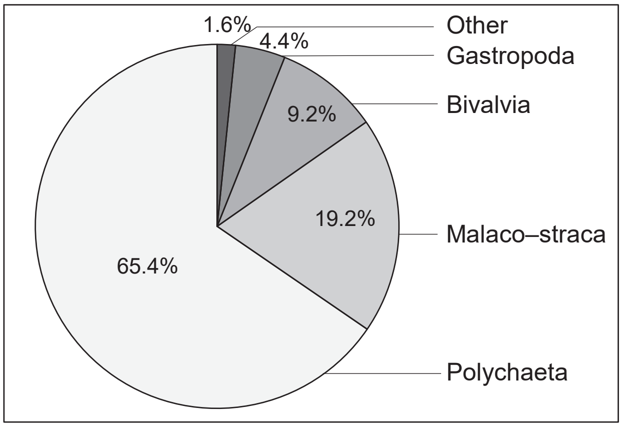

Figure 2: Numerical composition of benthic macrofauna by taxonomic classes collected on the continental shelf off southern Namibia

Table 1: Environmental variables (average ± SD) recorded for offshore and inshore stations, including water depth (m), TOC (Total Organic Content), TON (Total Organic Nitrogen), redox potential (mV) and sediment composition (i.e. percentage gravel, sand and mud). Station acronyms: BOG: Bogenfels, CHL: Channel, PPL: Purple, MB: Mud Belt, NS: North Shallow, CS: Central Shallow, CD: Central Deep, SS: South Shallow and SD: South Deep

Variables	Offshore						Inshore		
	MB	NS	CS	CD	SD	SS	PPL	BOG	CHL
% Gravel	0	2.97	3.10	4.27	0.49	1.68	0.07	2.18	1.35
% Sand	17.62	73.69	50.46	54.26	74.23	68.51	93.40	97.06	78.04
% Mud	82.23	23.34	46.45	41.46	25.28	29.80	6.52	0.76	20.61
Depth	100.95 (± 9.81)	135.63 (± 42.06)	113.91 (± 3.57)	139.08 (± 6.16)	134.07 (± 2.68)	122.91 (± 3.09)	60.88 (± 3.82)	54.43 (± 5.29)	50.87 (± 5.84)
TOC	1.35 (± 0.6)	0.41 (± 0.13)	1.04 (± 0.44)	1.98 (± 0.92)	0.44 (± 0.15)	0.59 (± 0.31)	0.28 (± 0.16)	0.08 (± 0.05)	0.54 (± 0.52)
TON	0.24 (± 0.09)	0.04 (± 0.01)	0.14 (± 0.05)	0.26 (± 0.08)	0.04 (± 0.01)	0.07 (± 0.04)	0.27 (± 0.05)	0.04 (± 0.02)	0.08 (± 0.05)
Redox (mV)	-167.94 (± 44.47)	-135.63 (± 42.06)	-155.30 (± 26.98)	-129.58 (± 51.95)	-131.36 (± 43.09)	-146.97 (± 35.24)	-108.93 (± 89.48)	141.03 (± 66.55)	-146.72 (± 116.64)

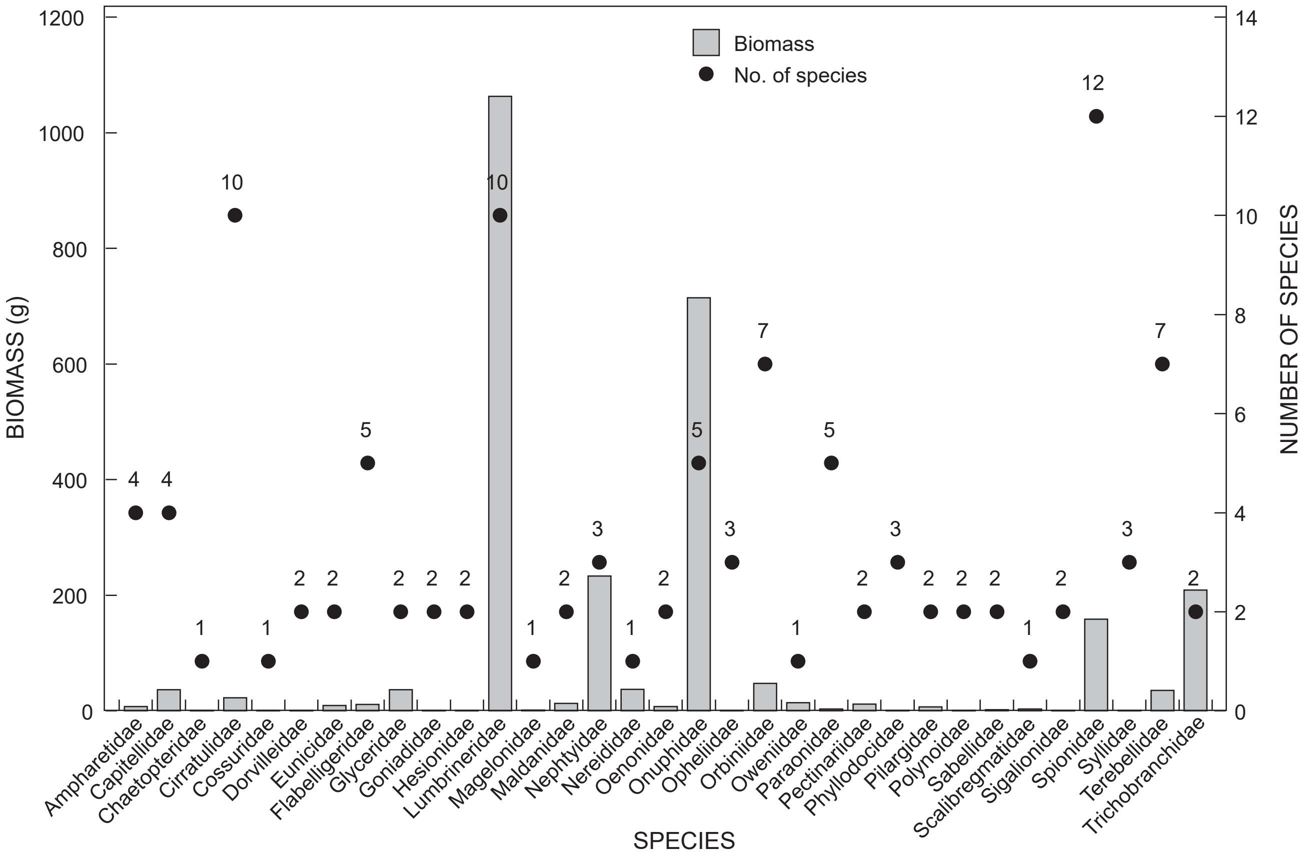

Figure 3: Total biomass in grams (grey bars) and number of species (dots) by polychaete family recorded across all samples

DNA Barcoding

Of the 29 voucher specimens, DNA from only ten specimens amplified successfully (according to data quality control standards). Overall, the similarity of genetic matches to taxa available on the reference databases (GenBank and Bold) were low, ranging between 79% to 98% with an 87% average (Table 2). Morphological identifications also matched genetic results up to the genus level for all taxa, except for *Lumberineris meteorana*, which yielded a close match with *Gallardoneris* sp. (98%), thereby placing it within that genus. The COI barcodes are listed in Supplementary Table S3.

Spatial and diversity patterns

Significant differences were observed in the spatial distribution of polychaete fauna in the study area. Offshore and inshore assemblages were evident in nMDS plots that are further separated by region, depth and latitude (Figure 4a−d; Supplementary Table S4). Offshore and inshore groupings were also evident in the CAP analysis plot (Figure 5). Offshore and inshore stations were separated and aggregated along the CAP1 axis. The average dissimilarity between offshore and inshore groups was 82%. Dominant taxa contributing to these differences were more abundant in either offshore or inshore stations, whereas some taxa were restricted to inshore (*Prionospio saldanha*, *Ampharete luederitz*i and *Magelona* sp.) or offshore (*Leitoscoloplos kerguelensis* and *Terebellides stroemii*) sites (Table 3). Additionally, regional separation of mudbelt polychaete taxa was mainly attributed to a higher abundance of *Sigambra parva*, *Pararionospio pinnata*, *Diopatra* cf. *monroi* and *Nepthys* cf. *hombergii* (Supplementary Table S5).

Heat maps were used to further visualise the spatial distribution and diversity patterns of inshore and offshore communities. In general, a higher number of taxa and Shannon diversity indices were recorded at offshore sites compared to shallower sites (Figure 6). Abundance was elevated and patchy throughout the central and northern offshore sites (Atlantic 1 MLA), while most of the biomass was recorded in the central region of Atlantic 1 MLA between 108 m and 116 m. It is important to note that since no samples were collected between the latitudinally separated inshore stations, these areas were subject to increased interpolation and are ultimately data deficient i.e. values indicated by the colour interpolation in these areas should be treated with caution.

Environmental influence on polychaeta

The pattern of inshore and offshore communities was significantly correlated with all environmental parameters (Table 4). This correlation can be visualised in the dbRDA (Figure 7) where category vectors indicate the measure of the relationship strength between that category and the axes. All environmental variables explained a significant component of the variation in polychaete communities

Table 2: DNA barcode results of the 10 voucher specimens sequenced from Atlantic 1 MLA, showing the morphological identification of the specimen and its highest genetic match with taxa available on GenBank (blast_nt) and BOLD. NMID: Voucher code; Morph ID: Identification of specimen based on morphology and taxonomic keys; Region: where specimen was collected (SD – South Deep, CD – Central Deep, NS – North Shallow, MB – Mudbelt, SS – South Shallow, CS – Central Shallow); accID: accession number for barcoded specimen; % similarity: percent genetic match

Voucher specimen				Genetic Match				
NMID	Morph ID	Region	accID	Family	Genus	Species	% Similarity	Database
SB-27798	*Leitoscoloplos kerguelensis*	SD	CBPM198-11	Orbiniidae	*Leitoscoloplos*	*Leitoscoloplos pugettensis*	79.51	blast_nt
SB-27801	*Scalibregma inflatum*	SD	ARIQ004-17	Scalibregmatidae	*Scalibregma*	*Scalibregma californicum*	87.60	BOLD
SB-27803	*Spiophanes* sp.	CD	KT307701	Spionidae	*Spiophanes*	*Spiophanes kroyeri*	94.09	BOLD
SB-27804	*Lumbrineris meteorana*	NS	OM237789	Lumbrineridae	*Gallardoneris*	*Gallardoneris sp.*	98.59	blast_nt
SB-27809	*Diopatra cuprea*	MB	MK690692	Onuphidae	*Diopatra*	*Diopatra victoriae*	81.72	blast_nt
SB-27810	*Sigambra parva*	SS	KY775643	Pilargidae	*Sigambra*	*Sigambra parva*	81.93	BOLD
SB-27813	*Paraprionospio pinnata*	SD	KU661498	Spionidae	*Paraprionospio*	*Paraprionospio patiens*	84.71	blast_nt
SB-27815	*Spiophanes* sp.	CD	KT307701	Spionidae	*Spiophanes*	*Spiophanes kroyeri*	94.09	BOLD
SB-27820	*Brada villosa capensis*	CD	LC056920	Flabelligeridae	*Diplocirrus*	*Diplocirrus nicolaji*	83.33	BOLD
SB-27822	*Terebellides stroemii*	CS	MN207183	Trichobranchidae	*Terebellides*	*Terebellides lilasae*	89.33	blast_nt

when tested individually (Marginal test) and cumulatively (Sequential test), explaining 33% and 38% of offshore and inshore community changes, respectively. Percentage mud explained most of the offshore faunal variability (17%), followed by percentage sand (16%), depth (14%), TON (14%) and TOC (12%). Conversely, percentage gravel and redox potential explained the offshore variability to a much lesser extent (3% and 2% respectively). In contrast, redox potential (20%) explained most of the inshore faunal variability, followed by latitude (13%), percentage mud (12%), percentage sand (11%), TON (10%) and TOC (9%). Depth and percentage gravel accounted for 3% and 2% of the inshore variability, respectively.

Discussion

This study provides a comprehensive overview of the polychaete community inhabiting the southern continental shelf of Namibia, where most research thus far has focussed on the macrozoobenthic communities off the northern continental margins (Zettler et al. 2009; Zettler et al. 2013; Eisenbarth and Zettler 2016; Amorim and Zettler 2023). Abundance and biomass-based hierarchical clustering analyses were performed, which yielded similar results and detected two main polychaete assemblages, separating into inshore (44 m to 67 m) and offshore (87 m to 146 m) communities. The structure of polychaete communities off southern Namibia was significantly driven by sediment composition, depth, latitude, redox potential, TOC and TON. Our results indicate that these are not the only variables driving polychaete community structure as more complexity exists through the interaction among various stressors, biotic interactions and ecological dynamics (Amorim and Zettler 2023).

Biogeographic records and diversity

Most of the polychaetes in southern Africa were identified by John H. Day who published an extensive monograph on the Polychaeta of Southern Africa (Day 1967). However, ongoing taxonomic revisions demonstrate that cosmopolitan or widely distributed local taxa mentioned in the monograph are species complexes characterised by distinct global and local distributions (Simon et al. 2022 and references therein). The records of these cosmopolitan or widespread polychaete species in southern Africa often arose from synonymies to single species, or the use of existing names, mostly from the Northern Hemisphere (Hutchings and Kupriyanova 2018). As a result, several species from southern Africa have been misidentified locally and are likely to be indigenous to the region, while several others may also have hidden cryptic diversity (Simon et al. 2022). Therefore, it is suggested that some of the species-level identifications presented in this study require validation and further research to confirm the records within this region. Although it is strongly advised that species-level identification include comparisons to original descriptions and ideally, type material (Hutchings and Kupriyanova 2018; Simon et al. 2022) which is not always possible for large-scale surveys such as the one presented here. To avoid perpetuating taxonomic errors, it is further recommended

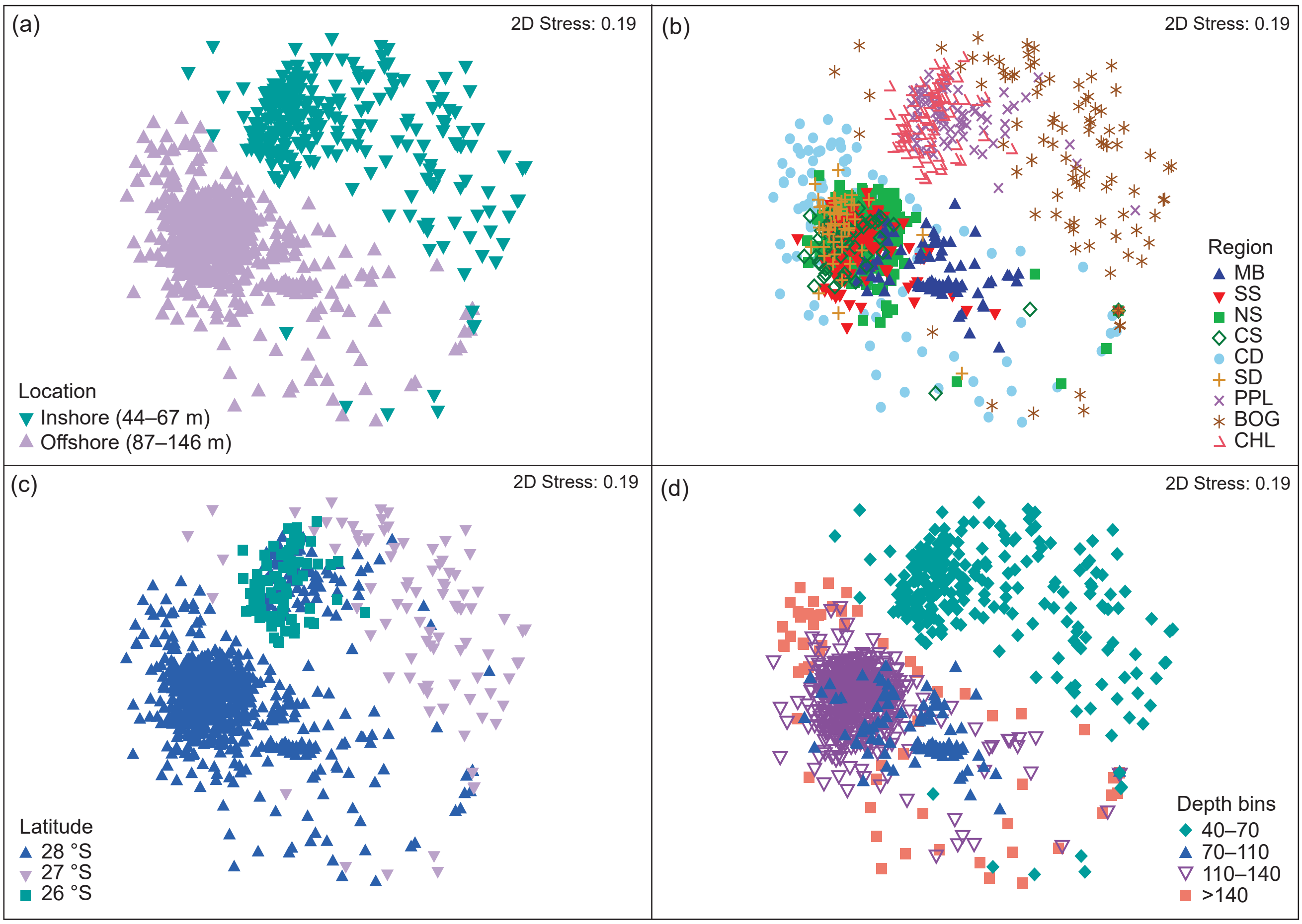

Figure 4: Distinct polychaete assemblages detected on the southern shelf off southern Namibia using non-metric multidimensional scaling analysis based on Bray–Curtis similarity, factoring (a) Location: inshore (44–67 m) and offshore (87–146 m, (b) Region: BOG: Bogenfels, CHL: Channel, PPL: Purple, MB: Mud Belt, NS: North Shallow, CS: Central Shallow, CD: Central Deep, SS: South Shallow, and SD: South Deep, (c) Latitude: 26 °S, 27 °S and 28 °S (d) Four depth bins: 40–70 m, 70–110 m, 110–140 m and >140 m

that future surveys carefully investigate taxa that are putative cosmopolitans or have wide local distributions. To facilitate this issue, we successfully barcoded 10 voucher specimens from Atlantic 1 MLA, of which nine matched with its given genus when based on morphology and taxonomic keys. In contrast, genetic matches exhibited a lower degree of similarity at the species level. This highlights the importance of taxonomists exercising caution when assigning species names and should rather adhere to the genus level. More importantly, it indicates that the reference database for polychaetes in the Southern Hemisphere is incomplete and an extensive amount of research is needed in this region.

Polychaetes numerically dominated the benthic macrofauna of the southern Namibian shelf and represented 66% of the total macrofaunal abundance and 37% of total biomass. The 112 polychaete taxa also comprised nearly half (48%) of the total number of macrofauna taxa collected. The diversity of these southern Namibian shelf samples is, however, lower than that recorded from northern Namibia (between 17°S and 25°S) where 130 (Eisenbarth and Zettler 2016) and 196 (Amorim and Zettler 2023) polychaete taxa have been reported. These northern shelf studies sampled a wider depth range between 25 m and 1 523 m (Amonrim and Zettler 2023) and 403 m to 1 370 m (Eisenbarth and Zettler 2016). According to Eisenbarth et al. (2016), species diversity of macrofauna was positively correlated with depth and this was attributed to the presence of severe hypoxic conditions (0.5 ml l^{-1}) and other environmental fluctuations on the continental shelf, while the environmental conditions present in deeper waters off the edge of the shelf were relatively more stable and conducive to a greater diversity of taxa.

In the present study, higher species richness and Shannon diversity indices were recorded at deeper sites (87 m to 146 m) compared to shallower stations (44 m to 67 m). This corroborates some previous studies of increased macrofaunal diversity with depth (Escaravage et al. 2009; Eisenbarth and Zettler 2016; Neal et al. 2018; Saeedi et al. 2022; Amorim and Zettler 2023). However, this trend is not consistent as some studies have found an inverse correlation between benthic polychaete species richness and depth (Ellingsen et al. 2007; Sobczyk et al. 2023), while others have demonstrated a positive correlation between the two (Hilbig and Blake 2006; Brandt et al. 2007).

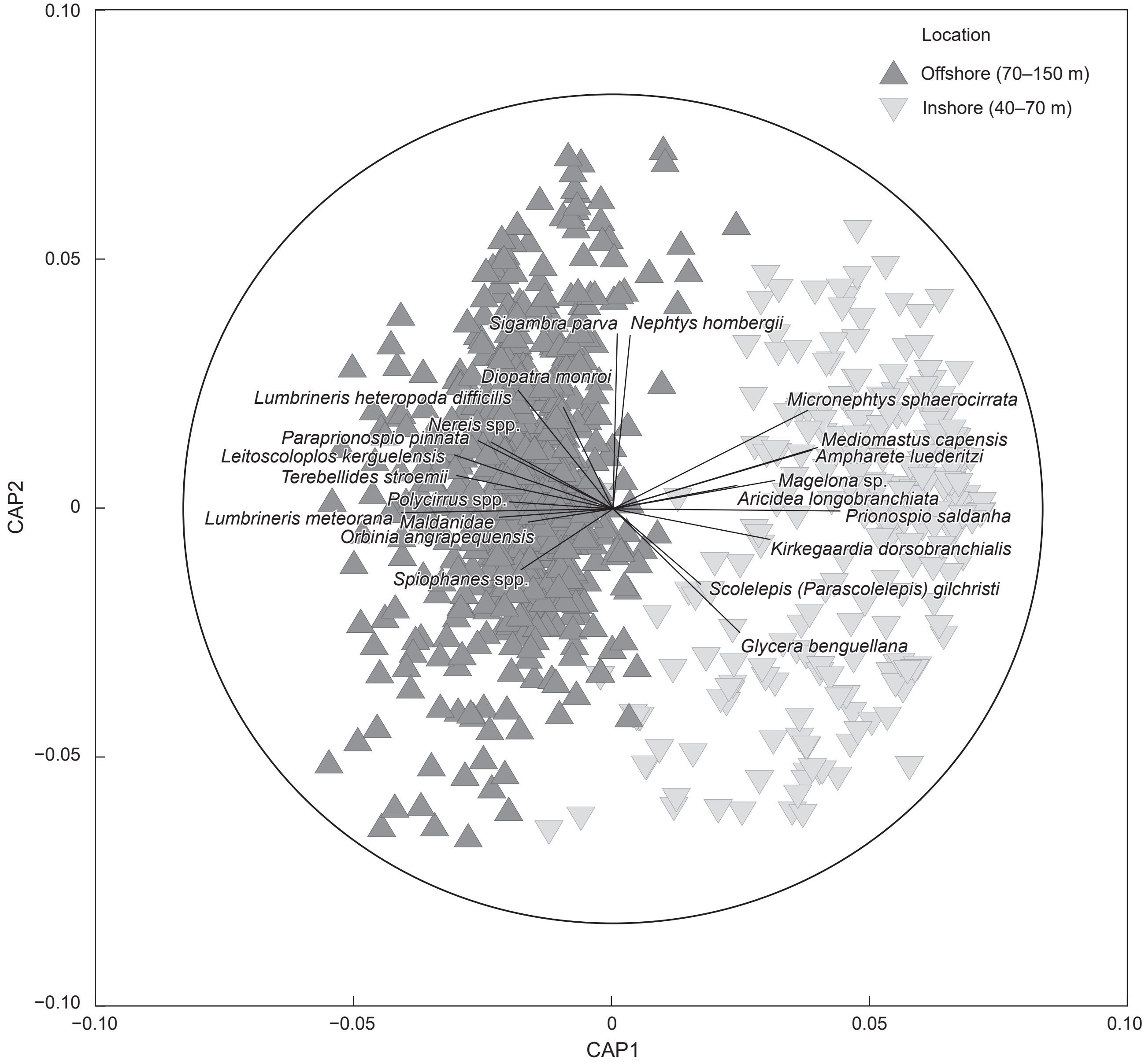

Figure 5: Canonical analysis of principal coordinates (CAP) on inshore and offshore polychaete assemblages identified in the shelf margin off southern Namibia. Dominant taxa driving the differences are plotted as vectors

Environmental drivers of polychaete assemblages

Hypoxic events occur throughout the Benguela region (Monteiro and Van der Plas 2006; Monteiro et al. 2008; Hutchings et al. 2009) and are often generated in regions of high phytoplankton production that is decomposed by bacteria, which in turn depletes the oxygen present in the water column (Diaz and Rosenberg 1995; Levin 2003; Helly and Levin 2004). Sulphide-oxidising bacteria generally dominate when oxygen levels are low as they substitute the oxygen, required for organic matter degradation, with nitrate reduction which allows efficient energy extraction (Knowles 1982; Tyrrell and Lucas 2002). The measurement of the redox potential in unconsolidated sediments can be used to interpret such organic chemical processes (Søndergaard 2009; Gerwing et al. 2018). Redox values at Bogenfels (BOG) were all positive, indicative of well-oxygenated sediments that are low in organic content (Søndergaard 2009; Gardiner and James 2012). This is consistent with the organic content results as BOG had lower TOC and TON measurements compared to other inshore areas (PPL and CHL).

In contrast, negative redox potential measurements are characteristic of marine environments that are de-oxygenated and consist mainly of fine sediments rich in organic matter (ZoBell 1946; Jørgensen 1977; Pearson and Stanley 1979; Weston 1990; Rosenberg et al. 2001; Gardiner and James 2012). The negative redox measurements observed in samples from offshore stations were consistent with the high organic content and fine muddy sediments found in Atlantic 1 MLA. In general,

Table 3: SIMPER results showing the dominant taxa that contributed to the dissimilarity among offshore and inshore groups. Av.Abund: average abundance; Av.Diss: average dissimilarity; Diss/SD: square distance divided by the standard deviation; Contrib%: percentage of contribution; Cum.%: cumulative contribution percentage

Taxa	Av.Abund (Offshore)	Av.Abund (Inshore)	Av.Diss	Diss/SD	Contrib%	Cum.%
Paraprionospio pinnata	1.6	0.25	5.46	1.37	6.67	6.67
Lumbrineris meteorana	1.49	0.03	5.21	1.71	6.36	13.03
Mediomastus capensis	0.89	1.53	5	1.11	6.11	19.14
Micronephtys sphaerocirrata	0.88	1.4	4.39	0.91	5.37	24.51
Leitoscoloplos kerguelensis	1.05	0	3.5	1.06	4.28	28.79
Prionospio saldanha	0	0.79	3.29	0.72	4.02	32.81
Spiophanes spp.	0.95	0.07	3.13	0.91	3.82	36.64
Kirkegaardia dorsobranchialis	0.21	0.75	3.08	0.72	3.77	40.4
Lumbrineris heteropoda difficilis	0.92	0.58	3.07	1.01	3.75	44.15
Nephtys hombergii	0.99	0.78	3.06	0.93	3.74	47.89
Aricidea longobranchiata	0.28	0.8	3.01	0.79	3.68	51.58
Diopatra monroi	0.79	0.12	2.88	0.88	3.52	55.1
Scolelepis (Parascolelepis) gilchristi	0.42	0.61	2.72	0.75	3.33	58.43
Ampharete luederitzi	0	0.72	2.59	0.74	3.17	61.6
Terebellides stroemii	0.67	0	2.23	0.93	2.72	64.32
Maldanidae	0.68	0.02	2.19	0.83	2.68	66.99
Magelona sp.	0	0.59	2.1	0.7	2.56	69.56

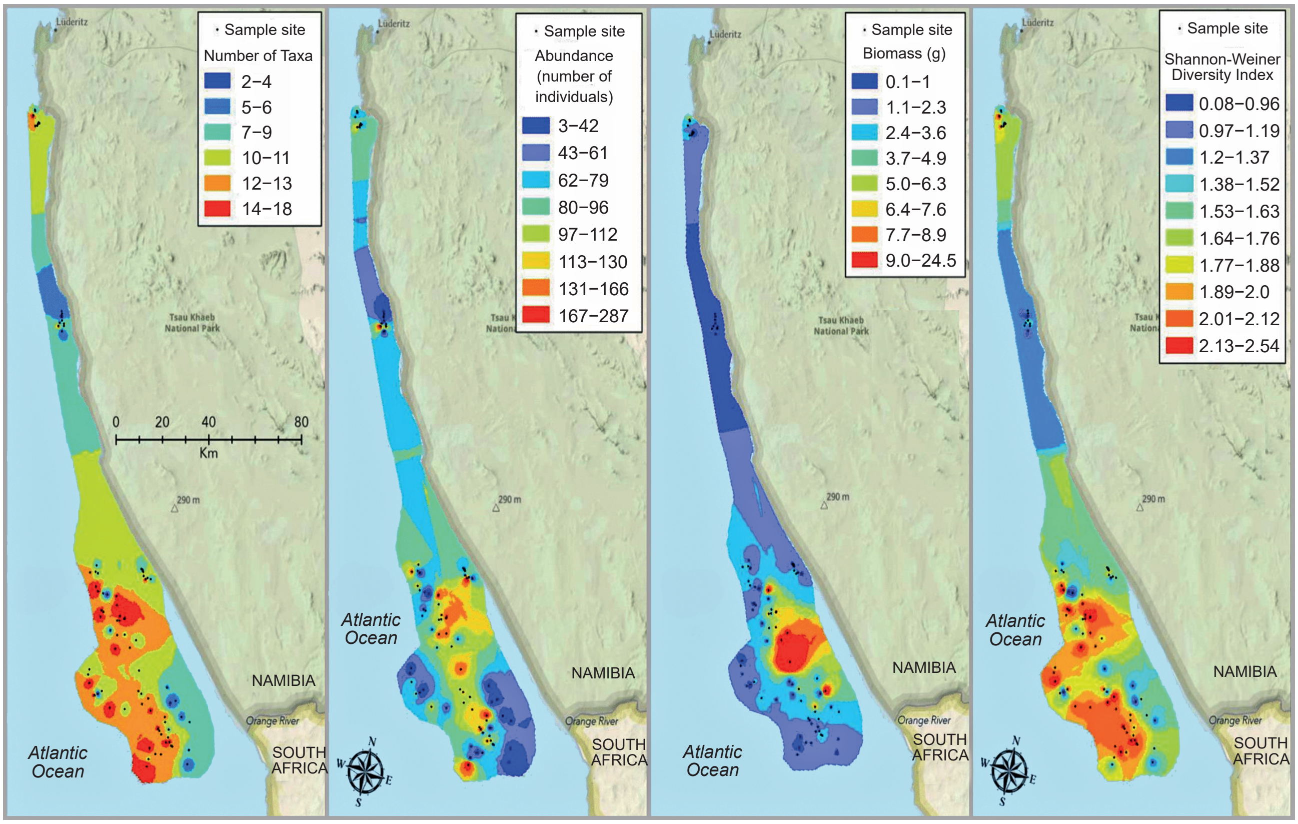

Figure 6: Heat maps displaying the spatial distribution of the total number of polychaete taxa, abundance (no. of ind.), biomass (wet mass g), species richness and Shannon index H' (Shannon, 1948)

lower organic and mud content and higher redox values were recorded inshore than offshore, and this pattern is especially apparent in mudbelt stations where the lowest recorded redox potential values were correlated with the highest percentage mud. The sediments in the mudbelt are mainly of fluvial origin, as Orange River plumes extend as far as 700 km from the river mouth (Rogers and Bremner 1991), with mud becoming more prevalent southward that is further dispersed northwards and westwards by ocean currents (Rogers and Rau 2006; Bluck et al. 2007). In the north and close to shore, sediment is sand dominated, well sorted by wave action and originates predominantly via aeolian transport of terrigenous material from the Namib Desert (Bremner 1981; Rogers and Bremner 1991), while mud, being more mobile, extends over the shelf to partly build up the shelf edge (Bluck et al. 2007). This is consistent with finding higher percentages of mud offshore than inshore, where sandy sediments are prevalent.

Two main polychaete assemblages were observed, separating into inshore and offshore communities. Given their smaller body size the abundance of dominant families (e.g. Spionidae, Cirratulidae) did not equate to a high biomass. Regardless, abundance-based and biomass-based hierarchical clustering analyses yielded similar results. Location, depth and latitude significantly influenced the separation of inshore and offshore polychaete communities. Latitudinal changes at inshore sites appear to be driven primarily by sediment geochemical properties rather than latitude itself. Similarly, Steffani et al. (2015) reported that the influence of latitude on macrofauna community compositions in the inner shelf of southern Namibia was minimal, and instead, attributed it to changes in sediment composition and depth that co-occur with latitude.

Adaptations of polychaete fauna to environmental stressors on the southern Namibian shelf

Significant regional separation of mudbelt sites from Atlantic 1 MLA stations was also apparent (Supplementary Table S6). Low abundance and diversity were detected at mudbelt stations. It is likely that the transportation of sediment from the Orange River disrupts the communities inhabiting the benthos in this area due to the seasonal influx of mud (Rogers and Bremner 1991). Dominant taxa (i.e. more abundant) in mudbelt stations are adapted to hypoxic conditions and the presence of hydrogen sulphide, including *Sigambra parva*, *Pararionospio pinnata*, *Diopatra* cf. *monroi*, and *Nepthys* cf. *hombergii* (Arndt and Schiedek 1997; Zettler et al. 2013; Eisenbarth and Zettler 2016). *Sigambra parva*, for example, is a biodiffuser with activities resulting in the diffusive transport of sediment to oxygenate the sediment (Michaud et al. 2005), while *Nepthys hombergii* has been shown to be adapted to hypoxic conditions by having a high phosphagen (phosphoglycocyamine) content – a primary energy source used during environmental stress or when using anaerobic glycolysis for energy production during hypoxic conditions (Arndt and Schiedek 1997). Additionally, most of the biomass recorded in the central region of Atlantic 1 MLA (108 m to 116 m) was attributed to relatively large polychaetes such as *Diopatra* cf. *monroi* that are equipped with pronounced branchiferous structures to cope with oxygen deficiency (Day 1967; Levin et al. 2009). Similarly, *Diopatra neapolitana capensis* contributed a high percentage of total polychaete biomass in northern Namibia (Eisenbarth and Zettler 2016).

Dominant taxa resulting in the dissimilarity of offshore to inshore stations were predominantly surface deposit feeders, three of which were restricted to inshore stations (e.g. *Prionospio saldanha*, *Ampharete luederitzi*,

Table 4: DistLM results for offshore and inshore polychaete community data and environmental variables. P: probability; Prop: proportion of the variability explained; Cumul: cumulative proportion of the variability explained; res.df: residual degrees of freedom

		Offshore						Inshore				
Marginal	Variables	Pseudo-F	*p*	Prop.			Variable	Pseudo-F	*p*	Prop.		
Test	%GRAVEL:	14.35	0.001	0.03			%GRAVEL:	4.51	0.003	0.02		
	%SAND:	104.65	0.001	0.16			%SAND:	30.62	0.001	0.11		
	%MUD:	105.81	0.001	0.17			%MUD:	34.17	0.001	0.12		
	Latitude	4.58	0.003	0.01			Latitude	35.19	0.001	0.13		
	Depth	83.23	0.001	0.14			Depth	8.29	0.001	0.03		
	TOC	69.96	0.001	0.12			TOC	25.40	0.001	0.09		
	TON	87.10	0.001	0.14			TON	27.76	0.001	0.10		
	Redox	12.60	0.001	0.02			Redox	62.18	0.001	0.20		
Sequential	Variables	Pseudo-F	*p*	Prop.	Cumul.	res.df	Variables	Pseudo-F	*p*	Prop.	Cumul.	res.df
Test	%Mud	105.81	0.001	0.17	0.17	531	Redox	62.18	0.001	0.20	0.20	242
	Depth	74.13	0.001	0.10	0.27	530	%SAND:	12.77	0.001	0.04	0.24	241
	TON	22.97	0.001	0.03	0.30	529	Depth	17.85	0.001	0.05	0.30	240
	TOC	8.97	0.001	0.01	0.31	528	TON	10.70	0.001	0.03	0.33	239
	%Sand	7.02	0.001	0.01	0.32	527	%GRAVEL:	7.52	0.001	0.02	0.35	238
	Latitude	5.49	0.001	0.01	0.33	526	Latitude	7.75	0.001	0.02	0.37	237
	Redox	4.56	0.001	0.01	0.33	525	TOC	4.85	0.001	0.01	0.38	236

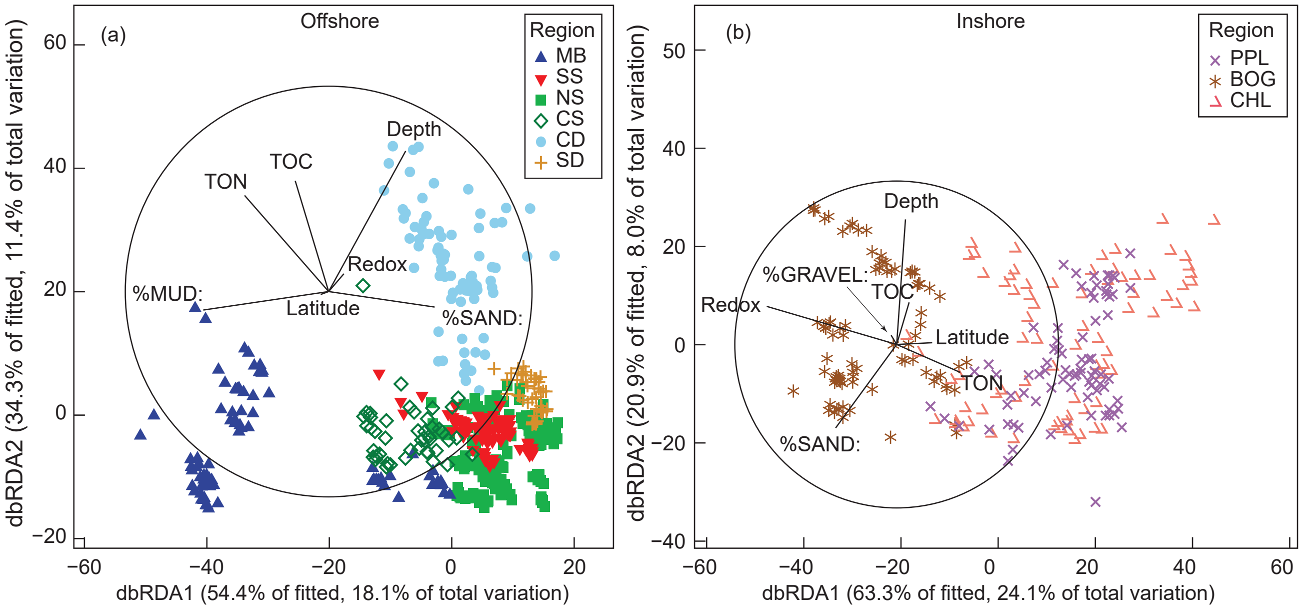

Figure 7: Distance-based redundancy analysis (dbRDA) of (a) offshore polychaete communities and (b) inshore polychaete communities. Vector showing the direction and strength of the environmental variables which significantly explained faunal variations, include: sediment composition (percentage mud, sand and gravel), water depth (m), latitude, redox potential (mV), TOC (Total Organic Carbon) and TON (Total Organic Nitrogen). Acronyms to regions – BOG: Bogenfels, CHL: Channel, PPL: Purple, MB: Mud Belt, NS: North Shallow, CS: Central Shallow, CD: Central Deep, SS: South Shallow and SD: South Deep

Magelona sp.), whereas offshore stations included a mixture of carnivores and deposit feeders. Although it has been found that the inner shelf of southern Namibia is dominated by habitat generalists (Steffani et al. 2015) with only a few species restricted to inshore areas, our results indicate a tendency for a dominance of deposit feeders inshore that transition to carnivores and deposit feeders offshore. It was previously found that on the Campeche Bank of the southern Gulf of Mexico, depth was the main factor influencing the distribution of feeding guilds of benthic polychaetes rather than sediment type (Castanedo et al. 2012). Similar to our results, Castanedo et al. (2012) also reported the presence of deposit feeders at sandy stations. This finding contrasts with the general assumption that deposit-feeders are more abundant in muddy habitats, and rather supports our finding that depth is the most important driver of polychaete feeding guilds in southern Namibia. It is also possible that predatory feeding behaviour further up the shelf could be the result of increased fluctuation in food sources occurring closer to the shelf edge (Wieking and Kröncke 2003; Eisenbarth and Zettler 2016). Although some species can modify their trophic habits in response to food availability (Castanedo et al. 2012), there is a clear pattern of trophic separation from shallow to deeper areas, suggesting an environmental influence on the trophic strategies adopted by benthic polychaetes on the shelf.

Conclusions

In general, polychaete communities off southern Namibia were significantly driven by depth, sediment composition, latitude, redox potential and organic content. However, sediment composition predominantly explained the variation observed in offshore polychaete community structure, mainly due to muddier sediment at mudbelt sites. Inshore variation in polychaete community structure was primarily explained by redox potential separating BOG from PPL and CHL. Although sediment texture is largely accepted as a key factor in influencing community structure (Arrighetti and Penchaszadeh 2010; Sobczyk et al. 2021; Sobczyk et al. 2023), the relationship between sediment composition and macrofaunal communities is not always clear (Steffani et al. 2015 and references therein), while additional environmental drivers have been found to influence macrozoobenthic communities, including temperature, hydrogen sulphide, sedimentation rates, dissolved oxygen and biological interactions (i.e. competition, niche partitioning, reproduction, settlement) (Chou et al. 2004; Wlodarska-Kowalczuk et al. 2004; Steffani et al. 2015; Eisenbarth and Zettler 2016; Donnarumma et al. 2019; Aliakbarian et al. 2020; Lamarque et al. 2022, Saeedi et al. 2022; Amorim and Zettler 2023). It is likely that differences between offshore and inshore polychaete communities are also a result of unmeasured variables that have been shown to influence benthic communities elsewhere.

Overall, the heterogeneity of this environment makes it challenging to determine the environment's influence on polychaete communities on the shelf that is also affected temporally (Martí et al. 2007; Aneiros et al. 2018; Kim and Yu 2021). It is suggested that increased sampling at greater depths, range of latitudes and temporal scales together with continuous in-situ measurements of additional environmental parameters (e.g., dissolved oxygen) can further assist in understanding the environmental influence on Namibian Polychaeta. This study has generated an extensive dataset and provides a baseline for further in-depth research on polychaete communities within the region (see Sobczyk et al. 2023). Here, we broadly contextualise the spatial patterns of Namibian Polychaeta on the southern continental shelf and demonstrate the importance of including genetic barcoding in future taxonomic and biogeographic research. Indeed, we have shown that the application of genetic barcoding is essential for distinguishing putative cosmopolitan species from those that have wide local distributions. Future studies should acknowledge these problematic taxa to prevent perpetuating potential errors in the distribution records of southern African Polychaeta and the use of genetic barcodes where possible.

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