Science of the Total Environment 957 (2024) 176794

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Review

Deep-sea ecosystems of the Indian Ocean >1000 m

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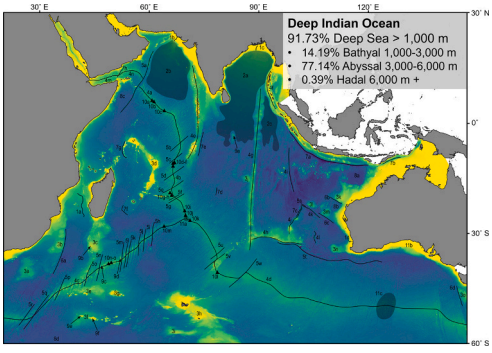
HIGHLIGHTS

- Over 90 % of the Indian Ocean is deeper than 1000 m but deep sea remains unknown.
- Biological research reviewed for deep-sea ecosystems of the Indian Ocean.
- Historical, socioeconomic, geological, and oceanographic research backgrounds presented.
- Ecosystem knowledge summaries provided for each major seafloor feature.
- Data gaps identified and four outstanding problems presented for future studies.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Olga Pantos

Keywords:
Indian Ocean
Deep sea
Benthic ecology
Seafloor geomorphology
Knowledge gaps

ABSTRACT

The Indian Ocean is the third largest of the world's oceans, accounting for ~20 % of the global marine realm. It is geomorphologically complex, hosting a wide variety of ecosystems across basins, trenches, seamounts, ridges, and fracture zones. While modern exploration has contributed significantly to our knowledge of its coastal ecosystems, deeper waters (>1000 m) remain relatively unknown despite accounting for over 90 % of its total area. This study provides the first comprehensive review of the Indian Ocean's diverse deep sea, presenting ecosystem knowledge summaries for each major seafloor feature, contextualised with the broader historical, socioeconomic, geological, and oceanographic conditions. Unsurprisingly, some ecosystems are better characterised than others, from the relatively well-surveyed Java (Sunda) Trench and hydrothermal vents of the Carlsberg, Central and Southwest Indian Ridges, to the unexplored Southeast Indian Ridge and hadal features of the western Indian Ocean. Similarly, there is a large depth discrepancy in available records with a clear bias towards shallower sampling. We identify four outstanding problems to be addressed for the advancement of deep-sea research in the Indian Ocean: 1) inconsistencies in research extent and effort over spatial scales, 2) severe lack of data over temporal scales, 3) unexplored deep pelagic environments, and 4) a need to place the Indian Ocean's deep-sea ecosystems in a global context. By synthesising and championing existing research, identifying knowledge gaps, and presenting the outstanding problems to be addressed, this review provides a platform to ensure this forgotten ocean is prioritised for deep-sea research during the UN Ocean Decade and beyond.

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https://doi.org/10.1016/j.scitotenv.2024.176794
Received 7 May 2024; Received in revised form 21 September 2024; Accepted 5 October 2024
Available online 18 October 2024
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1. Introduction

The Indian Ocean spans an area of 71,729,338 km^2, of which ~92 % is deep sea >1000 m (Table 1). It is the third largest of the world's oceans and is second only to the Pacific in its proportion of deep-sea area. Despite this, it is the least understood of the oceans, having been largely neglected scientifically until the late-1950s (Rogers, 2017). Modern exploration has greatly contributed to our knowledge of coastal biodiversity, yet its deeper waters (>1000 m) are still relatively unknown (Demopoulos et al., 2003; Wafar et al., 2011). Earlier reviews of deep Indian Ocean research have primarily focussed on the benthic communities of continental margins, slopes, and abyssal plains (Neyman et al., 1973; Demopoulos et al., 2003; Ingole and Koslow, 2005). Ramiro-Sánchez et al. (2023) further highlighted the data paucity for deep-sea habitats in the southern Indian Ocean, with many studies limited to the northwest and central regions (e.g. Wafar et al., 2011; Saraswat et al., 2022). As a result, the Indian Ocean is lacking a definitive baseline for deep-sea biodiversity research to inform future exploration and achieve the goals of the United Nations (UN) Decade of Ocean Science for Sustainable Development (2021–2030).

Here we provide a review of the deep-sea ecosystems of the Indian Ocean >1000 m, contextualised with geological and oceanographic conditions that collectively form this 20 % of the global ocean. We first provide background on the historical, socioeconomic, geological, oceanographic, and broad-scale biodiversity trends related to deep Indian Ocean research, then we present in-depth knowledge summaries for each major seafloor feature in terms of deep-sea ecosystems. Through this, we will identify knowledge gaps and present the outstanding problems that should be addressed for the advancement of deep-sea research in the Indian Ocean. A map of all major Indian Ocean seafloor features is presented in Appendix 1 (see Supplementary data) as a companion guide for this review. The aim is to provide a platform for future studies, to ensure this forgotten ocean is prioritised for deep-sea research during the Ocean Decade and beyond.

2. Geographical boundaries and data sources

The geographic extent of the Indian Ocean is defined here following Harris et al. (2014), modifying the boundaries set by 'The Limits of Oceans and Seas' (International Hydrography Organisation, 1953) to include bounding marginal seas and exclude Southern Ocean waters south of 60°S. The Indian Ocean is bordered to the north by the northern limits of the Red and Arabian Seas, and the Bay of Bengal; to the east by the Andaman Sea and Java Trench, the easterly limits of the Timor and Arafura Seas, and down the 146°55′ meridian from the southern point of Tasmania; to the south by the 60°S parallel of the Southern Ocean; and to the west by the 20°E meridian running from Cape Agulhas, South Africa. The Persian Gulf to the north of the Indian Ocean was excluded from this review as its maximum depth is <100 m. Names of seafloor features were verified following the IHO-IOC GEBCO Gazetteer of Under Sea Feature Names (GEBCO). Where features are not listed by GEBCO, names were aligned with the US BGN Advisory Committee on Undersea Features (ACUF).

Maps were produced in QGIS (v 3.32.2) using GEBCO_2023 bathymetric data and shapefiles downloaded from the following online repositories: shapefiles for the extent of the Indian Ocean and the national jurisdiction boundaries (EEZs) of Indian Ocean countries from marineregions.org (Flanders Marine Institute, 2023, https://marineregions.org/downloads.php, accessed 05/10/2023); marine protected areas from protectedplanet.net (https://www.protectedplanet.net/en/thematic-areas/marine-protected-areas, accessed 01/11/2023); and deep-sea mining contracts for areas beyond national jurisdiction from the International Seabed Authority webpage (https://www.isa.org.jm/exploration-contracts/maps/, accessed 11/10/2023). Bathymetric contour layers were used to generate polygons of areas exceeding 6000 m depth to determine the area and maximum depths of Indian Ocean hadal features, excluding polygons <2 km^2 for quality control. Note that these estimations are subject to variation based on the use of different map projections for GIS computations and are regularly updated with the availability of new, higher quality data (Stewart and Jamieson, 2018). Spatial analysis to determine the total area and proportion of different depth ranges across the Indian Ocean was conducted in ArcPro (v 3.0) using the Mollweide projection.

To study broad-scale sampling effort and biodiversity patterns in the Indian Ocean, data were downloaded from the open-access Ocean Biodiversity Information System (OBIS) mapper (https://mapper.obis.org/, accessed 15/11/2023). OBIS is the most complete and comprehensive open-access data repository on the biogeography of marine taxa, with access to 123 million records from over 5000 datasets (https://obis.org/; Vanden Berghe et al., 2010). Data were filtered for records >1000 m depth and for the following areas: Arabian Sea, Red Sea, Bay of Bengal, Andaman Sea, Arafura Sea, Timor Sea, Great Australian Bight, Laccadive Sea, Gulf of Aden, Mozambique Channel, Persian Gulf, Gulf of Oman, Indian Ocean, ABNJ: Indian Ocean, Gulf of Aqaba, and Gulf of Suez. The resulting 65,604 records were imported to R Studio (v 2023.09.1) for data manipulation and visualization. Data were cleaned to remove non-metazoans, blank records, and to check for erroneous depth records by removing those with depths recorded <1000 or >8000 m (deeper than the maximum depth of the Indian Ocean) and bathymetry recorded <1000 m, leaving 32,257 records. Where data were plotted by taxonomic group, phyla with low numbers of records (<300) were grouped as 'Other'. All figures were edited using Inkscape (v 1.3.2).

These OBIS data have been instrumental in identifying spatial, bathymetric, and ecosystem biases in marine exploration (Webb et al., 2010; Kennedy and Rotjan, 2023). There are, however, significant discrepancies between the open-access OBIS records and available metadata for research cruises, as shown for the Central and South Atlantic (Bridges et al., 2023). This suggests that not all datasets collected during research cruises have been uploaded to OBIS. Nevertheless, in the absence of data completeness, patterns can be derived and interpreted from the available data.

Table 1
Area (km^2) and relative proportion (%) of different depth ranges in the Indian Ocean, calculated using the Mollweide map projection and GEBCO_2023 bathymetry data in ArcPro (v3.0). EEZ: Exclusive Economic Zone, ABNJ: Area Beyond National Jurisdiction.

	Area (km^2)		
	Indian Ocean	EEZs	ABNJ
Total area	70,884,251	24,023,171	46,861,080
Deep sea (>1000 m)	65,023,066 (91.73 %)	18,275,565 (76.07 %)	46,747,501 (99.76 %)
Bathyal (1000–3000 m)	10,060,277 (14.19 %)	6,343,043 (26.40 %)	3,717,234 (7.93 %)
Abyssal (3000–6000 m)	54,683,224 (77.14 %)	11,842,225 (49.30 %)	42,840,999 (91.42 %)
Hadal (6000 m+)	279,565 (0.39 %)	90,297 (0.38 %)	189,268 (0.40 %)

3. Historical background

The first scientific study of the Indian Ocean began with the 19th century European expeditions. The *HMS Challenger Expedition* (1872–1876) contributed relatively little to scientific knowledge of the deepwater ecosystems of the Indian Ocean as it surveyed circumpolar waters south of the polar front. The later German *Valdivia Expedition* (Deutsche Tiefsee-Expedition) (1898–1899) covered a large part of the Indian Ocean and sampled deep-sea benthic fauna from depths up to 2490 m. The first half of the 20th century saw more European mounted expeditions surveying the Indian Ocean and providing some insights in deep-sea biodiversity, including the fourth Danish *Dana Expedition* (1928–1930), the Anglo-Egyptian *John Murray Expedition* (1930s) which yielded some samples of deep-sea bivalves (Knudsen, 1967), and the

Swedish *Albatross Expedition* (1947–1948), which collected deep benthic samples and sediment cores. The Danish *Galathea* (1950–1952) provided trawl samples from lower abyssal and hadal fauna in the west and central Indian Ocean. Trawling data from Soviet-led expeditions on the *R/V Vityaz* added to knowledge on bathyal and abyssal organisms (Bezrunov, 1963).

Deep-sea sampling on these early cruises was relatively opportunistic and the *International Indian Ocean Expedition* (IIOE 1960–65) was the first comprehensive international effort dedicated to improving knowledge on the Indian Ocean including its deep ecosystems, with ship time provided by 40 vessels from over 20 nations (Zeitzschel and Gerlach, 2012). Subsequently, and among others, the Royal Society *Indian Ocean Deep Slope Fishing Expedition* (1969) explored deep-slope resources in the Indian Ocean (Forster et al., 1970), Soviet/Ukrainian research institutes including YugNIRO led deep-sea fisheries explorations on plateaus, seamounts and ridges in the Indian Ocean (1970s–1980s; Budnichenko et al., 1997, Romanov, 2003, Parin et al., 2008), French expeditions to the Indian Ocean involved some deep-sea studies in the 1970s (e.g. *BENTHEDI Expedition*, Thomassin, 1977, Poupin, 2015), and the Netherlands *Indian Ocean Expeditions* explored deep-sea environments in the northern Arabian Sea and western Indian Ocean (1992–1993; van Weering et al., 1997). Roberts et al. (2020) provide a more detailed summary of historical fisheries and seamount exploration in the Indian Ocean. The *Second International Indian Ocean Expedition* (IIOE-2) (Hood et al., 2016) was initiated approximately 60 years after the conclusion of IIOE with a running time between 2015 and 2025.

Further international drilling project collaborations including the Deep Sea Drilling Project (1968–1983) and IODP (2013–2023) frequented the Indian Ocean deep sea, but were mainly geologically focussed. On the ecological side, the Census of Marine Life (CoML) had five deep-sea projects which were largely focused on the Atlantic but included Indian Ocean research on abyssal plains (CeDAMar – Stuart et al., 2008, Ebbe et al., 2010), seamounts (CenSeam – Consalvey et al., 2010, Stocks et al., 2012), chemosynthetic environments (ChEss – Baker et al., 2010, German et al., 2011), continental margins (COMARGE – Menot et al., 2010) and mid-ocean ridges (MAR-ECO – Bergstad et al., 2008).

Of the contemporary research cruises in the Indian Ocean, those targeting depths >1000 m remain the minority. However, important contributions to knowledge on Indian Ocean deep-sea biodiversity has come from cruises on national and private research vessels (e.g. Ingole and Koslow, 2005, Rogers and Taylor, 2011, Trotter et al., 2021, Zhou et al., 2022, Bond et al., 2023).

4. Socioeconomics and management

Approximately one-third of the Indian Ocean lies within the Exclusive Economic Zones (EEZs) of 36 countries, 76 % of which is deep sea >1000 m (Table 1, Fig. 1). Thirty of these countries have deep sea >1000 m within their EEZ, 21 have abyssal depths >3000 m, and only Indonesia and Australia have hadal depths >6000 m (Table 2, Bond and Jamieson, 2022). The governance of deep-sea environments within these EEZ is the responsibility of the countries that hold national jurisdiction over these areas (Table 2). However, access to assets such as vessels, research equipment, and funds for deep-sea exploration and research is low for Indian Ocean countries, despite the broad view that deep-sea environments are important across the region (Bell et al., 2023; Talma, 2022). Collaborations with the deep-water oil and gas industry have occasionally provided a platform for deep-sea exploration for countries with limited capacity (Gates et al., 2017a).

In Tanzania, ecological data collected as part of the SERPENT project (Scientific and Environmental ROV Partnership using Existing iNdustrial Technology) provided the basis for recommendations on the sustainable use of deep-sea resources and marine spatial management (Gates et al., 2021). Such partnerships have also facilitated the discovery of new biodiversity and interesting ecological observations, highlighting the

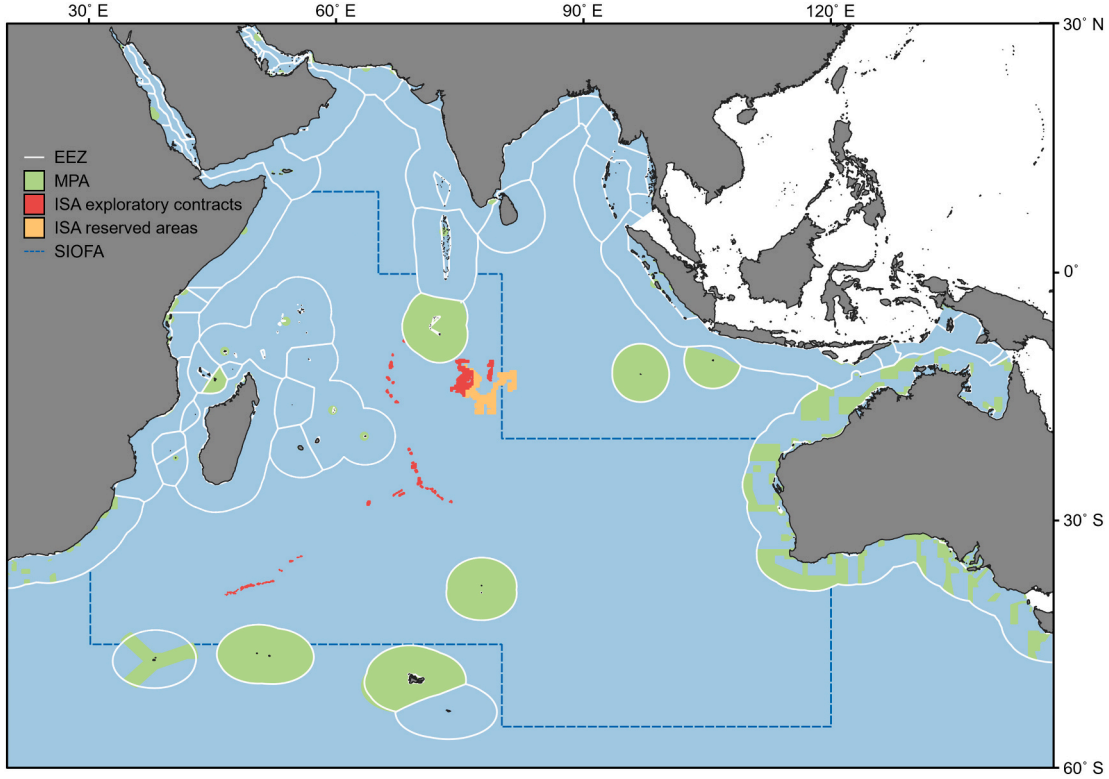

Fig. 1. Map of the Indian Ocean with exclusive economic zone (EEZ) boundaries of neighbouring countries (white lines), SIOFA management area (blue dashed lines), established marine protected areas (MPAs, green polygons), and International Seabed Authority (ISA) exploratory mining contracts (red polygons) and reserved areas (orange polygons). The blue area defines the limits of the Indian Ocean.

Table 2
Countries and their territories bordering the Indian Ocean and the depth classifications of their Exclusive Economic Zones. Bathyal: 1000–3000 m, abyssal: 3000–6000 m, hadal: >6000 m.

Countries and territories	Bathyal	Abyssal	Hadal
Australia°	X	X	X
- Christmas Island			
- Cocos (Keeling) Island			
- Heard and McDonald Islands			
Bahrain#	–	–	–
Bangladesh°	X	–	–
Chagos Archipelago*	X	X	
Comoros	X	X	–
Democratic Republic of Timor-Leste°	X	X	–
Djibouti	X	–	–
Egypt#	X	–	–
Eritrea#	X	–	–
Federal Republic of Somalia	X	X	–
France°	X	X	–
- French Southern and Antarctic Lands*			
- Mayotte			
- Réunion			
India	X	X	–
- Andaman and Nicobar			
Indonesia°	X	X	X
Iran	X	X	–
Iraq#	–	–	–
Israel#	–	–	–
Jordan#	–	–	–
Kenya	X	X	–
Kuwait#	–	–	–
Madagascar	X	X	–
Maldives	X	X	–
Mozambique	X	X	–
Myanmar	X	X	–
Oman	X	X	–
Pakistan	X	X	–
Papua New Guinea	–	–	–
Qatar#	–	–	–
Republic of Mauritius°	X	X	–
Saudi Arabia#	X	–	–
Seychelles°	X	X	–
South Africa	X	X	–
- Prince Edward Islands			
Sri Lanka	X	X	–
Sudan#	X	–	–
Tanzania°	X	X	–
Thailand	X	–	–
United Arab Emirates#	X	–	–
Yemen	X	X	–

*Disputed territory, #Red Sea or Persian Gulf only, °Signatories of BBNJ Treaty
Note that the French Southern and Antarctic Lands comprise the Crozet, Kerguelen, Saint Paul and Amsterdam, and Scattered Islands, and Adélie Land.

importance of deep-sea exploration in these areas (Moore and Gates, 2015; Gates, 2016; Gates et al., 2017b; Macreadie et al., 2018). Meanwhile, India has been working to expand its deep-sea research as part of its Deep Ocean Mission to explore and exploit the deep sea both within its EEZ and beyond (Atmanand, 2019). National collaborations with independent research institutes also increasingly provide a window into deeper waters and support national research agendas for EEZs, though biological observations predominantly remain limited to depths <1000 m (e.g. Monaco Explorations, 2022, Nekton Maldives Expedition, 2024, Ahusan et al., 2023, OceanX Seychelles Expedition, 2024). However, given the narrow continental shelves of many countries bordering the Indian Ocean, deep sea >1000 m is part of many EEZs. Partnerships, knowledge exchange, and capacity building support a comprehensive understanding of deep-sea habitats and biodiversity within EEZs and achieve national priorities as well as the aims of international agreements (Woodall et al., 2021).

Areas beyond national jurisdiction (ABNJ) comprise the other two-thirds of the Indian Ocean, almost 100 % of which is deep sea >1000 m (Table 1). This part of the seafloor, known as the 'Area', is governed by the International Seabed Authority (ISA) which was established under the United Nations' Convention on the Law of the Sea (UNCLOS) in 1994 (Thompson et al., 2018). Some factors impeding research effort for Indian Ocean ABNJ include the greater distance from shore, requiring significant funding and access to larger vessels, and a lack of incentive for research without direct national benefits. It is for these reasons that the southern Indian Ocean remains one of the least explored regions in the world (Ramiro-Sánchez et al., 2023). Yet the Area is also the target for emerging industries such as deep-sea mining. The ISA have granted four mining exploration contracts for polymetallic sulfides along the southwest, central, and southeast Indian ridges, as well as one contract and one reserved area for polymetallic nodules in the Mid-Indian Ocean Basin (ISA, 2022a, 2022b, Fig. 1). Two of these mining exploration contracts are held by the Government of India, yet the other three are held by countries that do not hold any national jurisdiction in the Indian Ocean, and no other ISA deep-sea mining contracts are held by Indian Ocean countries. Conversely, no established mining contracts exist for cobalt-rich ferromanganese crusts (CFC) in the Indian Ocean.

Marine conservation and sustainable management of marine resources is essential across the deep-sea environments of both EEZs and ABNJ. In EEZs, several marine protected areas (MPAs) have been designated in the Indian Ocean, the majority of which include depths >1000 m (Fig. 1). However, these MPAs offer varying levels of protection from anthropogenic threats such as fishing and mining (Grorud-Colvert et al., 2021) and are not necessarily effective conservation measures for deep-sea environments without full consideration of potential impacts (Thomas et al., 2021b) and management capacity. The recent finalisation and adoption of Biodiversity Beyond National Jurisdiction (BBNJ), a treaty which also sits within the framework of UNCLOS, was a promising step towards the conservation and sustainable management of marine biodiversity in ABNJ, including deep-sea environments (Mendenhall et al., 2023). However, the BBNJ treaty now requires ratification and adoption by the 83 member states who have signed the agreement to date, including only eight Indian Ocean countries (UN, 2023, Table 2), thus its effective implementation is not yet guaranteed.

The Indian Ocean is of high interest to commercial fisheries and fishing operations, some of which extend into waters >1000 m (Georgeson et al., 2020), though mainly concentrated on the ridges and seamounts in the southern part of the Indian Ocean (Clark et al., 2007). Most commercial deep-water fisheries have historically developed in these ABNJ without stock size and fishing effort assessments (Rogers et al., 2017), though some have been supplemented by research surveys and scientific monitoring (Romanov, 2003, Marsac et al., 2020a, b). Regional Fisheries Management Organizations (RFMOs) provide frameworks to manage fishing activity, including in ABNJ. The Southern Indian Ocean Fisheries Agreement (SIOFA) is an RFMO with 13 member entities and is responsible for the management of deep-water fishing activity in the Southern Indian Ocean including in ABNJs (Shotton, 2006, SIOFA Secretariat, 2023a, 2023b). The SIOFA has established 5 interim benthic protected areas (BPAs) - areas closed to bottom or midwater fishing due to their unique biodiversity value - and is actively undertaking research into the establishment of new protected areas (Ramiro-Sánchez et al., 2023; SIOFA, 2023). In addition, the Southern Indian Ocean Deep-Water Fisheries Operators Association (SIODFA), an industry-led body representing the interests of deep-sea fishing operators and an observer to SIOFA, has delimited 11 voluntary BPAs (Shotton, 2006, SIODFA Secretariat, 2016).

5. Geological history

The initial formation of the Indian Ocean is linked to the break-up of the Gondwana super-continent when Africa–South America (West Gondwana) separated from Madagascar–Greater India–Antarctica–Australia (East Gondwana) during the Middle Jurassic (~175 Ma) (Fig. 2; Schettino and Scotese, 2005, Müller et al., 2019). As

India-Madagascar continued to rotate south from Africa, the early rifting between the eastern and western Gondwana landmasses had developed into seafloor spreading within the Mozambique and Somali basin systems and the Davie Fracture Zone acted as the major transform fault to separate these two basins. Therefore, these regions recorded the oldest ocean floor in the Indian Ocean (Davis et al., 2016). Seafloor spreading between Africa and East Gondwana continued until the Early Cretaceous at ~120 Ma and the landmass continued to be broken into blocks of various sizes (Fig. 2; Gibbons et al., 2013). As a result, East Gondwana fragmented into the India-Madagascar-Sri Lanka-Seychelles dominated plate in the northwest and the unified Australian–Antarctic Plate in the southeast. Then, Greater India began separating from Australia's western margin, and subsequently unzipped from Antarctica at around ~120 Ma. This northward motion and anticlockwise rotation of Greater India created the Naturaliste, Wallaby–Zenith, and Exmouth plateaus and associated fracture zones during the drift. In the mid-Cretaceous period, there was increasing magmatic activity in the region, related to the development of the Kergulen Large Igneous Province from ~120 to 110 Ma, and formed the Kerguelen Plateau and the Broken Ridge (Fig. 2; Frey et al., 2000). The continued northward movement of the Indian plate caused the separation of Madagascar from the Indian continent during the Late Cretaceous (~90–85 Ma) and Neotethys became narrower. At the same time, there was a significant plate reorganization and an increase in the spreading rates along the Central and Southeast Indian Ridges (Scotese et al., 1988). Rifting was also initiated in the southwestern boundary between the Australia and Antarctica plates.

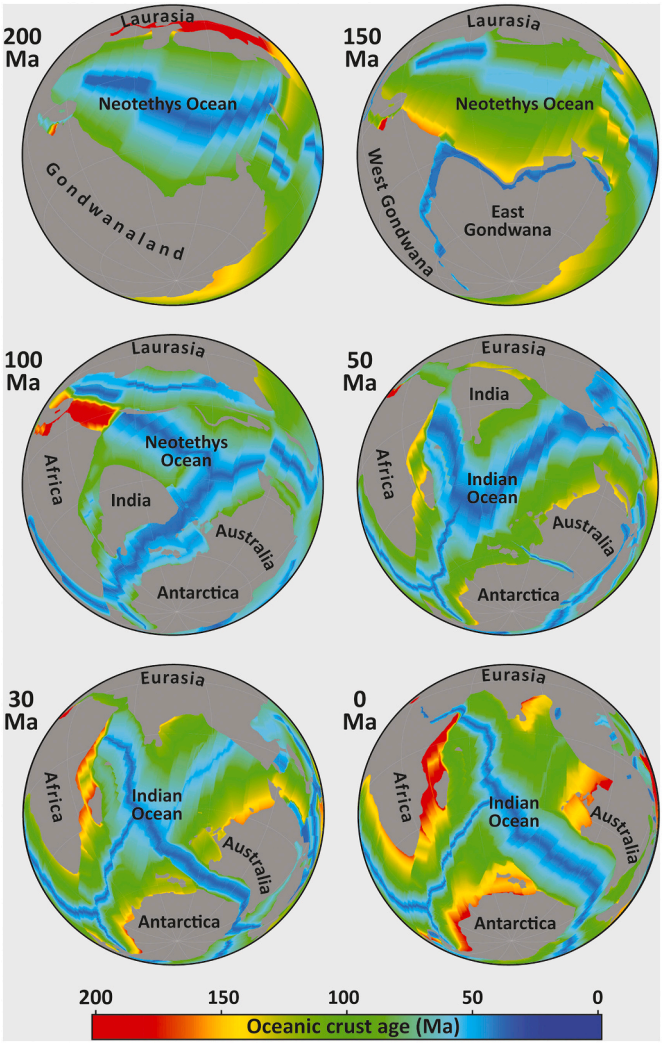

Fig. 2. Oblique view of the oceanic crustal age of the Indian Ocean region since 200 Ma to present day, showing the break-up of Eastern Gondwana continent and opening of the Indian Ocean. Images created using gPlates software (https://www.earthbyte.org/category/resources/software-workflows/pygplates/). Base maps are from Müller et al., 2019.

The first collision of the Indian continent with the islands of the south Asian subduction zones occurred, and therefore the northward movement of the Indian continent slowed down in the Early Eocene at ~53 Ma (Fig. 2; Scotese, 2021). Meanwhile, relatively slow seafloor spreading continued and separated Australia from Antarctica, marking the formation of the Indian, Australian, and Antarctic continents in the east Indian Ocean. The relative movement of the Indian and Antarctic plates continues along the transform fault, which is expressed as a deep trough located east of the Ninetyeast Ridge (Levchenko et al., 2021). During the Mid-Ecoene (~40 M) there was the second phase of plate reorganization due to the hard collision of the Indian and Eurasian plates. As the relative movement of the Indian and Australian plates along the transform boundary ceased, they merged into the single Indo-Australian Plate. When the Australian plate began to move rapidly northward during the late Eocene (40–35 Ma), it separated from the Antarctic Plate, and allowed the deep waters from the Indian Ocean to mix with the south Pacific Ocean for the first time through the Tasman Strait (Fig. 2; Hodel et al., 2021).

6. Geomorphology

The ocean can be delimited into different depth zones: the bathyal zone (1000–3000 m), the abyssal zone (3000–6000 m) and the hadal zone (>6000 m). Table 1 summarises the proportion of the Indian Ocean that reaches these depth zones, with over 77 % lying at abyssal depths. On the contrary, hadal depths represent <1 % of the total Indian Ocean area (0.35 %: Harris et al., 2014, 0.39 %: this study, Table 1). Excluding polar regions, which exhibit much lower levels of seafloor roughness, this is the lowest proportion of oceanic basin classified as hadal zone, globally (Harris et al., 2014; Jamieson, 2015). The geomorphological diversity of the Indian Ocean basin is important from an ecological and biological perspective, as different seafloor features are commonly associated with particular habitats (Harris and Baker, 2020).

The Indian Ocean is geomorphologically complex: it comprises 20 major seas and basins intersected by several active ridge systems (Appendix 1, Fig. 3); most notably, the Central Indian Ridge (CIR), Southwest Indian Ridge (SWIR) and Southeast Indian Ridge (SEIR), which meet at the central point of the Rodriguez Triple Junction (RTJ) at ~25.5°S, 70°E (Munschy and Schlich, 1989), dividing the western and eastern Indian Ocean. The topographic complexity of the western Indian Ocean is encapsulated by its diverse range of tectonic boundaries and mid-ocean ridge/fracture zone configurations (Parson and Evans, 2005). The CIR extends northwards from the RTJ, punctuated by several fracture zones including the Flinders, Mary Celeste, Argo, Vema Trench, and Vityaz Fracture Zones (Fisher et al., 1971). The Carlsberg Ridge runs northwest from the CIR to the Owen Fracture Zone (Tao et al., 2013), forming a barrier between the Arabian Sea and the Somali Basin (Fig. 3, Appendix 1). The Arabian Sea hosts the Indus Fan which extends 1500 km into the Indian Ocean from the Indus Canyon at the Pakistan continental shelf break (Clift et al., 2001). Into the Gulf of Aden, the East Sheba Ridge and West Sheba Ridge are offset by the Alula-Fartak Trough (Fournier et al., 2010), with the Red Sea to the northeast.

To the west of the CIR lies the Mascarene Basin, bounded to the east by the Mascarene Plateau, and Madagascar Basin, bounded by the Madagascar Plateau to the west and SWIR to the south (Fig. 3, Appendix 1). The Mozambique Basin is situated south of the Mozambique Channel, with its associated homonymous plateau and escarpment to the west. The ultraslow spreading SWIR extends southwest from the RTJ intersected by numerous fracture zones including the Melville, Discovery II, and Andrew Bain Fracture Zones (Sauter and Cannat, 2010). The

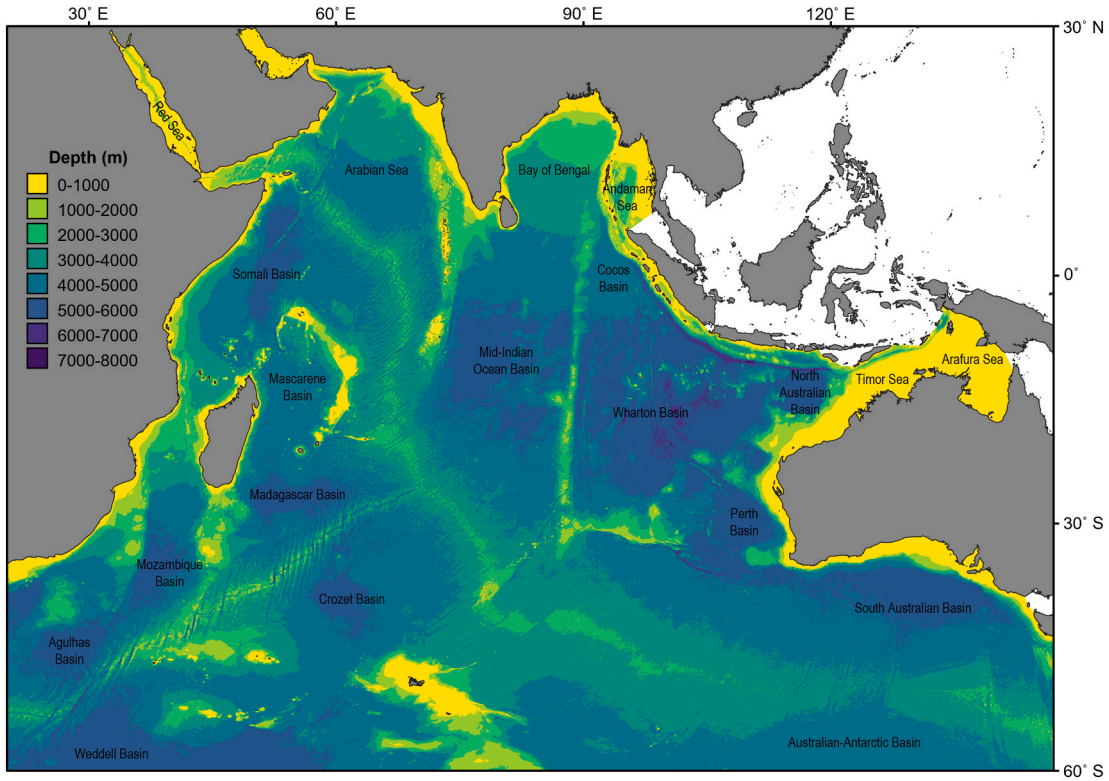

Fig. 3. Bathymetric map of the Indian Ocean with major basins and seas labelled. Note that the Persian Gulf to the north is not included in this study as it is shallower than 1000 m.

Elcano Rise extends west-east between the SWIR and the Crozet Islands, with the Crozet Basin lying to the northeast, bounded by the SWIR, SEIR, RTJ, and the Kerguelen Plateau to the south (Fig. 3, Appendix 1). At the western boundary of the Indian Ocean, the SWIR divides the Agulhas Basin to the north (with its homonymous plateau) from the Weddell Basin to the south, both of which extend beyond the limits of the Indian Ocean, into the Atlantic and Southern Oceans, respectively.

East of the CIR, the aseismic Chagos-Laccadive Ridge divides the Arabian Sea from the Mid-Indian Ocean Basin, running ~2000 km south from the western continental margin of India to ~9°S adjacent to the Vema Trench (Fig. 3, Appendix 1; Parson and Evans, 2005). To the northeast, the largest submarine fan globally, the Bengal Fan, extends 3000 km from the Swatch of No Ground Canyon (ACUF) at its head, along the length of the Bay of Bengal to the northern limits of the Mid-Indian Ocean Basin (Curray et al., 2003). East of this, beyond the Andaman-Nicobar Ridge, lies the marginal Andaman Sea, also known as the Burma Sea. In the Cocos Basin, the smaller Nicobar Fan extends southwards from between the Andaman-Nicobar Ridge and Ninetyeast Ridge (Pickering et al., 2020). The aseismic Ninetyeast Ridge intersects the east Indian Ocean, running almost meridionally for >4500 km from ~7°N, 90.4°E to ~34°S, 87°E and dividing the Mid-Indian Ocean Basin from the Wharton Basin to the east (Fig. 3, Appendix 1; Sclater and Fisher, 1974). At ~15°S, the Osborn Plateau juts out from the western side of the Ninetyeast Ridge, while the Broken Ridge extends to the east at 32.25°S. The eastern Indian Ocean basins are generally much deeper than western Indian Ocean (Fig. 3). The Wharton Basin, for example, is intersected by several north-south directional fracture zones including the so-called Investigator Ridge, resulting in a large number of discrete depressions within the basin reaching hadal depths (>6000 m; Weston et al., 2021, Jamieson et al., 2024).

Extending the length of Indonesia's continental margin, the Java, or Sunda, Trench is the only subduction trench in the Indian Ocean, formed by the subduction of the Indo-Australian Plate beneath the Eurasian Plate (Appendix 1; Jamieson et al., 2022). Its deepest point, and the deepest point in the Indian Ocean, is located in its eastern sector, south of Bali at 11.129°S, 114.942°E (Bongiovanni et al., 2022). At its eastern end lies the North Australian Basin and associated Argo Abyssal Plain, and the Timor Sea and associated Timor Trough (Wei et al., 2023), with the Arafura Sea denoting the eastern limits of the Indian Ocean north of Australia. Southeast of the Wharton Basin is a geomorphologically complex area of seafloor encompassing the Cuvier and Zenith Plateaus, Cuvier Abyssal Plain, Wallaby-Cuvier Escarpment, Lost Dutchmen and East Indiaman Ridges, Brouwer Trough, and the Wallaby-Zenith Fracture Zone (Appendix 1; Weston et al., 2021, Bond et al., 2023). The abyssal Perth Basin is bounded by the above features to the northwest and by the Naturaliste Plateau and Diamantina Fracture Zone to the south. The Diamantina Fracture Zone runs along the southern aspect of Broken Ridge, past Cape Leeuwin to the South Australian Basin, with its deepest point located at Dordrecht Deep (Bongiovanni et al., 2022). The South Australian Basin is enclosed to the north by the Great Australian Bight and separated by the SEIR from the more southerly Australian-Antarctic Basin, which extends from the Kerguelen Plateau to the southeastern boundary of the Indian Ocean (Fig. 3, Appendix 1). The SEIR has fewer named fracture zones than the SWIR and CIR – its most notable are the Geelvinck, Nieuw Amsterdam and Zeewolf Fracture Zones (Ma and Cochran, 1996). The SEIR is however interrupted by a region of anomalous geophysical and geochemical properties between 120° and 128° E, named the Australian-Antarctic Discordance (Sempéré et al., 1991).

7. Oceanographic setting

The Indian Ocean is characterised by unique oceanographic conditions with a profound influence on deep-sea habitats (Demopoulos et al., 2003). From a physical oceanographic perspective, the Indian Ocean has distinct features in the upper ocean layers, setting it apart from other oceans (Phillips et al., 2021). The primary flow regimes in the upper layers are monsoonal-forced circulation of the tropics and northern

hemisphere alongside the subtropical gyre of the south Indian Ocean (Talley et al., 2011). In the deep and bottom waters, the paths of bifurcation are controlled by the complex topography such as deep ridges and mixing with overlying waters.

From a global circulation perspective, the Indian Ocean functions as an upwelling region, much like the Pacific Ocean, and has a greater impact on global climate variability than historically thought (Schott et al., 2009). Over the past decade, higher resolution observations encapsulating broader spatial coverage have improved numeric simulations and provided a clearer picture of the oceanographic processes of the Indian Ocean (Phillips et al., 2021). Additionally, programs such as the second Indian Ocean Expedition (IIOE-2, https://iioe-2.incois.gov.in/IIOE-2/index.jsp), the Global Ocean Observing System for Indian Ocean (IOGOOS, https://incois.gov.in/iogoos/home.jsp) and the Global Ocean Ship-Based Hydrographic Investigations Program (GO-SHIP, https://www.go-ship.org/index.html) have improved our physical and biogeochemical understanding of this poorly understood basin (Hood et al., 2022).

There are major modes of variability which influence the upper layers of the equatorial Indian Ocean on seasonal and interannual timescales. The Madden-Julian Oscillation (MJO) drives thermodynamic responses in the upper Indian Ocean through atmospheric variability causing wind, surface heat flux and rainfall anomalies (Madden and Julian, 1971; Hendon and Salby, 1994; McPhaden and Foltz, 2013). The Indian Ocean Dipole (IOD) can be categorized as a positive or negative event, altering the monsoon season, and influencing global climate (Cai et al., 2009; Ihara et al., 2008). When positive, there is a cold sea surface temperature (SST) anomaly and anomalous upwelling in the southeastern tropical Indian Ocean (Saji et al., 1999, Webster et al., 1999, Horii et al., 2013). When negative, there is a warm SST anomaly in the southeastern tropical Indian Ocean and a cold SST anomaly in the central-western Indian Ocean (Horii et al., 2013). Wyrtki jets are semi-annually occurring narrow currents that flow eastward along the equator during inter-monsoonal periods (Wyrtki, 1973, Schott and McCreary, 2001, Nagura and McPhaden, 2010). Their structure causes a thermocline depression on the eastern side of the basin and uplift in the western basin (Wyrtki, 1973; Wiggert et al., 2006). Combined, these physical mechanisms impact biogeochemical processes at basin-wide scales in the upper Indian Ocean by impacting primary production and chlorophyll maximum depths, altering biological productivity, and therefore impacting higher trophic levels (Wiggert et al., 2006, Prasanna Kumar et al., 2012, Strutton et al., 2015). These changes in the biological productivity of the upper Indian Ocean in turn affect the influx of particles to the deep sea and as such the food availability at the deep seafloor (McCreary et al., 2013; Hood et al., 2017).

There is no high-latitude ocean cooling due to the Asian continental border at 30°N, driving monsoon dynamics to play a key role in shaping ocean circulation. Strong and seasonally reversing monsoon winds (northeast in boreal summer and southwest in boreal winter), drive many changes in the Indian Ocean (Vinayachandran et al., 2018). For example, reversal of western boundary currents (Zang et al., 2021), enhanced biological productivity (Thushara and Vinayachandran, 2016), and changes in the mixed layer depth (Kara et al., 2003). The Indian Ocean connects to the Pacific Ocean through the Indonesian Archipelago, forming the Indonesian Throughflow. Excess heat is transferred from the western Pacific Ocean to the eastern Indian Ocean (Schneider, 1998; De Deckker, 2016), creating a north-south density gradient that drives eastward surface currents between Australia and Madagascar and generates a uniquely southward-flowing eastern boundary current along Western Australia, the Leeuwin Current (Feng et al., 2015).

Off the continental shelf, complex topographic ridges separate the Indian Ocean into basins (Fig. 3, Appendix 1), generating intense mixing at the basin boundaries, contributing to internal wave energy generation (Scott et al., 2011; Huussen et al., 2012), and ultimately supporting meridional overturning circulation (Sloyan, 2006). The overturning of water mass in the Indian Ocean is driven by the lack of a northern deep-water source, resulting in net northward inflow in the cool deep water from the south, and outflow in the upper ocean, evident in the water mass properties at depth (Fig. 4). Circumpolar Deep Water (CDW) fills into the greater deep Indian Ocean as deep western boundary currents in the Crozet Basin, Central Indian Ocean Basin, and Perth Basin (Toole and Warren, 1993). North Atlantic Deep Water (NADW) enters the south-western Indian Ocean from the South Atlantic, driven by the topographic of the Madagascar Ridge and Mozambique Channel (Toole and Warren, 1993). Principle flows below 3500 m are northward along the deep channels leading to the Arabian Sea and the Bay of Bengal. In the Cape and Agulhas basins, there are isolated cyclonic flows around 4500 m (Reid, 2003). These water mass movements enable upwelling of the lower meridional overturning circulation (MOC) from abyssal waters through diffusive mixing and export the largest poleward heat flux of all Southern Hemisphere basins, contributing to global climate variability (Schott et al., 2009; Roxy et al., 2014).

8. Broad-scale biodiversity patterns

Mapping the available, cleaned OBIS data for metazoan occurrence records >1000 m in the Indian Ocean (32,257 records) highlights the regions that have been well versus poorly sampled (Fig. 5). There is a clear pattern of greater sampling effort along continental margins, particularly around India, within the Bay of Bengal, and south of Australia (Fig. 5a). There are also clusters of records for ABNJ that are of particular interest and have been targeted by research cruises such as in the Mid-Indian Ocean Basin, around the Crozet Plateau, at the Madagascar Plateau, and along the Southwest Indian Ridge (see subsequent knowledge summaries for abyssal plains and seamounts). Equally, there are large areas of the Indian Ocean that are seemingly void of sampling, especially in the southeast, however, this may simply be a symptom of collected data not being uploaded to OBIS. It is possible to see specific sampling transects from the data (Fig. 5b), for example the majority of Chaetognatha records appear to follow straight lines from north to south that can be attributed to the sampling transects of the first International Indian Ocean Expedition (IIOE). Similarly, clusters of annelid, arthropod, and echinoderm records in the Mid-Indian Ocean Basin can be attributed to India's research program to explore the basin's polymetallic nodule field (see IndOBIS database, https://indobis.in/). Arthropods make up a large proportion of the available records, especially in the northern Indian Ocean and Red Sea, while a high number of chordates have been recorded off southeast Australia, primarily by Australia's Commonwealth Scientific and Industrial Research Organisation (CSIRO) (Fig. 5b). These records off southern Australia can be attributed to the Great Australian Bight Research and Deepwater Marine programs, comprising six research cruises to the area between 2013 and 2017 (see subsequent summary for continental margins).

There is a clear bias towards shallower sampling, with the vast majority (>24,000) of deep Indian Ocean metazoan records from bathyal depths between 1000 and 3000 m (Fig. 6), compared to almost 8000 records from abyssal depths and only 66 records from hadal depths. Furthermore, there are no Porifera records from >6000 m, nor hadal records for other phyla such as Ctenophora (Fig. 6), despite the known existence of sponge and ctenophore species at these depths (Jamieson et al., 2022, Jamieson et al., 2023; see subsequent summary for subduction trenches). While this may be due to the lack of open-access data, the decrease in sampling effort with increasing depth is a well-documented trend, likely owing to the technical challenges of sampling at abyssal and hadal depths (Jamieson et al., 2013a, Bridges et al., 2023).

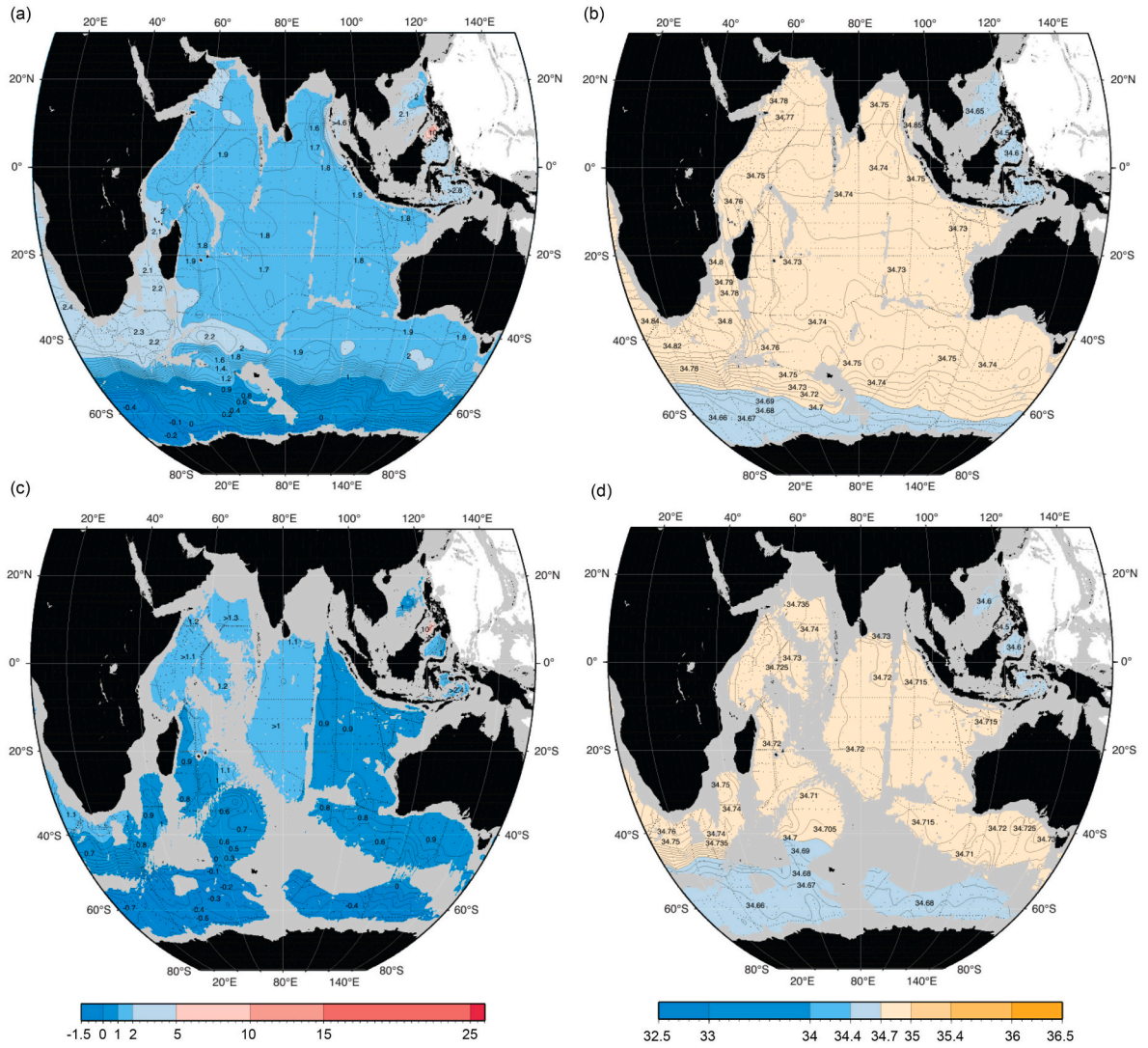

Fig. 4. Deep and bottom water properties of the Indian Ocean from the World Ocean Circulation Experiment Indian Ocean Atlas (Talley, 2013). (a) Potential temperature (°C) and (b) practical salinity at 2500 m, (c) potential temperature (°C) and (d) practical salinity at 4000 m.

9. Knowledge summaries by seafloor feature

9.1. Continental margins

Beyond the continental shelf, the ocean deepens to bathyal depths along high gradient slopes, the size and steepness of which vary along the continental margins of the Indian Ocean. These margins are geomorphologically complex, encompassing a variety of heterogenous deep-sea habitats, including canyons, oxygen minimum zones, fans, cold seeps, and cold-water coral reefs (Menot et al., 2010; Levin and Sibuet, 2012). The continental shelf is generally much narrower along the east coast of Africa compared to the Australian and northern continental margins; the Tanzanian shelf (200 m contour), for example, extends <10 km from shore in places (Gates et al., 2021). The mean Indian Ocean continental shelf width is only 37 km, while the slope has a mean width of 51.9 km (Harris et al., 2014). Consequently, the deep sea is very close to the coast in certain areas of the Indian Ocean, presenting an excellent opportunity to study deep continental margin habitats and faunal communities, as demonstrated for the oxygenated slopes of the Kenyan margin (Demopoulos et al., 2003) and the Tanzanian continental slope (Gates, 2016). The Census of Marine Life's (CoML) Continental Margin Ecosystems on a Worldwide Scale (COMARGE) project further investigated the various complex ecosystems of the global continental margins, summarised by Menot et al. (2010), though most of the research effort was focussed on the Atlantic Ocean.

Of the countries bordering the Indian Ocean, the Australian continental margin is perhaps the best understood (McEnnulty et al., 2011). For example, the western continental margin of Australia was surveyed during 2005 and 2007 as a contribution to the COMARGE project (Williams et al., 2010; McEnnulty et al., 2011; Poore et al., 2015). Geoscience Australia's 2008–2009 survey provided further observations of deep-water benthic habitats and biota from the western margin such as 38 different types of Lebensspuren (Daniell et al., 2009; Przeslawski et al., 2012). Most notably, the southern Australian continental margin has been subject to intense research interest, especially areas of the Great Australian Bight that have been earmarked as frontiers for oil and gas exploration (Rogers et al., 2013). The recent CSIRO-led Great Australian Bight Research Program and Great Australian Bight Deep-water Marine Program provided the deepest systematic biological sampling in Australian waters to date (Begg, 2018, Ross et al., 2018, Smith et al., 2018). These programs collectively recorded 1267 benthic invertebrate species from the Great Australian Bight's continental margin, including 401 new to science and numerous species records for the region (MacIntosh et al., 2018), and culminated in the publication of several studies of the margin's deeper ecosystems (Ross et al., 2017, Fulton et al., 2018, Hook et al., 2018, Ross et al., 2018, Williams et al.,

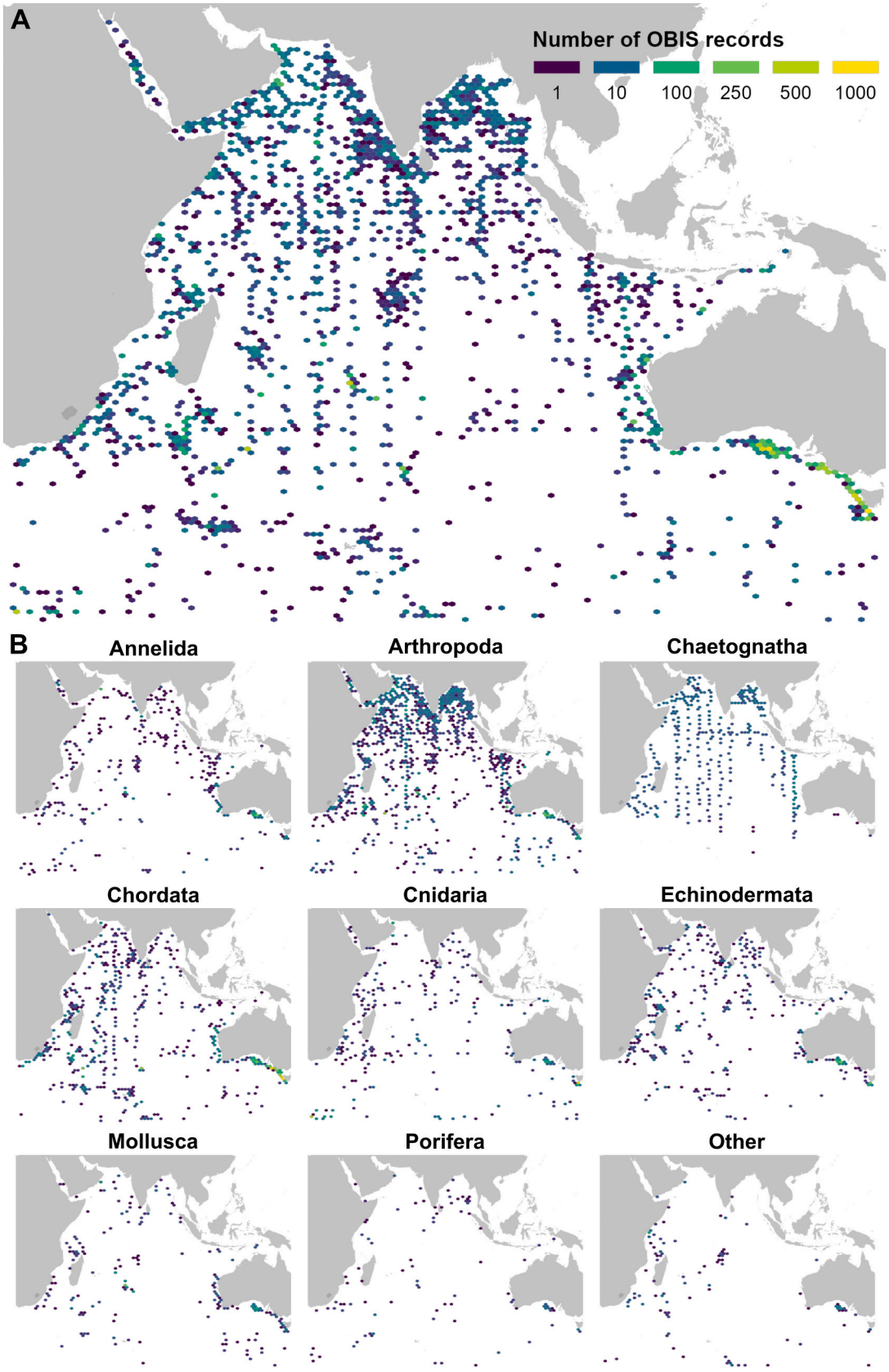

Fig. 5. Heat maps of metazoan biodiversity records, for all phyla (A) and across different phyla (B), in the deep Indian Ocean (>1000 m) using data from the Ocean Biodiversity Information System (OBIS). Other category includes phyla with low record numbers (<300): Brachiopoda, Bryozoa, Ctenophora, Hemichordata, Kinorhynca, Nematoda, Nemertea, Platyhelminthes, Priapulida, and Tardigrada.

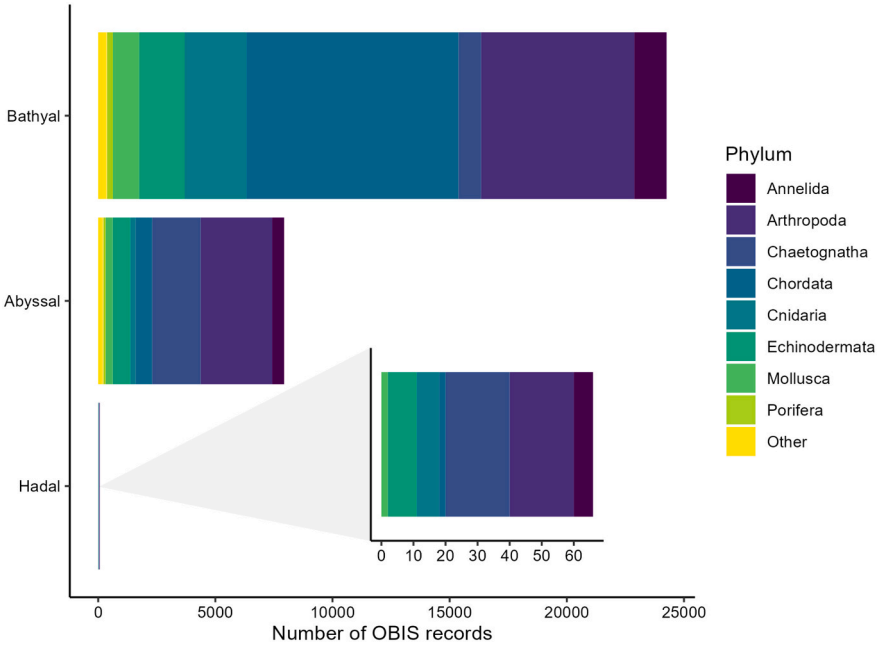

Fig. 6. Metazoan biodiversity records across different depth ranges in the Indian Ocean using data from the Ocean Biodiversity Information System (OBIS). Depth ranges – bathyal: 1000–3000 m, abyssal: 3000–6000 m, hadal: >6000 m. Other category includes phyla with low record numbers (<300): Brachiopoda, Bryozoa, Ctenophora, Hemichordata, Kinorhynca, Nematoda, Nemertea, Platyhelminthes, Priapulida, and Tardigrada.

2018a, Williams et al., 2018b, Farrelly and Ahyong, 2019, Barrett et al., 2020). As with Gates et al. (2017a, 2017b), these examples benefitted from collaborations with the oil and gas industry, highlighting how hydrocarbon exploration can lead to and incentivise deep-sea research. Similarly, fisheries surveys, such as the Royal Society Indian Ocean Deep Slope Fishing Expedition and YugNIRO expeditions in the 20th century, produced valuable biological datasets for continental slope communities, though many are restricted to the upper 1000 m (e.g. Forster et al., 1970).

9.2. Canyons

The continental slopes bounding the Indian Ocean are incised by numerous canyons that can reach several thousand meters deep. There are an estimated 1590 canyons in the Indian Ocean, with a cumulative total area of 760,420 km^2, accounting for 11.2 % of the continental slope (Harris et al., 2014). While some canyons are sub-sea extensions of large river systems (downwards formation, e.g., Indus and Swatch of No Ground Canyons), others have no direct connection with land, having either been isolated from their terrestrial inputs by sea level fluctuations (e.g., Perth Canyon) or forming via repetitive landslides along steeper margins of the continental shelf (retrogressive slope failures, e.g., Bremer Canyon). Linking the continental shelf and abyssal seafloor, canyons have been recognised as key areas of localised productivity resulting in hotspots of benthic biodiversity in the deep sea (De Leo et al., 2010; Robertson et al., 2020). However, most large studies to date have excluded the Indian Ocean's canyon systems. For example, a special issue from 2014 which presented 24 new studies on global submarine canyons did not include any research from the Indian Ocean (Huvenne and Davies, 2014).

A recent increase in research interest in Australia's submarine canyons has resulted in detailed surveys for several canyons along the Western and Southern Australian coast (Heap et al., 2008; Daniell et al., 2009; Currie and Sorokin, 2014; Conlan et al., 2015; Trotter et al., 2019; Post et al., 2021; Trotter et al., 2022a; Trotter et al., 2022b; Taviani et al., 2023). Geoscience Australia reported mapping 109 canyons along the western Australian continental margin in 2008–2009 (Daniell et al., 2009). The largest of these, the Perth Canyon, was first explored using an ROV during 2015, revealing a previously unknown deep-sea faunal community (Trotter et al., 2019). Perth Canyon is quiescent and described as a 'fossil canyon system', hosting extensive fossil coral graveyards that chronicle a history of thriving deep-water coral reefs during the last ice age (Trotter et al., 2019). In the modern day, the canyon is characterised by sporadic, localised hotspots of mega- and macrofauna that form relatively diverse communities along the canyon walls and rim, including sponges, corals, echinoderms, crustaceans, annelids, brachiopods, molluscs, and fish (Trotter et al., 2019). However, the Perth Canyon is relatively depauperate of life compared to the Bremer Canyon which lies further south, facing the Southern Ocean (Trotter et al., 2022b).

The dendritic Bremer Canyon system is comprised of several deeply incised submarine canyons extending over 4380 km^2, including the Bremer, Hood, Henry, and Knob Canyons (Trotter et al., 2022b). Both the Perth and Bremer canyon systems are disconnected from continental river systems so receive very little detrital input; however, the Bremer system benefits from a greater prevalence of hard substrates, relatively high dissolved oxygen concentrations, and enhanced upper ocean mixing (Trotter et al., 2022b). Consequently, the 2020 *RV Falkor* FK200126 cruise to the Bremer Canyon recorded flourishing benthic communities with bryozoan and sponge-dominated forests and extensive coral gardens (scleractinians, octocorals, antipatharians), which form important community centres for echinoderms (cactus urchins, basket stars, ophiuroids, crinoids), barnacles, anemones, crustaceans, and other taxa (Trotter et al., 2022b). Crucially, these studies demonstrate that the benthic communities of Australia's southwest canyons are comparable in diversity and density to the better-known nutrient-rich canyons of the North Atlantic and Northeast Pacific.

Similarly, the more northerly Cape Range and Cloates canyons off Exmouth are host to localised high densities of glass sponges and echinoderms, driven by the current-regulated sedimentation and nutrient availability (Post et al., 2020; Post et al., 2021). Another shallower study from a tributary of the Cape Range canyon system determined that these canyon habitats support richer fish assemblages than non-canyon habitats, with observed differences in the assemblages between the deeper and shallower areas of the canyon feature (Saunders et al., 2021). A comparison of macro- and megafaunal patterns at two topographically

contrasting canyons at the southern Australian margin (the shelf-incising du Couedic and slope-limited Bonney canyon) further revealed the need to explore different canyon types along the Indian Ocean's continental margin, as well as the effects of different water masses and bioregions, to fully comprehend localised biodiversity patterns (Currie and Sorokin, 2014; Conlan et al., 2015).

Several canyons have also been morphologically described along the African margin of the Indian Ocean, such as the Tugela Canyon off South Africa (Wiles et al., 2013) and the submarine canyons of northwest Madagascar (Wiles et al., 2019); however, there are no published data on their biological communities. Similarly, the benthic biodiversity of the large Swatch of No Ground and Indus canyons at the northern margins of the Indian Ocean have not been studied. Despite its name, the Zambezi Canyon is a north-south orientated submarine channel with no direct connection to the Zambezi River nor any other significant fluvial source (Wiles et al., 2017).

Owing to their proximity to terrestrial and coastal activities, submarine canyons are also of interest for the study of anthropogenic impacts to deep-sea environments. Canyons are considered potential sinks for marine litter (Hernandez et al., 2022) however, Australian canyons appear to be relatively devoid of human traces (Trotter et al., 2019; Taviani et al., 2023), possibly owing to their predominately upward formation. Comparatively, Perth Canyon has more macro-litter than other southwestern Australian canyons, presumably due to its proximity to urban developments and commercial shipping operations (Taviani et al., 2023). Nonetheless, the physical imprint of human activities is remarkably absent relative to global patterns (Trotter et al., 2019). Conversely, demersal trawling is an increasingly concentrated threat to Australia's southern canyons, with large portions of the upper and mid slope trawled over the last two decades (Currie and Sorokin, 2014, Conlan et al., 2015). Monitoring of continental shelf and slope environments is essential to understand the potential anthropogenic impacts to their related ecosystems, including canyons, yet the anthropogenic impacts faced by other Indian Ocean canyons remains understudied.

9.3. Fans

The northern Indian Ocean is host to the largest submarine fans in the world, accounting for more than half of the global fan area (Harris et al., 2014). Fans are depositional features that continuously deepen from their sediment source, usually at the mouth of a canyon (IHO, 2019). The largest, the Bengal Fan, extends 3000 km from the Swatch of No Ground Canyon to ~5000 m depth in the Mid-Indian Ocean Basin, spanning 1430 km at its widest point (Curray et al., 2003; Subrahmanyam et al., 2008). Sediments of the Bengal Fan have a maximum sub-seafloor thickness of 16.5 km, primarily derived from the Ganges-Brahmaputra River basin. To its east lies the smaller Nicobar Fan – an inactive sub-fan that was divided from the sediment supply of the Bengal Fan by the convergence of the Ninetyeast Ridge with the Java subduction zone in the late Pleistocene (Pickering et al., 2020). The Arabian Sea hosts the second largest submarine fan, the Indus Fan, which extends 1500 km from the Indus Canyon at the Pakistan continental shelf break and is >9 km thick at its thickest point (Clift et al., 2001). The natural significance of these fans lies in their transport of vast quantities of terrigenous sediments to the deep sea, serving as deep reservoirs of particulate organic carbon. As a result, the abyssal plain of the southern Bay of Bengal is among the flattest large areas of the Earth's surface (Demopoulos et al., 2003). However, modern sea-level conditions are less conducive for sediment transport along the Bengal Fan via its turbidity channels than past states (Curray et al., 2003). The Netherlands Indian Ocean Expeditions further provided insights to the depositional architecture and sediment facies of the middle and lower Indus fan (van Weering et al., 1997). The direct influence of the submarine fans on the deep-sea biodiversity of the region has never been studied.

9.4. Oxygen minimum zones

The enclosed nature of the northern Indian Ocean is unique among global oceans, resulting in a high productivity-low ventilation system with strong stratification (McCreary Jr. et al. 2013, Hermes et al., 2019). Consequently, major oxygen minimum zones (OMZs), with dissolved oxygen concentrations <0.5 mL/L, are located both in the Arabian Sea and Bay of Bengal at upper bathyal depths (Demopoulos et al., 2003; Rixen et al., 2020). These areas host ~21 % of the total global volume of oxygen-depleted waters and ~59 % of the Earth's marine sediments exposed to severe oxygen depletion (Rixen et al., 2020). Thus, despite the core OMZ (≤0.1 mL/L DO) occurring at depths shallower than 1000 m (~250–750 m at the Indus margin), these OMZ strongly influence the community dynamics of the deep benthos across the continental margins of both basins (Rogers, 2000; Gooday et al., 2010; Levin et al., 2013; Enge et al., 2014; Rixen et al., 2020). For example, strong edge effects of faunal diversity and density shifts with oxygen gradients have been observed across the OMZ boundaries at the Pakistan (Gooday et al., 2009; Hughes et al., 2009; Levin et al., 2009; Murty et al., 2009), Oman (Levin et al., 2000), and western Indian (Ingole et al., 2010; Levin et al., 2013; Enge et al., 2014) margins of the Arabian Sea, and in the Bay of Bengal (Gooday et al., 2010).

As well as shifts in oxygen concentrations, peaks in the abundance and diversity of deep-sea invertebrates at the lower boundaries of OMZs are thought to be strongly tied to the plentiful food supply available immediately beneath, resulting from the reduced utilisation of organic matter during its downwards flux through the anoxic water column (Rogers, 2000). At the Indian margin, foraminifera have been shown to rapidly process phytodetritus under almost anoxic conditions, suggesting they play an important role in short-term carbon cycling in this OMZ region (Enge et al., 2014). Furthermore, megafaunal aggregations at the lower OMZ boundary, including ophiuroids and *Encephaloides* spider crabs, have been shown to contribute substantially to the reworking and redistribution of organic matter at continental margins (Smallwood et al., 1999). There are however marked differences between the OMZs of the Arabian Sea and Bay of Bengal, primarily the occurrence of denitrification in the Arabian Sea and lack thereof in the Bay of Bengal (McCreary et al., 2013, Bristow et al., 2017). Consequently, differences in benthic faunal assemblages have also been observed between the two basins, as shown for foraminifera by Suokhrie et al. (2020). Demopoulos et al. (2003) provide a further summary of Indian Ocean OMZ research from the late 20th century.

9.5. Cold seeps and brine pools

Cold seeps are characterised by the expulsion of methane or other hydrocarbon-rich fluids from the seafloor and are associated with a diverse range of seafloor geomorphologies including mud volcanoes, pockmarks, diapirs, and brine pools (Foucher et al., 2009; Ceramicola et al., 2018). Various confirmed and inferred cold seeps occur along the northern continental margins of the Indian Ocean (Milkov, 2000; Ceramicola et al., 2018), in areas such as the Makran Accretionary Prism off Pakistan (von Rad et al., 2000; Fischer et al., 2012), the Cauvery-Mannar and Krishna-Godavari Basins off India (e.g. *methane hydrates*: Mazumdar et al., 2019, *pockmarks*: Mazumdar et al., 2021), and within the Red Sea (e.g. *brine pools*: Purkis et al., 2022).

Of the abundant brine pools in the Red Sea, there are at least 25 pool complexes located in deep water (>1000 m) along the basin's axial trough (Purkis et al., 2022), the deepest of which lies at 2850 m in Suakin Deep (Baumann et al., 1973). A further deep brine pool complex, named NEOM, was discovered in 2020 which extended the known range of Red Sea brine pools into the Gulf of Aqaba (Purkis et al., 2022). Despite their extreme conditions, cold seeps, including brine pools, are often host to distinct bacterial and faunal communities driven by chemosynthesis of abundant hydrocarbon seepage (Sibuet and Olu, 1998). The discovery of extremophile microbial diversity inhabiting

these environments has provided a promising source of pharmaceuticals, with evidence that the Red Sea brine pool communities may yield bioactive molecules with potential for biomedical applications including anticancer and antibacterial properties (Ziko et al., 2019; Renn et al., 2021).

Within the Red Sea, large assemblages of bivalves, tubeworms and sponges, as well as dense bacterial mats, have been associated with the fringes of brine pools (Antunes et al., 2011; Batang et al., 2012). Predators will also make use of the brine as part of their feeding strategies, feeding on animals shocked or killed by the anoxic, hypersaline pools (Purkis et al., 2022). A new species of Corbulidae clam, *Apachecorbula muriatica*, observed in narrow bands along the margins of Red Sea brine pools is suggested to be both tolerant of and endemic to the hypersaline, hypoxic conditions of this extreme environment (Oliver et al., 2015). Corbulid clam shells are adapted to withstand such toxicity, for example, their unequal and globose valves form a tight seal when closed while conchiolin layers afford protection from carbonate dissolution (Batang et al., 2012). While cold seep bivalves have been shown to harbour chemosynthetic bacterial endosymbionts in other regions (Duperron et al., 2013), there is currently no available evidence that *A. muricata*, nor the wider bivalve assemblages recorded along the perimeter of Red Sea brine pools, are chemosymbiotic (Oliver et al., 2015; Purkis et al., 2022).

On the Indian margin of the Bay of Bengal, several active cold seeps were discovered in 2018 at the Krishna-Godavari Basin between 900 and 1800 m deep, in association with shallow methane hydrates and supporting a rich biodiversity (Mazumdar et al., 2019; Dewangan et al., 2021; Sangodkar et al., 2023). Cold seep ecosystems have a long history at the Krishna-Godavari Basin with the discovery of cold-seep carbonate layers, including trace fossils of faecal pellet-filled burrow casts, deposited at least 46–58 kya (Mazumdar et al., 2009; Mazumdar et al., 2011). The modern faunal communities associated with the Krishna-Godavari cold seeps are diverse, with over 2300 individuals representing 18 macrofaunal families recorded (Sangodkar et al., 2023), and characteristic of global cold seep environments (Sibuet and Olu, 1998).

Unlike the Red Sea bring pools, the Krishna-Godavari cold seeps support chemo-endosymbiont bearing bivalves of the genera *Bathymodiolus*, *Calyptogena*, *Conchocele*, and *Acharax*, as well as other chemosymbiotic species such as provannid gastropods and *Sclerolinum* siboglinid polychaetes (Mazumdar et al., 2019). They also host heterotrophs including munidopsid and galatheid squat lobsters, *Amphiodia* ophiuroids, and *Neolepas* goose barnacles (Mazumdar et al., 2019; Sangodkar et al., 2023), some of which represent new distribution records for species that were not previously known from the Indian Ocean (e.g., *Shinkaia crosnieri*, Gonsalves et al., 2022). Isotopic analyses provided a glimpse into the trophic structure of the seep ecosystems, revealing that *Bathymodiolus* are dependent on methanotrophic symbionts while *Sclerolinum*, *Conchocele*, and *Acharax* host thiotrophic symbionts (Peketi et al., 2022). A parasitic relationship was further observed between *Bathymodiolus* and the polychaete *Branchipolynoe seepensis*, whereby the latter lives inside the mussel's mantle cavity and derives its food from its host's tissues (Mazumdar et al., 2019; Peketi et al., 2022). Meanwhile, the broad range of carbon and nitrogen isotope ratios are indicative of the variety of different food sources utilised by the heterotrophic fauna, from the soft tissues of the chemosynthetic organisms to suspended particulates to microbial mats and epibionts (Peketi et al., 2022).

Chemosynthetic organisms have similarly been recorded at cold seeps in the Cauvery-Mannar Basin between India and Sri Lanka, including *Lamellibrachia* tubeworms, *Munidopsis* squat lobsters, *Calyptogena* clams, and Buccinidae gastropods (Mazumdar et al., 2021). To date, the Krishna-Godavari and Cauvery-Mannar cold seeps are the only environments of their kind to be recorded within the Indian EEZ. Furthermore, as with the squat lobster *S. crosnieri* (Gonsalves et al., 2022), prior to their recent discovery, *Lamellibrachia* tubeworms had never been recorded from the Indian Ocean (Mazumdar et al., 2021), highlighting the need for further exploration and investigation of cold seeps and other reducing environments within the region.

9.6. Abyssal plains

Abyssal plains are extensive flat or gently sloping seafloor areas that occur at depths around 3000–6000 m (IHO, 2019). Commonly considered the largest environment on Earth, abyssal plains dominate the abyssal depth zone and comprise ~35 % of the Indian Ocean seafloor (Ramirez-Llodra et al., 2010; Harris et al., 2014). Abyssal plain habitats form the vast proportion of the seafloor environment of all major Indian Ocean basins, namely the Argo, Cuvier, Perth, Enderby, and Somali abyssal plains. Abyssal plains are generally characterised by vast areas of fine sediment tens to hundreds of metres thick, formed by the deposition of organic material from surface waters (Ebbe et al., 2010). However, recent research has revealed the heterogeneity of the abyssal seafloor with extensive hard substrate availability, including nodules and rocky outcrops (Fig. 7B, G, H), especially when associated with more complex features such as fracture zones (Riehl et al., 2020). Similarly, abyssal hills (<1000 m elevation) have also been recognised as sources of increased habitat heterogeneity and thus increased faunal biomass and diversity compared to surrounding plains (Durden et al., 2015). A boulder harbouring a diverse community of sponges and cnidarians observed in the North Australian Basin exemplifies this paradigm (Fig. 7H), and given the geomorphological complexity of the Wharton Basin, this region of the eastern Indian Ocean may demonstrate comparable abyssal habitat heterogeneity (Fig. 3).

The biodiversity and biogeography of abyssal plain communities are poorly known (Lörz et al., 2023). Low food availability and oligotrophic conditions in the abyss often result in low faunal abundance and biomass across the plains, while abyssal species richness has also been recorded as paradoxically high (Snelgrove and Smith, 2002; Ebbe et al., 2010). In contrast, Parulekar et al. (1982, 1992) report rich fauna and high biomass for the abyssal benthos of the western and central Indian Ocean, linked to high organic production in the overlying euphotic zone. There are two major components to benthic abyssal plain communities, the epifauna and infauna, both of which play an important role in ecosystem functioning (e.g., bioturbation). Abyssal plain epifaunal communities tend to be dominated by deposit feeders like holothurians (Fig. 8A-D; Thurston et al., 1994, Iken et al., 2001). A 2005 cruise to the Crozet Plateau and surrounding plains resulted in the discovery of several new species of abyssal elasipodid holothurians (Cross et al., 2009; Rogacheva et al., 2009), demonstrating that even the most ubiquitous and conspicuous deep-sea taxa remain unknown from Indian Ocean abyssal plain habitats.

While smaller holothurians are also characteristic of abyssal infaunal communities, nematodes and copepods dominated the abyssal meiofaunal assemblage in the Arabian Sea, with an average total meiofaunal density of 234.99 ± 61.60 individuals per 10 cm^2 (Sautya et al., 2021). Meiofauna hold broad importance as bioindicators of ecosystem health that are capable of predicting global change (Zeppilli et al., 2015); however, further research is required to determine how the community patterns across abyssal plains influence the ecosystem's functioning (Sautya et al., 2021).

Another key feature of abyssal plains is the abundance of lebensspuren or 'life traces', which can often be more conspicuous than the organisms that make them (Jamieson and Onda, 2022). For example, trails, burrows, spiral loops, and faecal casts were recorded at abyssal habitats at the western flanks of the Carlsberg Ridge in the Somali Basin (Glasby, 1973), as well as star-shaped feeding traces of echiuran worms in the Bay of Bengal (Ohta, 1984). Abyssal plain ecosystems are also host to benthopelagic mobile scavenger communities, including fish and crustaceans, which can be studied using baited deployment systems (see subsequent section on organic food falls; Bailey et al., 2007).

Indian Ocean abyssal plains are rarely prioritised for biological research. The little research effort that has occurred is spatially patchy

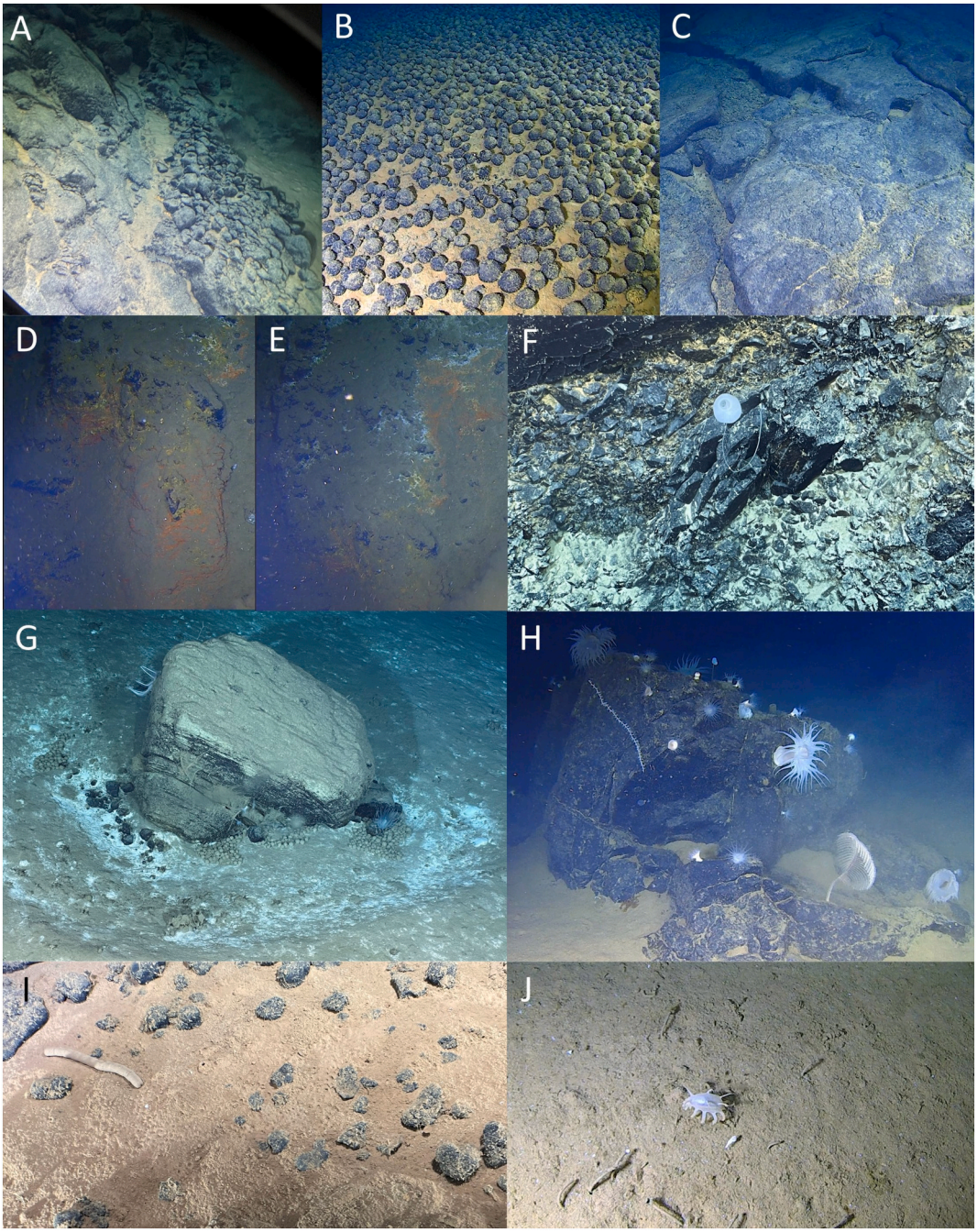

Fig. 7. Examples of substrate and habitats of the deep Indian Ocean, where A = debris fields within a fracture zone, B = manganese nodules, C = volcanic crust of seamount, D-E = putative bacterial mats on trench forearc, F = rock face of escarpment, G-H = large boulder puncturing abyssal plain sediments, I = cobble and soft sediment mix on fracture zone floor, and J = soft sediment on subduction trench floor. All images from between 3000 and 7300 m in the East Indian Ocean.

such that not all basins are represented equally in the literature. Perhaps the best-known abyssal region in the Indian Ocean is the Mid-Indian Ocean Basin, also known as the Central Indian Ocean Basin (Ingole and Koslow, 2005; Wafar et al., 2011). Seafloor surveys have been conducted here by Indian researchers since the 1980s to explore resource potential and inform environmental impact assessments for deep-sea mining of the central Indian Ocean nodule field (Ansari, 2000; Mukhopadhyay et al., 2002; Wafar et al., 2011). Data on the type and distribution of the area's meio-, macro-, and megabenthic fauna are suggestive of an extremely rich and diverse abyssal community (Ingole and Koslow, 2005). However, this research represents only a limited area within the Mid-Indian Ocean Basin and given its driving objective to understand mining impacts (e.g., Ingole et al., 2005), these patterns may not reflect the faunal trends for the entire region (Ingole and Koslow, 2005). Other abyssal plain research programmes in the Indian Ocean have focussed on the influences of surface productivity on particulate mass fluxes and the biomass and diversity of seafloor communities within the Arabian Sea (BIGSET project: Lochte and Pfannkuche, 2000, Pfannkuche and Lochte, 2000, Turnewitsch et al., 2000, Witte, 2000, Witte and Pfannkuche, 2000, Treude et al., 2002), Somali Basin (Netherlands Indian Ocean Expeditions 1992–93: van Weering et al., 1997), and Crozet Basin (CROZEX project: Hughes et al., 2007, Ebbe et al., 2010). In these basins, seafloor activity and community composition were found to be closely tied to the surface productivity patterns, though these interactions were complex and varied seasonally, often influenced by monsoonal dynamics (van Weering et al., 1997; Lochte

Fig. 8. Benthic biodiversity of the deep Indian Ocean, where A-D = Holothuiroidea, E = Asteroidea, F = Brisingida, G = Echinoida, H-J = Polychaeta, K = Enteropneusta, L = Sipuncula, M = Gastropoda, N-O = Isopoda, P-R = Decapoda, S = Pantopoda, T-U = cf. *Caulophacus*, V-W = cf. Hyalonematidae, X-Y = Actiniaria, Z = Antipatharia, Aa = Phlebobranchia. All images from between 1000 and 7300 m in the East Indian Ocean.

and Pfannkuche, 2000; Ebbe et al., 2010).

In contrast, there is a paucity of abyssal plain data elsewhere in the Indian Ocean. Bond and Jamieson (2022) highlighted the lack of research effort to understand abyssal plain ecosystems in Australia's EEZ, despite abyssal depths accounting for 46 % of its jurisdiction. A recent report on Australia's Gascoyne Marine Park noted only that the Cuvier Abyssal Plain appeared to be typical of the habitat type in its vast homogenous sedimented plains interspersed with holothurians, cusk eels, xenophyophores, and glass sponges (Post et al., 2021). Furthermore, data were found to be sparse for deep-sea habitats across the southern Indian Ocean, particularly in the south-eastern region (Ramiro-Sánchez et al., 2023). Thus, clear knowledge gaps remain regarding the

spatial and temporal biodiversity patterns, connectivity, productivity, and ecosystem functioning of abyssal plains in the Indian Ocean.

9.7. Nodule fields

Polymetallic nodule fields, also known as (ferro)manganese nodules, are common across the abyssal seafloor and are especially abundant in areas with oxygenated bottom waters and low sedimentation rates (Fig. 7B; Hein et al., 2013). Nodules are derived from the precipitation of metals from seawater forming concentric micro-layers around a nucleus, resulting in potato-sized (1–12 cm) deposits that can be rich in manganese, cobalt, nickel, and copper (Kuhn et al., 2017). These seafloor features provide important habitat heterogeneity through the availability of hard substrate for the benthic community (Fig. 8J, S, X), with significantly higher densities of sessile and mobile epifauna recorded at areas with dense nodule coverage compared to nodule-free areas of the abyssal plain (Vanreusel et al., 2016).

In the Indian Ocean, nodule fields are primarily known from the Mid-Indian Ocean Basin (central Indian Ocean nodule field), Diamantina Fracture Zone (Cape Leeuwin nodule field), and Mozambique Basin. Of these, the central Indian Ocean nodule field (IONF) is the best characterised (see Mukhopadhyay et al., 2018a, 2018b for a summary of IONF biota), owing to the deep-sea mining interest in the region (Hein et al., 2013; Mukhopadhyay et al., 2019). The IONF is comprised of two ~150,000 km^2 areas that have a combined estimated nodule resource of ~1300 million metric tonnes, making this the world's second greatest nodule deposit in extent, abundance, and metal content (Mukhopadhyay et al., 2002; Mukhopadhyay and Ghosh, 2010). As such, the Government of India holds an exploratory mining contract for a 75,000 km^2 area of the IONF, and a further 150,000 km^2 is reserved by the ISA for developing states to access deep-sea mineral resources (ISA, 2019, Mukhopadhyay et al., 2019; Fig. 1).

The Indian Deep-sea Environment Experiment (INDEX) was launched in 1995 to simulate and predict the environmental impacts of nodule mining in the IONF (Desa, 1997). Meio- and macrofaunal communities were sampled before, 1 month after, and ~3.7 years after a simulated mining disturbance (Ansari, 2000; Ingole et al., 2000; Ingole et al., 2001; Rodrigues et al., 2001; Ingole et al., 2005). Benthic communities experienced a significant decrease in both meiofaunal and macrofaunal densities post-disturbance, with the top 2 cm of sediment experiencing the greatest physical disturbance (Ingole et al., 2000; Ingole et al., 2001). Similarly, benthic megafaunal populations, characterised by xenophyophores, holothurians, and sponges, experienced a 32 % reduction post-disturbance (Rodrigues et al., 2001). While there was some recovery in nematode and oligochaete populations after 3.7 years, polychaete and crustacean populations did not recover to their pre-disturbance baseline (Ingole et al., 2005). Furthermore, a study integrating these results with 10 other simulated mining disturbance experiments from global sites concluded that the effects of nodule mining are likely to be long lasting (Jones et al., 2017).

Despite not appearing on recent maps of global nodule distribution (Hein et al., 2013; Miller et al., 2018), the Cape Leeuwin nodule field has been known since the 1970s and forms an extensive 1 million km^2 nodule pavement along the southern edge of the Diamantina Fracture Zone, from the Broken Ridge into the South Australian Basin (Kennett and Watkins, 1975; Frakes et al., 1977; Bond and Jamieson, 2022). However, the Cape Leeuwin deposits are of a lower grade and therefore are not currently of interest for deep-sea mining (Pettis and de Forest, 1979; Frakes, 1982). As such, there are no published studies of the benthic faunal communities associated with the Cape Leeuwin nodule field. Likewise, the Mozambique Basin nodules also have low-grade combined nickel, copper, and cobalt contents (Rogers, 1995); therefore there is a lack of interest in the region despite a relatively high nodule abundance of 37.1 kg/m^2 and growth rate up to 248.3 mm/Ma (Geodekyan and Rozanov, 1984; Ovechkina et al., 2021).

Nodules have also been recorded in the Wharton Basin at the Zenith Plateau (Weston et al., 2021), Wallaby-Zenith Fracture Zone (Niyazi et al., 2024), south of Christmas Island (Exon et al., 2002), at the western flank of the Carlsberg Ridge (Glasby, 1973), and south of Tasmania (Watkins and Kennett, 1971, Watkins and Kennett, 1977, Bolton et al., 1988). Similarly, Nagender Nath et al. (1992) report nodules from the Mascarene and Somali Basins. Indeed, manganese nodule deposits appear to occur across the extent of the abyssal Indian Ocean, with varying degrees of nodule density and grade (Mukhopadhyay et al., 2018a, 2018b). Despite this, very little work has been done to understand the importance of these areas for seafloor faunal communities in the Indian Ocean, with a focus on the economic value of the nodule fields instead and most polymetallic nodule research globally is concentrated in the high-grade Clarion-Clipperton Zone in the Pacific.

9.8. Organic food falls

In an environment largely dependent on the transfer of food sources from surface waters, the deposition of animal carcasses and large plant matter to the seafloor is considered to play an important role in the nutritional needs of deep-sea species, including scavengers, predators and chemosymbiotic specialists (Smith et al., 2015; Jamieson, 2016). Such events are termed 'food falls' or 'organic falls' and can include sunken whales (Smith and Baco, 2003), large fish (Higgs et al., 2014), masses of gelatinous invertebrates (Billett et al., 2006), pelagic crustaceans (Christiansen and Boetius, 2000), macroalgal rafts like kelp (Bernardino et al., 2010), and wood (Bienhold et al., 2013).

As naturally occurring food falls are ephemeral and extremely difficult to locate on the deep seafloor (Jamieson, 2016), several studies have used experimental deployments to study the faunal communities associated with these environments, using different types of bait to mimic the various food fall types (e.g., Hilario et al., 2015; Amon et al., 2017; McClain et al., 2019). Baited camera and trap systems have been used in the deep Indian Ocean since the 1970s (Bailey et al., 2007) and have been successfully employed to study the assemblage composition and distribution of deep-sea scavengers (e.g. amphipods, macrourid fish, penaeid decapods) and other mobile bait-associated species (e.g. *Bassozetus*) across the Indian Ocean (Fig. 9D-E & G-O; *Arabian Sea*: Witte, 1999, Janßen et al., 2000, *Crozet Plateau*: Cousins et al., 2013, *Wallaby-Zenith Fracture Zone*: Weston et al., 2020, Weston et al., 2021, *Red Sea*: Pearce et al., 2023).

Other food fall experiments have focussed on the species colonising the bait itself, rather than mobile scavengers and opportunists captured on camera. These experiments often utilise packages of fresh mammal bones and are left for longer periods to simulate the latter enrichment-opportunist and sulfophilic stages of food fall communities (Smith and Baco, 2003). For example, the deployment of pig bones for two years on a mooring system on the Southwest Indian Ridge resulted in the first Indian Ocean records of the famous bone-eating zombie worms, *Osedax* (Zhou et al., 2020). A further two experiments, using whale bone and wood packages, were deployed at the Coral and Atlantis Bank seamounts on the Southwest Indian Ridge and left for two years (Amon et al., 2017); however, these deployments occurred at depths shallower than the remit of this review (≤750 m).

While several natural whale falls have been observed in the Atlantic, Pacific and Southern Oceans (Smith et al., 2015, Li et al., 2022a), to date only one has been recorded in the Indian Ocean (Trotter et al., 2021, Trotter et al., 2022b). This is surprising given the numerous whale populations and migrations that occur in the Indian Ocean (e.g. *blue whales in the northern Indian Ocean*: Anderson et al., 2012; *breeding and migrating humpback whales*: Jenner et al., 2001, Fossette et al., 2014; *pygmy blue whales in the eastern Indian Ocean*: Thums et al., 2022; *southern right whales in the southeast*: Carroll et al., 2011; *widespread occurrence of sperm whales*: Laran et al., 2017, Chambault et al., 2021), and perhaps highlights the paucity of exploratory deep-sea expeditions and reduced research capacity (e.g. ROV and submersible availability) in the region. Similarly, there are no studies of natural wood falls from

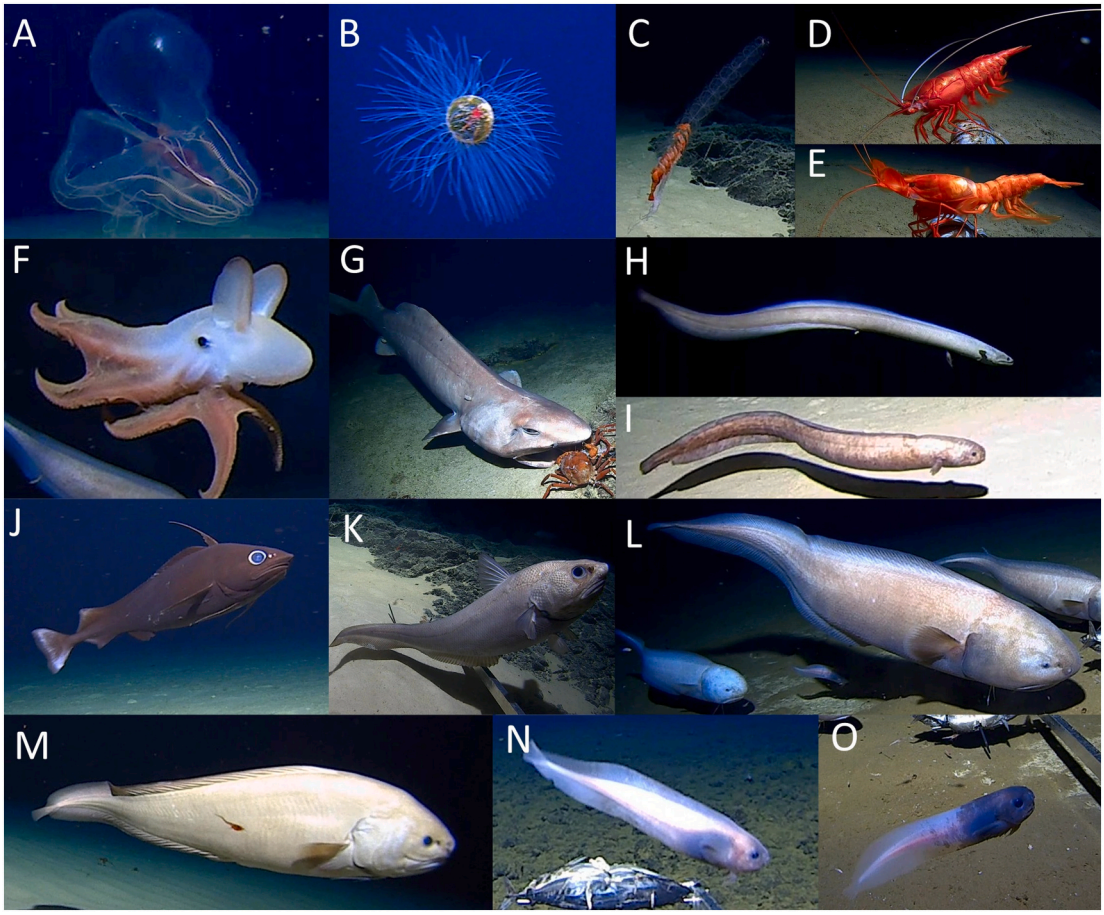

Fig. 9. Pelagic and demersal biodiversity of the deep Indian Ocean, where A = lobate Ctenophore, B = Trachymedusae, C = remosiid siphonophore, D-E = penaeid decapods, F = cirrate octopus, G = *Pseudotriakis microdon* (false catshark), H-I = Synaphobranchid eels, J = Morid (blue hake), K = Macrourid (grenadier), L-M = Ophidiid (cusk eel) and N-O = Liparid (snailfish). All images from between 1000 and 7300 m in the East Indian Ocean.

the Indian Ocean, despite the likelihood of wood debris transported into the Bay of Bengal during monsoon season (Lee et al., 2019; Wohl and Iskin, 2021) and observations of sunken wood in the Java Trench and off Tanzania (Gates et al., 2021; Jamieson et al., 2022). The only other records of natural organic falls in the Indian Ocean include observations of mass depositions of *Charybdis smithii* swimming crabs and *Crambionella* jellyfish in the Arabian Sea, in 1995 and 2002 respectively, both of which resulted in significant organic carbon fluxes that exceeded annual records by more than an order of magnitude (Christiansen and Boetius, 2000; Billett et al., 2006).

9.9. Plateaus

Plateaus are large, relatively flat areas elevated from the surrounding relief with at least one steep side or escarpment (IHO, 2019). They most often present as single features and can present from continental or oceanic affinities formed through volcanic activity, tectonic uplift of ocean crust, or rifting of continents where large fragments are left offshore. Several plateaus in the Indian Ocean abut continental margins and slope down on all remaining sides (e.g., Exmouth Plateau and Madagascar Plateau) whilst others are isolated offshore features, steep on all sides (e.g., Zenith Plateau and Mascarene Plateau). It is important to note that plateaus formed from isolated volcanic activity create large igneous provinces which are geochemically different from mid-ocean ridges created at divergent plate boundaries (Frey et al., 2000). Occasionally, these two processes interact, and a plateau can break apart, form two isolated structures with escarpments where they once adjoined. Such is the case with Kerguelen Plateau and Broken Plateau which rifted apart at Broken Ridge.

The Kerguelen Plateau is the largest plateau (1,226,230 km^2) in the Indian Ocean and third largest in the world (Harris et al., 2014). It rises >2000 m from its surrounding basins and has been the focus of many geological surveys due to its enigmatic and geodynamic complexities (see Bénard et al., 2010). Clasts of continental crust have been found within the Kerguelen Plateau's basaltic flows which represent slithers of the Indian plate, left behind as India broke away from Antarctica and moved north (Frey et al., 2000). The Kerguelen Plateau has long been an important commercial fishing ground (Duhamel and Williams, 2011). From the 1970s, Soviet trawlers targeted marbled rockcod, mackerel icefish and grey notothen. Since the establishment of French and Australian EEZs in 1978 and 1979, unrestricted trawling activity has gradually been replaced with longliners targeting Patagonian Toothfish (*Dissostichus eleginoides*) in 500–2300 m water depth (Lord et al., 2006; Park et al., 2008; Palomares and Pauly, 2011). Whilst fishing activity in these Kerguelen plateau EEZs is managed and regulated, the area did see a period of unregulated illegal longline fishing activity between 1997 and 2004 (Duhamel and Williams, 2011).

Fortuitously, this commercial fishing activity has broadly facilitated observer contributions (Gasco, 2011) and scientific research on a broad range of topics in an otherwise remote, isolated and hostile location, including: Southern Indian Ocean fronts (Belkin and Gordon, 1996), slope currents (Park et al., 2008), cephalopod fauna and predator feeding behaviour (Cherel et al., 2004), the feeding ecology of two deep-sea skates (Faure et al., 2023), the macroinvertebrate assemblage (Martin et al., 2023), and life history and spatial distribution of fish (Péron et al., 2016). Less isolated plateaus such as the Exmouth Plateau

off Western Australia are easier to access, however research there is also driven by extraction operations.

The Exmouth Plateau abuts the mid-west coastline of Western Australia and is rich in subsea hydrocarbon deposits. Permission to extract these deposits has required facility operators to undertake environmental assessments and monitoring, resulting in biological and ecological knowledge at depths and locations often forgotten (Macreadie et al., 2018; McLean et al., 2022). Although most operations exist on the top of the plateau, advances in technology have resulted in extraction and associated subsea infrastructure installed beyond 1000 m. The marine community on the slope of Exmouth Plateau beyond 1000 m loosely reflects that of the shelf break off Western Australia (Williams et al., 2001; Douglas, 2021). Future research at Exmouth Plateau beyond 1000 m will likely be driven by the exploration and extraction of hydrocarbons, however areas without extraction – oil and gas, fisheries or otherwise – may remain largely unexplored. One such area is the Naturaliste Plateau.

The Naturaliste Plateau is a large (90,000 km^2) marginal plateau off the southwestern coast of Western Australia and, like the Kerguelen Plateau, has geological ties to the greater India and Antarctica plates after the break-up of Gondwana (Halpin et al., 2008). Three of its steep sides extend from 2000 m to beyond 5000 m, and its southern face edges to hadal depths at the eastern margin of the Diamantina Fracture Zone. Despite its proximity and physical presence, a lack of commercial interest in this plateau has not compelled any biological or ecological research beyond 2000 m.

The Zenith Plateau and Cuvier Plateau (also known as the Wallaby Plateau) are two more plateaus that rise in the eastern Indian Ocean, situated in a geologically complex area surrounded by ridges and deep fracture zones. Like other plateaus in the Indian Ocean, their geology, formation and evolution are relatively well-described (see Symonds et al., 1998, Sayers et al., 2002, Daniell et al., 2010, Gibbons et al., 2012) compared to their biological community. Bond et al. (2023) classified the broad scale geomorphology of the Wallaby-Cuvier Escarpment on the southern margin of the plateau (Fig. 7F) and linked this to ecology, finding the highest diversity of organisms in the rocky debris field interlaced with soft sediment. The assemblage of macrobenthic organisms on the plateau and its slopes and escarpments are described as diverse but with exceptionally low abundance of animals (Daniell et al., 2010; Przeslawski et al., 2012; Bond et al., 2023). Low abundance of organisms could be a result of the oligotrophic conditions in the eastern Indian Ocean (Johannes et al., 1994; Lourey et al., 2006).

Conditions differ in the southeast Indian Ocean where iron-rich plateaus fertilise surrounding waters. Like the Kerguelen Plateau, the Crozet Plateau is located on the northern boundary of the Southern Ocean and within a larger region known to have high-nutrient, but low-chlorophyll, primarily due to low iron (Blain et al., 2007; Pollard et al., 2009). However, waters surrounding the plateaus like Crozet and Kerguelen are isolated hotspots of productivity caused by dissolved iron leaching from the shelf (Pollard et al., 2007; Wolff et al., 2011). Pulses of chlorophyll occur once irradiance increases during the austral spring and summer which sinks to the deep sea and increases the amount of organic matter available to organisms (Pollard et al., 2009; Wolff et al., 2011). Areas with high surface productivity induced by iron fertilisation have a different assemblage of macrobenthic organisms and fish compared to low iron areas nearby (Wolff et al., 2011; Cousins and Priede, 2012). Plateaus like Crozet and Kerguelen play a nuanced role in shaping the biological community of their surrounding deep sea and understanding this role better, warrants further research.

The Indian Ocean hosts several other plateaus of note as listed in Appendix 1, including the Mascarene Plateau, the second largest in the Indian Ocean (Fisher et al., 1967), and the Agulhas, Mozambique and Madagascar Plateaus that lie off southeast Africa (Goslin et al., 1980; Parsiegla et al., 2008; Jacques et al., 2019). These plateaus have also been subject to commercial interest from fisheries, and consequently research interest (see Roberts et al., 2020), especially at the Madagascar (Clark et al., 2007; Rogers, 2012) and Mozambique (Budnichenko et al., 1997; Parin et al., 2008) Plateaus. However, there remains a paucity of biological data at depths >1000 m for these features, especially for benthic environments.

9.10. Ridges

A ridge is an elongated elevation with steep sides of varying complexity and size (IHO, 2019), some of which may be seismically active while others are aseismic. The Indian Ocean has four main active spreading ridges: the Central Indian Ridge (CIR) which extends into the Carlsberg Ridge (CR) to the north, the Southwest Indian Ridge (SWIR) which is connected to the Mid-Atlantic Ridge system, and the Southeast Indian Ridge (SEIR) which is connected to the Pacific-Antarctic Ridge. Each of these ridge systems have differing characteristics and spreading rates, though their crusts are generally considered to be thinner than normal because of their slow spreading rates (Suo et al., 2016). They also host a diverse range of geological formations including guyots, seamounts and hydrothermal vents; the biodiversity of which are discussed in subsequent sections of this review.

The SWIR is the second slowest spreading ridge in the world at an ultraslow rate of ~15 mm/year (Patriat et al., 1997; van der Most et al., 2023). Investigations of the SWIR were instrumental in the discovery of ultraslow spreading ridges globally (Dick et al., 2003). One key artifact of the SWIR is its hypothesised role as a corridor for gene flow between the world's oceans (e.g., for hydrothermal vent fauna, German et al., 1998). Exploration of the ridge has resulted in the discovery of new species and new geographic records such as the sponge-associated polychaete *Bathymoorea*, a genus previously only known from the northeast Pacific (Periasamy et al., 2023e). Conversely, the SEIR has a more uniform and intermediate spreading rate of 69–75 mm/year while the CIR has a slow to moderate spreading rate of ~48 mm/year (Sempéré and Cochran, 1997; Kumagai et al., 2008; van der Most et al., 2023). Variation in spreading rates and the resulting stability of ridges often leads to differences in their biology (Copley et al., 2016). The CR to the north has a slow spreading rate of 22–32 mm/year (Murton and Rona, 2015; van der Most et al., 2023). Sautya et al. (2017) provided the first quantitative exploration of the benthic megafaunal assemblages on the CR, recording eight different substratum types and 90 megafaunal taxa from seven phyla, including cnidarians, echinoderms, poriferans and chordates. As with the SWIR, investigations of the CR have resulted in the discovery of new taxa including a new genus and species of glass sponge, *Indiella ridgenensis* (Sautya et al., 2011b). In contrast, the SEIR remains one of the least biologically studied regions of the Indian Ocean, including for seamount and hydrothermal vent ecology (see subsequent sections), despite being a major active spreading centre. Indian Ocean ridges have also been a focal area for fisheries operations, with fishery activity historically covering most ridges of the Indian Ocean (Budnichenko et al., 1997, Romanov, 2003; see subsequent section on seamounts).

Other Indian Ocean ridges of note include the Ninetyeast Ridge, the longest linear intraplate rise globally which formed via hotspot trace of the Kerguelen mantle plume (Levchenko et al., 2021), the associated Broken Ridge (Frey et al., 2000), and the similarly formed Chagos-Laccadive Ridge via the Réunion hotspot trace (Sreejith et al., 2019); all of which are examples of aseismic ridges driven by intraplate volcanism.

9.11. Seamounts

The seafloor is scattered with volcanically derived features of discrete elevation that form at ridge-transform fault intersections, overlapping spreading centres, in intraplate regions and at hotspots, and that can occur as chains, clusters or in isolation (Fig. 7C; Iyer et al., 2012). According to the IHO (2019), there are four distinct features that fall under the general umbrella of this definition, though applied

definitions vary between studies (Rogers, 2018). *Seamounts* are conically shaped features with elevations >1000 m from the surrounding seafloor, although the term 'seamount' is also readily used for features of lower elevations (>100 m) in ecology (Wessel, 2007), *guyots* are flat-topped seamounts, *knolls* have a rounded profile but with <1000 m elevation, and *hills* are irregularly shaped knolls. The number of seamounts that occur globally varies depending on the estimation method and definitions used (Kitchingman et al., 2007; Clark et al., 2010; Yesson et al., 2021), with recent estimates for the Indian Ocean ranging from 1082 seamounts and 28 guyots (Harris et al., 2014) to 4023 seamounts and 19,909 knolls (Yesson et al., 2011). Despite improvements in modern datasets, 'phantom seamounts' derived from misinterpretations of no-bottom-sounding data persist in updated predictions, with the majority of those identified concentrated in the Indian Ocean (Yesson et al., 2021). However, even by Harris et al.'s (2014) more conservative estimate, the Indian Ocean's seamounts occupy a considerable proportion of the ocean basin, with a collective area almost twice the size of Madagascar. For the purpose of this review, the term seamounts will encompass all these features hereafter (Clark et al., 2010).

Seamounts are globally recognised as areas of biological importance in the deep sea, supporting abundant benthic communities and forming complex habitats at their summit and flanks (Clark et al., 2010; Rogers, 2018). Seamounts are also known to attract mobile megafauna such as cetaceans, sharks and large fish (Rogers, 2018), the physical processes associated with their topography enhancing productivity or food supply within their vicinity (Rogers, 2012). In the Indian Ocean, seamounts are mostly associated with ridge systems and among others found in abundance in the Mid-Indian Ocean Basin and along the Southwest Indian Ridge. Iyer et al. (2012) further provided a summary of the differing formation and emplacement of Indian Ocean seamounts with descriptions of several known seamounts, primarily in the northern and central Indian Ocean. However, research effort to explore the faunal communities and ecology of Indian Ocean seamounts is particularly poor compared to other regions (Clark et al., 2010).

Demopoulos et al. (2003) called for complete benthic habitat descriptions for Indian Ocean seamounts, yet scientific knowledge 20 years later is still lacking. Roberts et al. (2020) summarise the history of seamount exploration and fisheries research in the Indian Ocean. Species records collated by the SeamountsOnline initiative up to 2010 are limited for the Indian Ocean, with only 1148 records for 279 species compared to 12,010 records for 1953 species in the Pacific and 6588 records for 1141 species in the Atlantic (http://seamounts.sdsc.edu/). Seamounts in the southern Indian Ocean support aggregations of commercially important fish species, and biological datasets predominantly come from the deep-sea fishing industry or from national fisheries research programmes (Romanov, 2003). Furthermore, the majority of these Indian Ocean records are from Walters Shoal, a collection of shallow (18 m) seamounts at the Madagascar Plateau (Rogers, 2012), thus are not representative of the biodiversity of deeper seamounts in the region. Similarly, extensive seamount chains and abundant isolated seamounts have been mapped in the Mid-Indian Ocean Basin (Das et al., 2007), yet their faunal communities remain unknown.

Most seamounts in the Indian Ocean have summits >1000 m, with a mean summit depth of ~2400 m (Yesson et al., 2011), yet these deeper seamounts are rarely explored (Clark et al., 2010). Instead, the little benthic research that has been conducted for Indian Ocean seamounts has generally been restricted to those with shallower summits (<1000 m depth), primarily at the SWIR. Two major research cruises surveyed the area in 2009 and 2011 as part of the NERC/IUCN Seamounts Project, specifically targeting the Coral, Melville Bank, Middle of What, Sapmer Bank, and Atlantis Bank seamounts (Rogers and Taylor, 2011; Rogers et al., 2017). The SWIR seamounts are of biogeographical interest owing to the Agulhas, Subtropical and Subantarctic Fronts that demarcate the region (Pollard and Read, 2017; Read and Pollard, 2017; Rogers et al., 2017). These surveys resulted in the discovery of several new species including octocorals (Taylor and Rogers, 2017), carnivorous sponges (Hestetun et al., 2017) and holothurians (O'Loughlin et al., 2013). Diverse faunal communities were also discovered from within coral rubble and carbonate material atop the seamounts, including 34 different polychaete families (Narayanaswamy et al., 2017). Furthermore, given the commercial interest in seamount-based fisheries in the region, a strong focus was placed on understanding the productivity dynamics and pelagic communities of the SWIR seamounts (Budnichenko et al., 1997; Djurhuus et al., 2017; Laptikhovsky et al., 2017; Letessier et al., 2017; Rogers, 2017; Rogers et al., 2017; Sonnekus et al., 2017; Rogers, 2018; Cherel et al., 2020).

The megabenthic communities of seamounts have also been explored in the Andaman Sea, whereby two seamounts with different summit depths were surveyed and compared to the biodiversity of the adjacent basin floor. Faunal abundances were found to be greatest at the seamounts compared to the surrounding basin, with the highest number of taxa observed at their flanks (Sautya et al., 2011a). Distinct faunal communities were recorded between the shallow- (434 m) and deep-summited (1336 m) seamounts, the deeper of the two dominated by porifera and cnidaria at its summit, as well as arthropods and other taxa at its more biodiverse flank (Sautya et al., 2011a). Six ophiuroid species were also collected at the Andaman seamounts, all of which were new records for the Andaman Sea including two new species (Stöhr et al., 2012).

The research conducted at the SWIR and Andaman Sea highlights the biological importance of seamounts and emphasises the need to pursue similar exploratory studies for deeper seamounts in the Indian Ocean (Clark et al., 2010). Further, seamounts are highly variable in morphology and depth ranges, with implications for seamount ecology. For example, five seamounts mapped at the Southwest Indian Ridge (SWIR) differed in their seascape composition and configuration despite belonging to the same geological feature (Swanborn et al., 2023a). The varied seascapes and spatial heterogeneity of seamount habitats influenced the biodiversity supported by these seamounts and likely their ecological functioning (Swanborn et al., 2023a, 2023b). However, such interactions have not yet been explored for the majority of Indian Ocean seamounts, compounding the need for increased ecological research.

Recent surveys as part of baseline environmental and benthic ecological assessments for deep-sea mining in the Indian Ocean have been a catalyst for new biodiversity discoveries for deep-summited seamounts. Such exploration has resulted in the description of several new species and new species distribution records for seamounts on the Central Indian Ridge and SWIR, including bamboo corals (Periasamy et al., 2023a), black corals (Periasamy et al., 2023b), octocorals (Periasamy et al., 2023c), carnivorous sponges (Periasamy and Ingole, 2022), *Spongicoloides* shrimp (Periasamy et al., 2022), and squat lobsters (Periasamy et al., 2023d). As well as improved research effort for deeper seamounts and for Indian Ocean seamounts in general, future research should also include more detailed study of the flanks and bases of seamounts given the indications that these areas support distinct assemblages (Baco, 2007, Sautya et al., 2011a, 2011b). For example, autonomous landers deployed to the base of the Afanasij Nikitin Seamount (~4700 m) in the Mid-Indian Ocean Basin in 2017 resulted in the collection of seven amphipod species including two potentially new abyssal species of *Hirondellea* and *Cyclocaris* (Weston et al., 2021).

The anthropogenic threats to Indian Ocean seamounts are stark. Demersal and benthopelagic fish have been trawled at SWIR seamounts since the 1970s (Marsac et al., 2020a, b). Today, seamount fisheries are prominent in the southern Indian Ocean including seamounts at the Southwest Indian Ridge, Conrad Rise, Mozambique and Madagascar Plateaus, and Ninetyeast and Broken Ridges (Clark et al., 2007: Table 17.9). Five SWIR seamounts were classified as SIOFA BPAs (Walters Shoal, Coral, Middle of What, Atlantis Bank and Fools Flat) in 2018. While these seamounts were part of the voluntary SIODFA BPAs prior to this (Shotton, 2006), the SIOFA designation provides active conservation and management measures prohibiting bottom fishing in the BPAs (Marsac et al., 2020a, b, SIOFA, 2023, SIOFA Secretariat, 2023a,

2023b). As with other deep-sea environments, marine litter often pollutes seamounts, the majority associated with lost fishing gear (Woodall et al., 2015; Rogers, 2018), and microplastic fibres have also been found in the sediments and biota of SWIR seamounts (Woodall et al., 2014; Taylor et al., 2016). Finally, although no mining contracts have yet been agreed for Indian Ocean seamounts, they may nonetheless be future deep-sea mining targets for the cobalt-rich ferromanganese crusts (CFC) that form at their summits (Halbach et al., 2017; Miller et al., 2018), thus improved research effort is critical for understanding potential CFC mining impacts in the region.

Like seamounts, oceanic islands are topographic elevations rising from the seafloor that penetrate the sea surface instead. They often form part of larger chains but have never been connected to the mainland (Dawson, 2016). Several nations bordering the Indian Ocean have oceanic islands in their territory, such as the Seychelles and Maldives in the western Indian Ocean, India's Lakshadweep Islands, and Australia's Cocos-Keeling archipelago in the eastern Indian Ocean. Deeper slopes of oceanic islands in the Indian Ocean equally exhibit complex geomorphology hosting rich biodiversity. For example, a 2022 expedition to the Cocos-Keeling archipelago revealed variety of deepwater habitats and species potentially new to science along atoll slopes, providing data that will also assist management plans (O'Hara, 2022). However, atoll slopes >1000 m typically remain under-sampled in the Indian Ocean, despite their importance for marine management in national waters.

9.12. Hydrothermal vents

Several Indian Ocean ridge systems are associated with hydrothermal vents. Hydrothermal vents are insular, chemosynthetic environments that occur in geothermally active areas where seawater percolates into the oceanic crust and is reemitted as superheated, mineral-rich fluid, which precipitates to form large chimney structures and supports a plethora of life via chemosynthesis (Van Dover, 2000). Active hydrothermal vent communities were first discovered in the Indian Ocean in 2000, with the description of faunal assemblages at the Kairei vent field just north of the Rodriguez Triple Junction on the Central Indian Ridge (CIR) (Hashimoto et al., 2001). Earlier evidence of a potential active vent community was recorded from the Southeast Indian Ridge (SEIR), with the retrieval of a vent-associated *Neolepas* barnacle from a dredge at the Site 21 vent field (Scheirer et al., 1998; Watanabe et al., 2018); however, this vent field has never been directly observed and no further publications have confirmed faunal activity at this site. Including Site 21, a total of 15 active vent fields have been observed: three along the Carlsberg Ridge (CR), seven on the Central Indian Ridge (CIR) (including two newly discovered sites), three on the Southwest Indian Ridge (SWIR), and two on the Southeast Indian Ridge (SEIR) (Table 3; van der Most et al., 2023, Jang et al., 2023).

Despite falling short compared to the research effort in the North Pacific and at the Mid-Atlantic Ridge (Thaler and Amon, 2019), hydrothermal vents are undoubtedly the best biologically characterised deep-sea ecosystem in the Indian Ocean, as summarised by Perez et al. (2021) and van der Most et al. (2023). This is likely owing, in part, to the deep-sea mining interest for the polymetallic sulfides that form the chimney structures of hydrothermal vents. Exploratory mining contracts have been granted by the International Seabed Authority (ISA) to the China Ocean Mineral Resources and Development Association (COMRA), Federal Institute for Geosciences and Natural Resources of Germany (BGR), and the Governments of India and Korea (Table 3, Fig. 1). Within the Indian Ocean, the region most in need of increased hydrothermal vent study is the SEIR, with 50 inferred active vent fields listed on the InterRidge global database that have been identified by plume activity but never observed directly (Beaulieu and Szafranski, 2020).

Indian Ocean vents form their own biogeographic province, hosting several unique species that have not been recorded elsewhere (Van Dover et al., 2001; Rogers et al., 2012; Copley et al., 2016; Perez et al., 2021), including, most notably, the scaly-foot snail *Chrysomallon squamiferum* (Chen et al., 2015). The Indian Ocean also hosts a high degree of locally endemic species known only from a single vent field, such as the gastropod *Dracogyra subfusca* (Chen et al., 2017, Perez et al., 2021, Thomas et al., 2021a,b). Further, four newly described species of *Anatoma* gastropods are considered endemic to vents in the central Indian Ocean (Hoffman et al., 2022). Such high levels of biodiversity uniqueness contributed to the evaluation that Indian Ocean vent species are under the greatest threat of extinction from deep-sea mining of the nine global vent biogeographic provinces (Thomas et al., 2021a,b). Using

Table 3
Known active hydrothermal vent fields in the Indian Ocean, adapted from van der Most et al., 2023 and Jang et al., 2023. Colours denote the proposed biogeographical subdivision of hydrothermal vent communities by Zhou et al., 2022 and Jang et al., 2023, with dashed lines denoting proposed geographic boundaries within a ridge system. Mining contracts – Korea: Government of Korea, BGR: Federal Institute for Geosciences and Natural Resources of Germany, India: Government of India, COMRA: China Ocean Mineral Resources and Development Association. Biogeographic sub-provinces – CR: Carlsberg Ridge, (n/s) CIR: (north/south) Central Indian Ridge, (n/s) SWIR: (north/south) Southwest Indian Ridge, SEIR: Southeast Indian Ridge.

Ridge	Vent field	Depth (m)	Mining contract	Biogeographic sub-province		Key references
				Zhou et al., 2022	Jang et al., 2023	
Carlsberg Ridge	Daxi	3450	–	CR	CR	Wang et al., 2021, Zhou et al., 2022
	Wocan	2973–3105	–	CR	CR	Wang et al., 2017, Zhou et al., 2022
	Tianxiu	3500	–	CR	CR	Zhou et al., 2022, Qiu et al., 2023
Central Indian Ridge	Onnare	2984	Korea	–	nCIR	Kim et al., 2020, Jang et al., 2023
	Onbada	2523	Korea	–	nCIR	Kim et al., 2020, Jang et al., 2023
	Onnuri	1990–2170	Korea	CIR–nSWIR	nCIR	Kim et al., 2020, Jang et al., 2023
	Dodo	2745	#	CIR–nSWIR	sCIR	Nakamura et al., 2012
	Solitaire	2606	#	CIR–nSWIR	sCIR	Nakamura et al., 2012
	Edmond	3290–3320	BGR	CIR–nSWIR	sCIR	Van Dover et al., 2001
	Kairei	2415–2460	BGR	CIR–nSWIR	sCIR	Hashimoto et al., 2001
Southwest Indian Ridge	Tiancheng	2682–2729	India	CIR–nSWIR	nSWIR	Tao et al., 2014, Zhou et al., 2018, Sun et al., 2020
	Duanqiao	1732	COMRA	sSWIR	sSWIR	Tao et al., 2014, Zhou et al., 2018
	Longqi	2755	COMRA	sSWIR	sSWIR	Tao et al., 2012, Copley et al., 2016, Zhou et al., 2018
Southeast Indian Ridge	Pelagia	3659	BGR	–	SEIR	Gerdes et al., 2019
	Site 21*	~2800	–	–	SEIR	Scheirer et al., 1998, Watanabe et al., 2018

*Note that vent activity has not been directly observed at Site 21 and the presence of a faunal community is evidenced only by the collection of *Neolepas* barnacles by dredge sampling (Scheirer et al., 1998). #The Dodo and Solitaire vent fields lie within the Mauritius EEZ under national jurisdiction.

vent-endemic molluscs as representative taxa and given the incidence of several deep-sea mining contracts within the region (Fig. 1), 60 % of species assessed were found to be Critically Endangered with 100 % considered threatened (Thomas et al., 2021b). Furthermore, van der Most et al. (2023) determined that all active vent fields in the Indian Ocean meet the scientific criteria for protection under CBD, IMO and FAO guidelines. At a higher taxonomic level, however, there are broad similarities between the faunal communities of vent fields in the Indian Ocean and those in the Atlantic, Pacific and Southern Oceans (e.g., *Kiwa* yeti crabs, *Rimicaris* shrimp, *Neolepas* barnacles, *Bathymodiolus* mussels, *Lepetodrilus* limpets, *Alviniconcha* gastropods, *Hesiolyra* polychaetes; Bachraty et al., 2009, Copley et al., 2016, Roterman et al., 2018, Zhou et al., 2018, Gerdes et al., 2019a, Wang et al., 2020).

Within the Indian Ocean province, there is a documented trend of continuous biogeographic transitions between the CR, CIR, and SWIR (Zhou et al., 2022). Distinct biogeographic subdivisions of the Indian Ocean province have been inferred accordingly, based on community structure and genetic differentiation of species located across multiple vent fields (Table 3). The distinctive clustering of vent communities between the proposed sub-provinces of the CR, CIR (including the Tiancheng vent field on the northern SWIR), and southern SWIR, is suggested to be linked to the numerous transform faults and fractures that scar these ridge systems (Sun et al., 2020; Zhou et al., 2022). A further phylogeographic boundary was also proposed between the Onnuri and Solitaire vent fields on the CIR based on the genetic divergence of *Alviniconcha* gastropods (Jang et al., 2023). At a local scale, faunal communities at Indian Ocean vent fields follow patterns of spatial zonation from chimneys with high hydrothermal activity, to areas of diffuse flow, to the vent periphery (Watanabe and Beedessee, 2014; Perez et al., 2021), as observed at other global vent fields (e.g., Marsh et al., 2012). For example, endemic *Rimicaris* shrimp often dominate the active venting chimneys, with abundant chemosymbiont-hosting *C. squamiferum* and *Gigantopelta* gastropods in areas of diffuse flow venting (Copley et al., 2016; Wang et al., 2021). In contrast, the vent periphery is largely host to organic-enrichment opportunists that are also capable of colonising other reducing environments, rather than vent specialists, such as the holothurian *Chiridota hydrothermica* (Thomas et al., 2020, Thomas et al., 2022).

The faunal communities at inactive hydrothermal vents are far less understood than active sites, despite the probability that these inactive sites will be the primary focus of prospective polymetallic sulfide mining activity (Van Dover, 2011; Gerdes et al., 2019b). Inactive and diffuse venting sites are often closely associated with active vent fields, which hampers their exploration as they are rarely prioritised. Inactive vents are those that do not currently exhibit fluid flow but are distinguished from extinct vents by their geological connection to an active source, such that they may potentially become active again in future (Jamieson and Gartman, 2020). The Duanqiao vent field on the SWIR was initially thought to be inactive, until vent-endemic taxa were discovered colonising an edifice with weak, but active, fluid venting (Zhou et al., 2018; Van Dover, 2019).

There are indications that inactive vent sites may host their own specialist communities (Gerdes et al., 2019b; Van Dover, 2019; Kniesz et al., 2022). For example, two previously unknown species of *Amphisamytha* polychaetes collected from an inactive chimney at the Longqi vent field have not been recorded elsewhere and are potentially specific to this environment (Zhou et al., 2018; Zhou et al., 2019). By studying a stand-alone inactive vent field, Gerdes et al., 2019b confirmed that the faunal assemblage at the hydrothermally extinct Gauss field is statistically distinct from the communities at the adjacent Edmond vent field, its periphery, and the surrounding hard- and soft-substrate non-vent areas. This discovery supports the existence of unique faunal assemblages related to inactive vent sites (Gerdes et al., 2019b). Furthermore, inactive polymetallic sulfides at the Kairei and Pelagia vent fields were found to host abundant microbial communities including microorganisms that are unique to the site or rare elsewhere (Han et al., 2018). Further known inactive hydrothermal fields in the Indian Ocean include the MESO Zone on the CIR and Mount Jourdanne on the SWIR, however, the true number of inactive deposits remains unknown and requires more exploration of the Indian Ocean's ridge systems, especially further away from the ridge crest (Jamieson and Gartman, 2020).

9.13. Subduction trenches

The deepest known point in the Indian Ocean is located in the Java Trench which is a subduction trench that reaches a maximum depth of 7187 m (±13 m) (Bongiovanni et al., 2022). Subduction trenches form at convergent plate boundaries. The Java Trench is formed as the Indo-Australian Plate subducts beneath the Eurasian Plate (Jamieson et al., 2022). Of all the trenches known globally, the Java Trench is the only subduction trench extending into the hadal zone in the Indian Ocean, making it a relatively geographically isolated hadal ecosystem (Jamieson et al., 2022). Consequently, hierarchal cluster analysis of hadal 'isolation' grouped the ~3200 km long Java Trench with West Pacific hadal sites rather than others in the Indian Ocean (Stewart and Jamieson, 2018).

Note that not all seafloor features named as trenches are associated with the hadal zone nor active subduction. For example, the Amirante Trench is a ~5200 m deep structure located south of Seychelles within the Mascarene Basin which has attracted the interest of geoscientists due to its enigmatic morphology. The Amirante Ridge/Trough Complex shares characteristics with subduction zones, transform faults and mid-oceanic ridges (Damuth and Johnson, 1989; Stephens et al., 2009; Rodriguez, 2020) and early theories posited it might be a potential asteroidal impact site (Hartnady, 1986). Recent research suggests that its origin may be linked to spreading along the Carlsberg Ridge and the India-Seychelles breakup events occurring around 63–65 Ma (Mukhopadhyay et al., 2012; Rodriguez, 2020). A full-coverage high-resolution map of the Amirante Trench was produced in 2020 (Caladan Oceanic, 2020), however, further research is required to uncover the ecosystems and biodiversity the Amirante Trench hosts.

Jamieson et al. (2022) summarised the biodiversity of the Java Trench, recording over 70 putative species across 10 phyla and 21 classes. A five-day expedition to the Java Trench in 2019 represents the only modern biological survey of this hadal trench, yielding several new species records and range extensions, including: the first record of hadal liparid snailfish in the Indian Ocean (Jamieson et al., 2022), first hadal cephalopod (Fig. 9F; Jamieson and Vecchione, 2020), deepest global larvaceans (Jamieson and Linley, 2021), and deepest Indian Ocean decapods (Swan et al., 2021). Additionally, the first hydrographic profiles of the trench were also recorded, providing bottom water conditions of 1.54 °C for in-situ temperature and 34.70 for practical salinity (Kolbusz et al., 2024). The diverse biological community of the Java Trench is characterised by elasipodid holothurians, amphipods including the supergiant *Alicellea gigantea*, *Bassozetus* cusk eels, and hexactinellid sponge aggregations (Jamieson et al., 2021; Jamieson et al., 2022). These faunal patterns are typical of hadal trenches (e.g., Jamieson et al., 2013b; Mironov et al., 2019). There are, however, some noticeable distinctions between Java and other global trench systems, such as the absence of *Hirondellea* amphipods despite their prevalence elsewhere at hadal depths (Weston and Jamieson, 2022; Jamieson and Weston, 2023).

The Java Trench seafloor can be categorized into six different habitat types which drives benthic species distributions within the trench (Jamieson et al., 2022). For example, faunal community shifts are apparent between the flat, fine-grain sediment-covered trench and plateau floors, and the steeper, bedrock-exposed slopes, with holothurians and brittle stars or anemones and asteroids dominating these respective communities (Fig. 7J; Jamieson et al., 2022). Patchiness in species distributions can also be linked to this habitat heterogeneity, exemplified by the discovery of the dense hexactinellid sponge aggregations only beneath overhangs of the upper trench slope (Jamieson

et al., 2022).

Likewise, spatial patchiness may be a feature of the potential hadal chemosynthesis observed in the Java Trench. Numerous putative chemosynthetic bacterial mats were observed exploiting the structural weaknesses in the exposed bedrock of the forearc escarpment (Fig. 7D, E), however, it remains to be seen whether they are restricted to these steep, structurally complex areas within the trench (Jamieson et al., 2022). Similar bacterial mats were recorded in association with outcrops and talus at Sirena Deep in the Mariana Trench (Hand et al., 2020) and it is possible the hadal chemosynthesis phenomenon may occur in other areas of structurally weak bedrock on the fore-arcs of global subduction trenches (Blankenship-Williams and Levin, 2009; Jamieson et al., 2022).

Sedimentation rates vary within and between trench systems, in turn influencing this habitat heterogeneity (Stewart and Jamieson, 2018). For example, the accumulation of sediment in the deepest part of trenches (see 'trench resource accumulation depth' in Jamieson et al., 2010) often supports higher species abundances, typified in the Java Trench by increases in the number of holothurians and anemones observed at the trench floor and towards the base of the trench slope, respectively (Jamieson et al., 2022). However, despite lying within the ultra-productive Sunda-Arafura Sea Coastal biogeochemical province (Longhurst, 2007), particulate organic carbon (POC) flux models suggest the Java Trench receives lower annual POC input than >50 % of other major global trenches (Lutz et al., 2007; Stewart and Jamieson, 2018).

9.14. Transform faults and fracture zones

Transform faults are the active perpendicular offsets between two ridge segments of a mid-ocean spreading centre which extend into inactive fracture zones either side of the main ridge system (Hensen et al., 2019), collectively referred to here as fracture zones. Some of these fracture zones can reach hadal depths (>6000 m), of which there are eight in the Indian Ocean (Table 4, Fig. 10). Only two of these have been mapped and their hadal status confirmed: the Wallaby-Zenith Fracture Zone (WZFZ) to the east (6675 m, Niyazi et al., 2024), and the Diamantina Fracture Zone (DFZ) in the southeast (7019 ± 17 m, Bongiovanni et al., 2022). There are several other named fracture zones that intersect the mid-Indian Ocean ridges (Appendix 1).

Compared to subduction trenches, the WZFZ is a small hadal feature (Weston et al., 2021) but is an area of tectonic importance as a consequence of the breakup of Greater India and Australia-Antarctica subcontinents and the opening of the Indian Ocean (Ali and Aitchison, 2005; Gibbons et al., 2012; Olierook et al., 2015). Published accounts of the fauna at WZFZ to date include amphipods (Weston et al., 2020, 2021), fish (Jamieson et al., 2021), decapods (Swan et al., 2021), and the functional feeding strategies of demersal and benthic macrofauna (Niyazi et al., 2024). Weston et al. (2020) described a new genus and two new species of amphipod from the WZFZ from abyssal depths within the fracture zone. Furthermore, cluster analysis of community structure compared to those of other hadal features in the Pacific Ocean suggested that the assemblage hadal amphipods at WZFZ is merely an extension of the abyssal community, despite the abundant presence of the hadal specialist *Bathycallisoma schellenbergi* (Weston et al., 2021, 2022). As such, and conversely to community structure shifts observed in subduction trenches, Weston et al. (2021) postured that the WZFZ represents an area of transitional community composition from abyssal to hadal, likely owing to the comparable seafloor topography between the upper Zenith Plateau and the flat bottom of the hadal fracture zone.

First discovered in 1960 (Jempson, 2019), the DFZ is also an area of geological importance for studying ancient tectonic patterns, including the breakup of Australia from Antarctica (Markl, 1978; Mammerickx and Sandwell, 1986). Like the WZFZ, the DFZ is one of the smallest hadal areas globally (Stewart and Jamieson, 2018). It is, however, the deepest of the Indian Ocean's fracture zones and its deepest point, the Dordrecht Deep, was once believed to be the deepest part of the Indian Ocean (Stewart and Jamieson, 2019). For this reason, the Five Deeps Expedition, which mapped the deepest points in each ocean, surveyed the Dordrecht Deep in 2019 and found it to be <200 m shallower than the Java Trench (Bongiovanni et al., 2022). A single lander deployment made at the Dordrecht Deep recovered amphipods, including the cosmopolitan hadal species *B. schellenbergi*, which is also known from WZFZ and the Java Trench (Weston et al., 2022). Due to the surveys of

Table 4
Hadal features (>6000 m) of the Indian Ocean. We determine approximately 20 seafloor features with associated hadal areas in the Indian Ocean (see Fig. 10). Maximum depths are derived from GEBCO_2023 bathymetry or from confirmed studies where definitive multibeam bathymetry is available. Areas were calculated using GEBCO data in QGIS.

Feature type	Feature name	Total hadal area (km^2)	Max. depth (m)		References
			GEBCO	Confirmed	
Subduction trenches	Java Trench	78,303	7210	7187	Bongiovanni et al., 2022, GEBCO_2023
	Total (trenches)	78,303 (28 %)			
Fracture zones	Diamantina Fracture Zone	12,670	7174	7019	Bongiovanni et al., 2022, GEBCO_2023
	Wallaby-Zenith Fracture Zone	1357	6649	6675	Niyazi et al., 2024, GEBCO_2023
	Vema Trench Fracture Zone	284	6315	–	GEBCO_2023
	Melville Fracture Zone	722	6653	–	GEBCO_2023
	Atlantis II Fracture Zone	490	6450	–	GEBCO_2023
	Gazelle Fracture Zone	54	6223	–	GEBCO_2023
	Gallieni Fracture Zone	477	6374	–	GEBCO_2023
	Andrew Bain Fracture Zone	1826	6673	–	GEBCO_2023
	Total (fracture zones)	19,391 (7 %)			
Troughs, basins and other features	Wharton Basin	174,430	7371[#]	–	GEBCO_2023
	Langseth Trough	164	6607	–	GEBCO_2023
	Brouwer Trough	1427	6404	–	GEBCO_2023
	South Australian Basin	57	6573	–	GEBCO_2023
	Madagascar Basin	844	6766	–	GEBCO_2023
	Mozambique Basin	567	6253	–	GEBCO_2023
	Agulhas Basin	1091	6325	–	GEBCO_2023
	Weddell Basin	79	6091	–	GEBCO_2023
	Zenith Plateau*	209	6088	–	GEBCO_2023
	Lost Dutchmen Ridge*	382	6345	–	GEBCO_2023
	Dirck Hartog Ridge*	1511	6363	–	GEBCO_2023
	Total (basins)	179,250 (65 %)			
	Total (all)	276,944			

*Note that, in the absence of definite names, these hadal areas are clustered under adjacent seafloor features and are not necessarily associated with the geological formation of these features. [#]Note that this max. depth is altimetrically derived and is unlikely to be the deepest point in the IO.

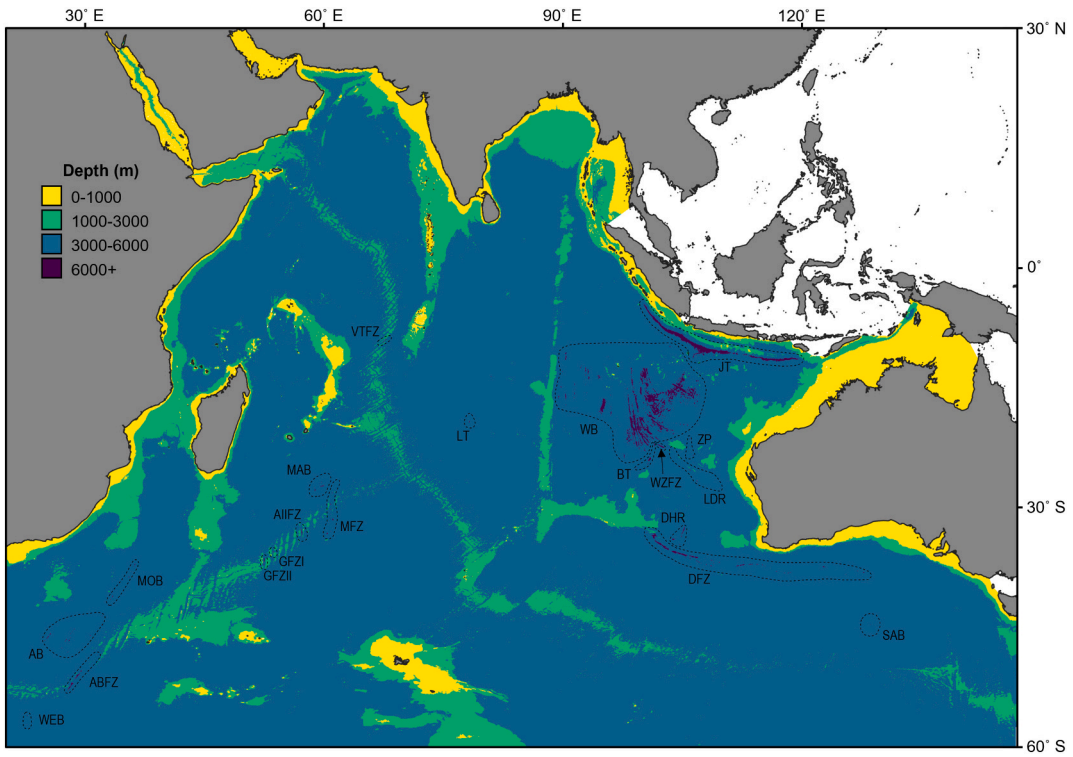

Fig. 10. Hadal features of the Indian Ocean, with hadal depths >6000 m and hadal features marked by dashed lines. AB: Agulhas Basin, ABFZ: Andrew Bain Fracture Zone, AIIFZ: Atlantis II Fracture Zone, BT: Brouwer Trough, DFZ: Diamantina Fracture Zone, DHR: Dirck Hartog Ridge, GFZI: Gazelle Fracture Zone, GFZII: Gallieni Fracture Zone, JT: Java Trench, LDR: Lost Dutchmen Ridge, LT: Langseth Trough, MAB: Madagascar Basin, MFZ: Melville Fracture Zone, MOB: Mozambique Basin, SAB: South Australian Basin, VTFZ: Vema Trench Fracture Zone, WB: Wharton Basin, WEB: Weddell Basin, WZFZ: Wallaby-Zenith Fracture Zone, ZP: Zenith Plateau.

Geoscience Australia (2017), the Five Deeps Expedition (Bongiovanni et al., 2022), and multibeam data from the search for flight MH370 (Picard et al., 2018) the WZFZ and DFZ are remarkably well-mapped deep-sea areas of Indian Ocean.

There are no available biological data for any of the other six hadal fracture zones in the Indian Ocean. Contrary to its moniker, the Vema Trench is in fact a fracture zone which offsets the Central Indian Ridge by ~300 km between 7°40′ and 10°40′ S, ranging from depths of 3000–4000 m at its peripheries to >6000 m at its deepest point (Dhawaskar et al., 2018). The Vema Trench was once thought to be the deepest point in the western Indian Ocean (Heezen and Nafe, 1964); however, other features appear to be deeper based on modern bathymetric data (Table 4). There are no published biological surveys of the area, and most geological surveys are from the 1960–70s (e.g., Heezen and Nafe, 1964, von Herzen and Vacquier, 1966, Fisher et al., 1967, 1971). Incidentally, one of the most prominent fracture zones in the Atlantic Ocean is also named Vema (Devey et al., 2018); both sites seemingly named after the RV *Vema* (Heezen and Nafe, 1964).

Many hadal areas in the central and western Indian Ocean have never been explored and their depths, currently derived from satellite altimetry data, have not been verified by multibeam echosounder bathymetry. This variation in the quality of available bathymetric data demands caution in the interpretation of the extent and maximum depth of hadal features (Table 4), especially in lesser-known areas where values may be overestimated, such as the western Indian Ocean (Jamieson et al., 2024).

The paucity of biological studies for the hadal fracture zones in the Indian Ocean demonstrates how non-subduction hadal features are rarely prioritised for biological research even by modern deep-sea exploration programmes. Studies of the hadal zone have largely focussed solely on subduction trenches to date, overlooking non-subduction features such as fracture zones and troughs, despite their importance in unravelling the ecology and evolution of hadal biodiversity (Weston et al., 2021). Although less conspicuous and often shallower than subduction trenches, the discovery of endemic hadal species from these relatively small and isolated fracture zones is suggestive of their importance in the global connectivity of hadal environments (Jamieson and Stewart, 2021; Weston et al., 2022). Since 2021, the Minderoo-UWA Deep-Sea Research Centre has undertaken research cruises to both the WZFZ (DSSV *Pressure Drop* 'Indomitable' expedition) and DFZ (*Pangea Ocean Explorer*) to fill these knowledge gaps. Using baited landers and a manned submersible, these cruises aimed to map habitat types (Fig. 7A, I) and study the biological communities in these areas (Figs. 7–9; Niyazi et al., 2024). However, no such expeditions have been conducted or planned for the hadal fracture zones of the central and southwestern Indian Ocean.

9.15. Deep troughs and basins

As well as subduction trenches and fracture zones, hadal areas are also found scattered across Indian Ocean basins (Fig. 10). A deep trough is defined here as a "long depression generally wide and flat bottomed with symmetrical and parallel sides", and basin is defined a "depression more or less equidimensional in plan and of variable extent" as per the definitions in IHO (2019). Despite their names, features such as the Chagos Trough (~5900 m, Raghukumar et al., 2004) are not considered here as they do not reach hadal depths. Of the Indian Ocean's hadal features, the Wharton Basin in the northeast is the largest in terms of total area > 6000 m (Table 4, Fig. 10; Weston et al., 2021). The significant hadal footprint of the Wharton Basin, across ~10 degrees of latitude, is comparable to the extensive hadal basins of the northwest Pacific (Jamieson et al., 2024). Indeed, deep troughs and basins account for 65 % of the total hadal area in the Indian Ocean (Table 4) yet remain understudied. They could provide complex connectivity networks for hadal-obligate species, sustaining gene flow between isolated hadal features (Weston et al., 2021). For example, the eight north-south

trending compartments of the Wharton Basin may act as dispersal corridors between the Java Trench and the Wallaby-Zenith and Diamantina Fracture Zones, with ~1.4 million km^2 of seafloor deeper than 5600 m between the three features (Jacob et al., 2014; Weston et al., 2021). Given the range of different hadal features all within close proximity, including troughs, basins, fracture zones and a trench (Fig. 10), the East Indian Ocean represents one of the most interesting opportunities to explore these connectivity patterns, globally. In contrast, the deep troughs and basins of the central and western Indian Ocean are much smaller in area and, as with lesser-known fracture zones, require further investigation to verify their status as hadal features (Table 4). As greater recognition is given to their significance for hadal research (Jamieson and Stewart, 2021), these aseismic hadal features should be prioritised for future research expeditions.

10. Pelagic environments

It is widely recognised that global knowledge of the pelagic ocean, that is the mid-water environment between the ocean's surface and the seafloor, is extremely poor (Webb et al., 2010). To date, pelagic research in the Indian Ocean has been largely restricted to the upper 1000 m, with most pelagic surveys occurring at epipelagic (0–200 m) and mesopelagic (200–1000 m) depths (Vipin et al., 2012, Wafar et al., 2011, Obura, 2015, Bernal et al., 2020a, 2020b). Similarly, existing demersal surveys for groundfish in the Indian Ocean are generally limited to depths <1000 m (Venu, 2013; Aneesh Kumar et al., 2017). Moreover, a large proportion of the available pelagic Indian Ocean literature is focussed on the summits of shallow seamounts, charismatic megafauna, or species targeted by fisheries (Vipin et al., 2012, Ebert, 2013, Ménard et al., 2013, Ebert, 2014, Rogers, 2017, Rogers et al., 2017, Cherel et al., 2020, Marsac et al., 2020a, b, Roberts et al., 2020). Meanwhile, limited sampling of invertebrates and fish at all depths of the water column renders the systematic assessment of total deep pelagic biodiversity impossible (Obura, 2015).

While seminal in the promotion and compilation of Indian Ocean research, the International Indian Ocean Expedition (IIOE, 1960–1965) primarily focussed on understanding biological oceanographic processes, primary productivity, and monsoon seasonality (Ryther, 1963; Hood et al., 2016; Urban Jr., 2020). The Second IIOE (IIOE-2, 2015–2025) likewise aimed to advance understanding of oceanic, atmospheric, and geologic process and interactions in the Indian Ocean (Hood et al., 2015, Hood et al., 2016, see special issues for IIOE-2 research in Deep Sea Research Part II: Topical Studies in Oceanography – e.g., Hood and Beckley, 2019 volume 1). Thus, while the IIOE programs provided a significant scientific foundation for our modern understanding of the Indian Ocean including insights into the pelagic realm (Zeitzschel and Gerlach, 2012; Hood and Beckley, 2019), they do not directly address the biological communities of the deep pelagic Indian Ocean.

11. Synthesis

Twenty years ago, Demopoulos et al. (2003) concluded that the deep Indian Ocean remains poorly known and is still waiting to be discovered and understood. Now, 20 years later, we review how deep-sea ecosystem research has advanced, synthesising our updated knowledge of deep-sea habitats and biodiversity in the Indian Ocean, and presenting outstanding problems for this field of research going forward.

Most deep-sea research in the Indian Ocean has been focused on certain ecosystems in specific regions. In the eastern Indian Ocean, the best characterised deep-sea ecosystems are the Australian continental margin especially its submarine canyons, the Java Trench, and other geologically complex features such as the Diamantina and Wallaby-Zenith fracture zones. Conversely, the varying ecosystems of the Wharton and South Australian basins and Southeast Indian Ridge have scarcely been surveyed and require targeted future exploration. Similarly, the remote southern Indian Ocean, especially the Australian-Antarctic Basin, is thoroughly lacking in deep-sea research, save for limited surveying at the Kerguelen and Crozet plateaus. Meanwhile, the primary deep-sea research focus in the western Indian Ocean has been the seamounts and hydrothermal vents of the Southwest Indian Ridge, as well some industry-driven research at the continental margins of eastern African countries such as Tanzania and Kenya. Despite this, there is a disparity in deep-sea research between the western and eastern Indian Ocean exemplified by the lack of hadal exploration for the western Indian Ocean's numerous fracture zones. Hydrothermal vent research continues northwards along the Central Indian Ridge and Carlsberg Ridge to the Arabian Sea, where existing research has focussed on the faunal communities and productivity patterns at the abyssal seafloor. Cold seeps and oxygen minimum zones dominate deep-sea research interest in the northern Indian Ocean, alongside the brine pools of the Red Sea, while the primary research target in the central Indian Ocean is the polymetallic nodule field of the Mid-Indian Ocean Basin. In contrast, the deep-sea ecosystems of major seafloor features such as the Mascarene Plateau, and Chagos-Laccadive and Ninetyeast ridges remain unexplored.

11.1. Inconsistencies over spatial scales

Spatial inconsistencies pose a significant hurdle to the advancement of deep-sea research in the Indian Ocean, both in research extent and effort. Of the countries bordering the Indian Ocean, India and Australia are leading the way for deep-sea research within EEZs, likely owing to greater access to resources including equipment and ship time. Meanwhile exploration in ABNJ has generally been restricted to specific sites of interest such as seamounts and hydrothermal vents along the mid-ocean ridge systems and potential industry targets such as the Mid-Indian Ocean basin. There are also bathymetric inconsistencies in sampling effort whereby the majority of biological data collected are from shallower bathyal depths (Fig. 6), a trend seen across other global oceans and likely linked to the increase in resources and technology required for deeper surveys (Bridges et al., 2023). This bias towards shallower sampling limits our ability to gain a holistic understanding of the deep Indian Ocean system.

At a regional scale, a lack of consistency in the defining limits of the Indian Ocean means data from holistic Indian Ocean studies are not directly comparable. For example, a global study of ophiuroid diversity unconventionally delimited the Indian Ocean at ~90° E and ~ 30° S, such that records from the majority of the eastern Indian Ocean are attributed instead to the Indo-Pacific region while records from the southern Indian Ocean are split between the 'South Africa' and 'South Pacific' regions (Stöhr et al., 2012). A further study reviewing the state of knowledge of coastal and marine biodiversity in the Indian Ocean similarly considered only the northwestern region of the Indian Ocean (Wafar et al., 2011). Meanwhile, the Australian Hydrographic Office regards the south Australian margin, including the Great Australian Bight, as the northerly limit of the Southern Ocean rather than the internationally accepted 60° S.

To achieve a spatially comprehensive and accurate understanding of large-scale ecological and biodiversity patterns in the deep Indian Ocean requires:

1) wider access to technologies for deep-sea exploration within EEZs via capacity building initiatives and national collaborations (Gates et al., 2017a, Woodall et al., 2021),
2) targeted research initiatives in ABNJ, especially regions that are known to be under-sampled (e.g., SEIR),
3) improved open-access data via the use of global databases like OBIS and the promotion of FAIR data principles (Klein et al., 2019; Levin et al., 2019), and

4) consistency in the use of terminology and defining limits used for ocean basin-wide studies to allow for regional and global comparisons.

11.2. Data gaps over temporal scales

At present, there is no targeted long-term monitoring of deep-sea ecosystems in the Indian Ocean. Deep Indian Ocean research is consequently lacking data over temporal scales whereby existing discrete data are unlikely to capture any seasonal or annual shifts in the faunal communities and abiotic features of deep-sea habitats that may occur in response to natural events or anthropogenic impacts (Wafar et al., 2011). Some research programmes have conducted multi-year sampling to study such trends, including the INDEX project examining the environmental impacts following a simulated mining event in the Mid-Indian Ocean Basin (1997–2001; Ingole et al., 2005), and the BIGSET project's study of the coupling between monsoon-driven productivity cycles and benthic processes in the Arabian Sea (1995–1998; Lochte and Pfannkuche, 2000). However, there remains a paucity of continually sustained monitoring and time-series studies essential for recording temporal change in deep-sea ecosystems to the degree seen in other ocean basins (Glover et al., 2010).

Elsewhere, long-term monitoring via observatories or repeated surveying have facilitated the collection of valuable time series datasets. The Porcupine Abyssal Plain Sustained Observatory (PAP) in the North Atlantic and Station M in the North Pacific represent two of the best examples of long-term observing in the deep ocean, with over 30 years of in situ data collected from abyssal depths (PAP: 4850 m, Station M: ~4000 m; Lampitt et al., 2010, Smith Jr. et al., 2017, Smith Jr. et al., 2020, Hartman et al., 2021). Meanwhile, cabled observatories such as the Monterey Accelerated Research System (MARS) provide the power and network accessibility of an onshore laboratory thus enabling long-term, real-time experiments and testing of new deep-sea equipment like the benthic rover (Henthorn et al., 2010), however they are often restricted to shallower depths (e.g., MARS: 891 m). Indeed, other than the Indian Ocean and South Pacific, some form of long-term multidisciplinary deep-sea monitoring has been undertaken via observatory systems in all other global oceans (Glover et al., 2010), including MABEL – Southern Ocean (Cenedese et al., 2004; Gerber and Clauss, 2010), HAUSGARTEN – Arctic Ocean (Soltwedel et al., 2005; Bergmann et al., 2011), and DELOS – South Atlantic (Vardaro et al., 2013). The integration of long-term observatories and repeated surveying would foster a new era of deep-sea exploration and increase research capacity in the deep Indian Ocean.

11.3. Unexplored deep pelagic environments

In keeping with the available literature, much of this review is dedicated to the benthic habitats and communities of the Indian Ocean. The chronic under-exploration of the deep pelagic ocean and lack of a biodiversity baseline for this environment leaves a substantial gap in our knowledge of the deep Indian Ocean (Robison, 2009; Webb et al., 2010). Establishing a biodiversity baseline for the Indian Ocean's (and indeed the Earth's) largest habitat by volume is essential to identify the regional patterns in community composition and the main environmental or ecological drivers across different depth gradients (Haddock and Choy, 2024). As such, a greater focus is required for the mid-water communities of bathypelagic, abyssopelagic and hadal depths (Webb et al., 2010), as well as the mesopelagic zone (Haddock and Choy, 2024), to fully catalogue and understand the deep-sea biodiversity patterns of the Indian Ocean. The recent drive to prioritise deep pelagic research and mid-water ecology, as well as the integration of new sampling techniques such as eDNA, has resulted in knowledge advancements for biodiversity distribution and population monitoring in the Pacific and Atlantic Oceans (Li et al., 2022b). Similar effort should now be given to prioritise deep pelagic research in the Indian Ocean.

11.4. Placing the deep Indian Ocean in a global context

The final consideration for the future promotion of deep-sea research in the Indian Ocean is the need to consider the Indian Ocean in a global context. The Indian Ocean is too often overlooked in global studies or disregarded for the supposition of its lack of data. While there are certainly data limitations, as summarised above, this review highlights that the Indian Ocean's deep-sea ecosystems are better-known than commonly considered. Furthermore, studying the Indian Ocean in isolation neglects the interconnectivity of global ocean processes and faunal biogeography. For example, several studies have demonstrated the importance of the Indian Ocean as a potential connectivity pathway for hydrothermal vent fauna between the Atlantic and Pacific Oceans, whether as a dispersal corridor supporting modern gene flow (German et al., 1998, Hwang et al., 2022) or as an evolutionary corridor creating a melting pot of Atlantic and western Pacific vent species in the Indian Ocean (Perez et al., 2021). Likewise, on a global scale, the Indian Ocean is often considered a single biogeographic province (e.g., lower bathyal province BY11 and abyssal province AB8 – Watling et al., 2013; hydrothermal vents – Rogers et al., 2012). However, recent studies have suggested multiple biogeographic subdivisions for hydrothermal vent fauna, effectively dividing the Indian Ocean's ridges into four subregions (Table 3; Zhou et al., 2022, Jang et al., 2023). Future research should consider whether similar biogeographic patterns arise for other deep-sea ecosystems in the Indian Ocean. Greater recognition of the regional and local heterogeneity of the Indian Ocean's deep-sea ecosystems, as well as the uniqueness of its abiotic characteristics, would highlight its importance for understanding global ocean processes thus promoting further research interest and prioritisation in these areas.

As with our recommendations for improving data inconsistencies over spatial scales, newly collected data should be published in open-access data repositories so that they are readily available for use in future global studies (Klein et al., 2019). This need is exemplified by the comparative lack of OBIS records for the deep Indian Ocean (>1000 m), with ~5–16 times the number of records per 1 million km^2 available from other global oceans, pre-quality checks and data cleaning (Appendix 2; https://mapper.obis.org/, accessed 03/04/2024). Ensuring these data are available for future studies will provide greater international recognition of the significant deep-sea research effort that has arisen from Indian Ocean exploration to date. Utilising this existing research in conjunction with global oceanographic and geomorphic patterns will provide the background to ensure the deep Indian Ocean is not overlooked nor misrepresented on a global stage.

12. Conclusion

We provide the most comprehensive review of deep-sea ecosystem research in the Indian Ocean to date. By recognising and championing the deep-sea research effort undertaken thus far, this review provides the necessary platform to inform future studies and ensure the Indian Ocean is prioritised for deep-sea exploration. Addressing the knowledge gaps and outstanding problems identified by this review will foster the advancement of deep-sea research in the Indian Ocean during the UN Ocean Decade and beyond.

CRediT authorship contribution statement

Elin A. Thomas: Writing – review & editing, Writing – original draft, Visualization, Project administration, Investigation, Conceptualization. **Todd Bond:** Writing – review & editing, Writing – original draft. **Jess L. Kolbusz:** Writing – review & editing, Writing – original draft. **Yakufu Niyazi:** Writing – review & editing, Writing – original draft, Visualization. **Denise J.B. Swanborn:** Writing – review & editing, Writing – original draft. **Alan J. Jamieson:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This review was supported by the Minderoo-UWA Deep-Sea Research Centre, funded by the Minderoo Foundation and Inkfish. We thank the two anonymous reviewers for their helpful feedback to improve this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.176794.

Data availability

No data was used for the research described in the article.

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