An assessment of the offshore marine natural values of Australia's Indian Ocean Territories.

Timothy D. O'Hara

Museums Victoria

Final Draft, July 2021

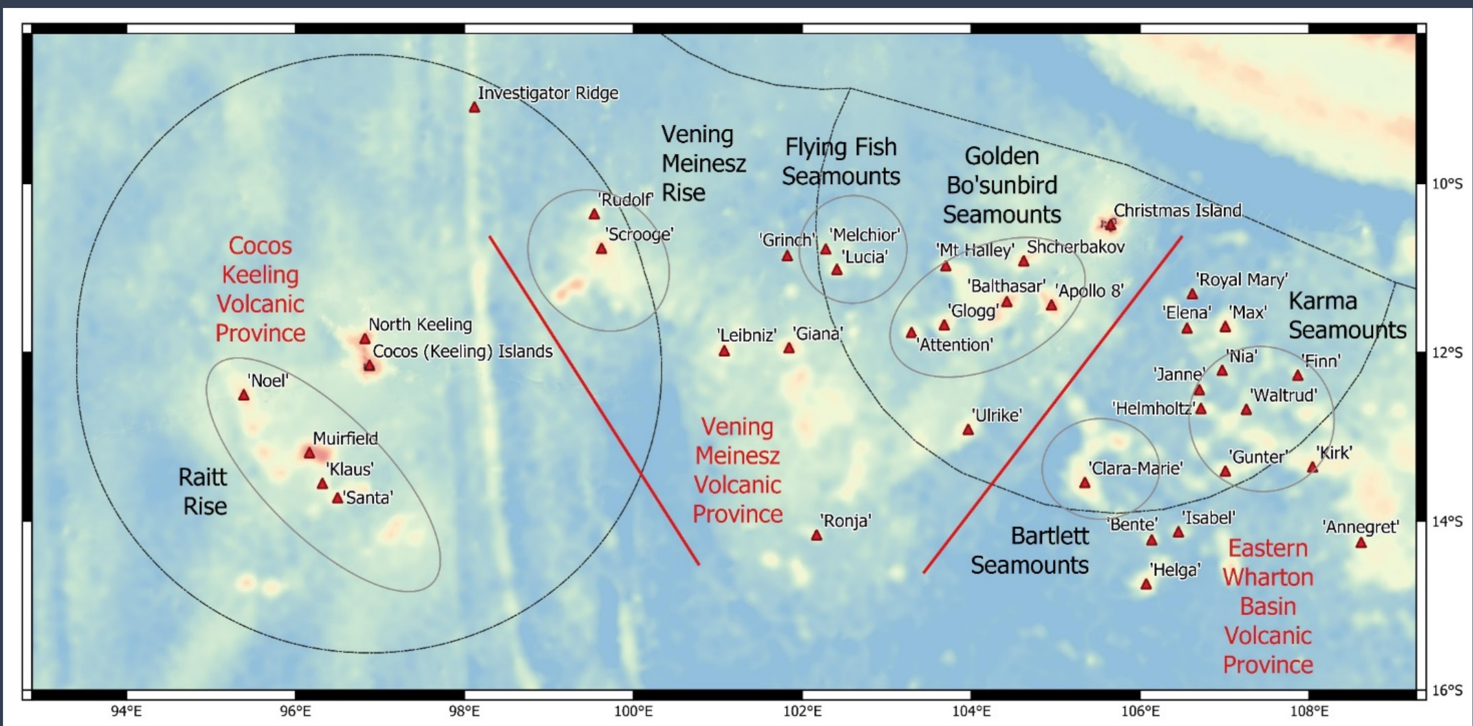

Table of Contents

Executive summary

Most of our knowledge of marine biodiversity of Australia's Indian Ocean Territories (IOT) is largely restricted to coastal waters around Christmas and Cocos (Keeling) Islands. However, we do know that the vast majority of the marine realm across the two territories is deep-sea, with seafloor consisting of seamounts and ridges, abyssal and hadal plains. This bio-assessment draws upon knowledge of the IOT shallow water fauna, infrequent observations from scientific voyages to the area, and from better-surveyed deep-sea habitats elsewhere.

Depth (and its oceanographic correlates temperature, salinity, oxygen, nutrients and carbonate dissolution) and surface primary production are likely to be the major determinants of seafloor community composition at large scales. At smaller spatial scales, substratum type (rock vs soft sediment) and current velocity will also be important.

Different communities are likely to occur in coastal (0-30 m), mesophotic (30-200 m), upper bathyal (200-1000 m), mid bathyal (1000-2000 m), lower bathyal (2000-4000 m), abyssal (4000-6000 m) and hadal (>6000 m) depths. Although, the boundaries between these layers are only approximate and individual species may inhabit only a part of one depth layer or parts of two or more layers.

Primary productivity varies in a NE to SW direction across the IOT, with the highest productivity occurring near Indonesia and the lowest in the mid Indian Ocean. This will alter the abundance and diversity of benthic communities.

There are three seamounts in the IOT that support rare mesophotic and upper bathyal habitats (30-1000 m). These occur on the flanks of seamounts that underlie Christmas and Cocos Islands, and the peaks of the Muirfield Seamount, to the SW of Cocos. Seamount biodiversity is generally structured by on-going or historical migration from surrounding regions that reflect predominant current patterns. As the currents at mesophotic and upper bathyal depths are similar in strength and direction to those at the sea-surface, it is probable that the biodiversity will reflect patterns seen in IOT coastal waters. Thus we can expect the mesophotic and upper bathyal biological assemblages to be a mixture of Pacific and Indian Ocean species and populations characteristic of this depth, that arrive on the westward flowing South Equatorial Current from Indonesia and the South Java Current from the NE Indian Ocean. The biodiversity on these three seamounts are likely to be distinct, due to different primary productivity regimes and individual migration and environmental history.

Other seamounts, particularly in the Golden Bo'sunbird chain southwest of Christmas Island, peak between 1000 and 2000 m (mid bathyal). These seamounts experience a mixture of intermediate-depth water originating from the south, north and east and so their community composition will reflect this complex biogeography. The majority of seamounts in the region, and the Investigator Ridge, peak between 2000-4000 m (lower bathyal) and experience deep-water masses originating in the south. The NE to SW gradient in primary productivity will alter benthic community composition and abundance. The Golden Bo'sunbird chain (Christmas Island EEZ) is in an area of relatively high productivity, while the Raitt seamount chain (Cocos Islands EEZ) is in an area of relatively low productivity. The abyssal plain is very deep across the IOT, frequently below 5000 m and consists of siliceous sediments and manganese nodules. There are also some seafloor at hadal (> 6000 m) depths to the east and south of Christmas Island, and to the SE of Cocos Islands. The fauna on and around manganese nodules has been found elsewhere to differ from that found on soft sediments.

A number of marine mammals, seabirds, turtles and fish feed in offshore waters. Species that breed on or around the islands typically forage in the surrounding waters, including the endemic Abbott's booby and Christmas Island frigatebird. Migrating predators such as tuna, mackerel, dolphins, sharks, and seabirds tend to aggregate in the open ocean around schools of small fish that are in turn reliant on patches rich in plankton. The spatial and temporal distribution of these aggregations is unknown. Pelagic planktivores such as manta rays and whale sharks are known to occur around the two island groups. Whale sharks are known to target the abundant larvae of the Red land crab around Christmas Island during summer. The entire Christmas Island EEZ is part of the only known spawning site for Southern bluefin tuna.

The oceanic seamount and island communities (30-2000 m) in the IOT are rare examples of these habitats in the eastern tropical Indian Ocean and are of national to international conservation significance. The presence of rocky substrata at lower bathyal depths, manganese nodules at abyssal depths, and troughs at hadal depths are significant in a regional context.

1. Introduction

1.1. Context for this report

Most of our knowledge of the marine biodiversity values of Australia's Indian Ocean Territories (IOT) around the Cocos (Keeling) and Christmas Islands is largely restricted to coastal waters. However, through the surveys and studies that have occurred, we know that the vast majority of the marine realm across the two territories is deep-sea, with seafloor consisting of seamounts and ridges, abyssal and hadal plains. Nevertheless, most areas have not been mapped with modern multibeam technology and only rarely been surveyed by research vessels, which have largely focused on the geology or oceanography.

To assist with planning and future management of new marine parks in the IOT, Parks Australia has asked Museums Victoria to help fill this research and planning gap. Museums Victoria led a mid-2021 RV *Investigator* voyage to the IOT that explored the deep sea around Christmas Island. Unfortunately, the Cocos (Keeling) Island leg of the voyage was postponed and is expected to be rescheduled to 2022. Three versions of this report will be produced as knowledge and understanding of IOT waters expands through these voyages:

1. The first version (this document) relies on information available as at June 2021 (before the RV *Investigator* voyages.
2. The second version (expected to be available in late 2021) will incorporate new information from the RV *Investigator* voyage to Christmas Island.
3. The third version (expected to be available in late 2022 will incorporate new information from the postponed RV *Investigator* voyage to Cocos (Keeling) Islands

This report, a broad assessment of the offshore natural values of the IOTs is complemented by the report *Proposed offshore Key Ecological Features and Biologically Important Areas of Australia's Indian Ocean Territories*, also by Museums Victoria.

1.2. Background

Christmas Island (137.4 km^2) and the Cocos (Keeling) Islands (27 islands, 15.6 km^2) are two of Australia's remote offshore territories. They are surrounded by Territorial Sea (to 12 nm) and Exclusive Economic Zones (EEZs, 12-200 nm). The area of the Christmas EEZ is 325,021 km^2 and the Cocos EEZ is 463,371 km^2.

The marine environment is predominantly abyssal plain punctured by clusters of massive ancient seamounts that formed 120-47 million years ago. The two island groups (Christmas and Cocos) are both the summits of tall seamounts that rise over 5,000 m from the abyssal plain. Another seamount, Muirfield, rises to within 16 m of the surface. The others have summits at 1000-3000 m below sea-level. The Investigator Ridge runs south-north through the eastern Cocos EEZ at lower bathyal depths (< 2500 m).

These waters are managed by the Commonwealth of Australia, although some functions associated with the delivery of government services in the IOTs are outsourced to other agencies. As at June 2021 two IOT national parks extend a short distance into marine waters. The first is Pulu Keeling National Park that includes North Keeling Island and surrounding seas. The second is the Christmas Island National Park that extends 50 m offshore in places where the terrestrial part of the park meets the sea.

A variety of names have been applied to seamounts, clusters of seamounts, rises and volcanic provinces within the IOT marine regions. To avoid confusion, this assessment uses the unofficial seamount names of Werner et al. (2009) placed in quotation marks (Fig. 1) as they refer to single identifiable features mapped using multibeam sonar. However, many seamounts are still unnamed (see Appendix 1 for more explanation).

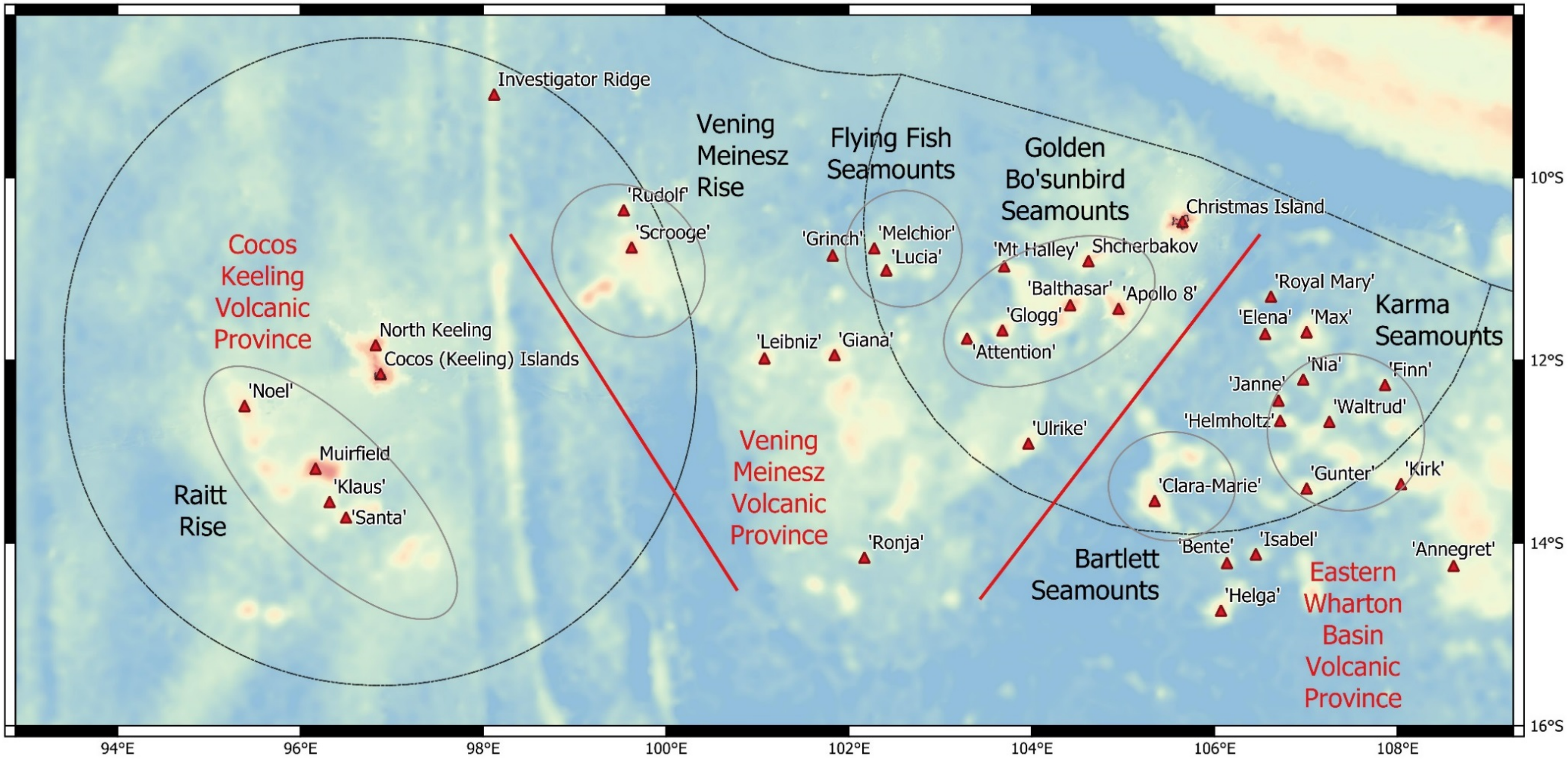

Figure 1. Topographical names given to features in the IOT. Volcanic Provinces follow Hoernle et al. (2011). The ellipses show approximate locations of seamount clusters named in the GEBCO gazetteer. The names in quotes are unofficial seamount names from Werner et al. (2009). The bathymetry is from AusSeaBed.

2. Physical Setting

The IOT sit in the Wharton Basin, part of the northward moving Indian-Australian plate that is slowly being subducted under the Eurasian plate in the Sunda Trench that occurs offshore of Java and Sumatra. But the Wharton seafloor and seamount clusters were formed long ago under different geological conditions. In general, the seamounts formed alongside a series of underwater ridges that have been subducted under the Eurasian plate over time. One hundred and forty million years ago, the Indian-Australian plate was part of Gondwana and much further south than today. The northern edge was bounded by a mid-ocean spreading (Neo-Tethyan) ridge that separated the westward rotating Gondwana from the northwards moving Meso-Tethys plate that formed the seafloor of the central section of the Tethys Sea [1]. The ancient seamounts of the Argo Basin (115˚E, east of the Christmas Island EEZ) formed as off-ridge volcanos 136 mya [2]. Although new seafloor was continually laid down along the Neo-Tethyan Ridge, the Meso-Tethys plate was gradually reduced in size through subduction along its northern margin [1], until the ridge Neo-Tethyan Ridge itself started to subduct (105 mya). Another cluster of seamounts (Eastern Wharton) formed south of the ridge on the Australian plate (115-95 mya) [2]. A third cluster of off-ridge seamounts (Vening Meinesz) formed 95-64 mya [2]. Around 100-80 mya, Gondwana proceeded to break-up, India accelerated northwards and a new spreading (Wharton) ridge was formed between the Indian and Australian plates [1]. The final cluster of IOT seamounts was formed in the Cocos Basin (56-47 my) to the east of the Wharton Ridge [2]. The Meso-Tethys was largely subducted by 55 mya. The Australian Plate accelerated northwards, once again merging with the Indian Plate and extinguishing the Wharton Ridge (43-36 mya). These IOT seamount provinces formed much further south (at ~35-45˚S) than they are at present.

The Investigator Ridge is a ~1,800 km long north-south orientated ridge in the oceanic crust of the Wharton Basin, which is assumed to have formed prior to the plate tectonic reorganization of the circum-Indian area at 90 to 100 million years ago [3]. Due to the collision of India with Asia, the western part of the Indo-Australian Plate has been prevented from moving further northwards, while the eastern half of the plate is being subducted beneath Indonesia. This difference in movement is producing north-south aligned fracture zones in the ocean crust, part of a developing plate boundary. The younger crust to the west of the Ridge appears to be offset by ~900 km from the older crust to the east. There is a steep west-facing scarp along most of the fracture zone, which implies recent reactivation of older fractures [3].

Many of the IOT seamounts are massive, over 70 km in diameter, and rise 3-5 km above the seafloor. Some appear to have been at sea level at some point. They have flattened wave-formed summits [3] (called 'guyots') and are covered in Cretaceous (75-65 million years ago) limestones that contain shallow-water reef-building fossils, including (now extinct) rudist and *Inoceramus* bivalves [4]. However, the seamounts were heavier than, and gradually subsided into, the relatively young oceanic crust, and many now summit 2-3 km below sea-level.

There are two exceptions to this scenario of seamount subsidence. The seafloor of the Australian plate flexes upwards as it is forced to subduct into the Sunda Trench [5]. The Christmas Island seamount sits just trench-wards of the bulge and has been uplifted 361 m above sea-level. Several seamounts to the south-west of Christmas Island have risen to be now 1000-1500 m below sea-level. This flexing of the oceanic crust has led to secondary bouts of volcanic activity at Christmas Island during the Eocene (43 to 37 million years ago) and Pliocene (4.5 to 4.2) periods [5].

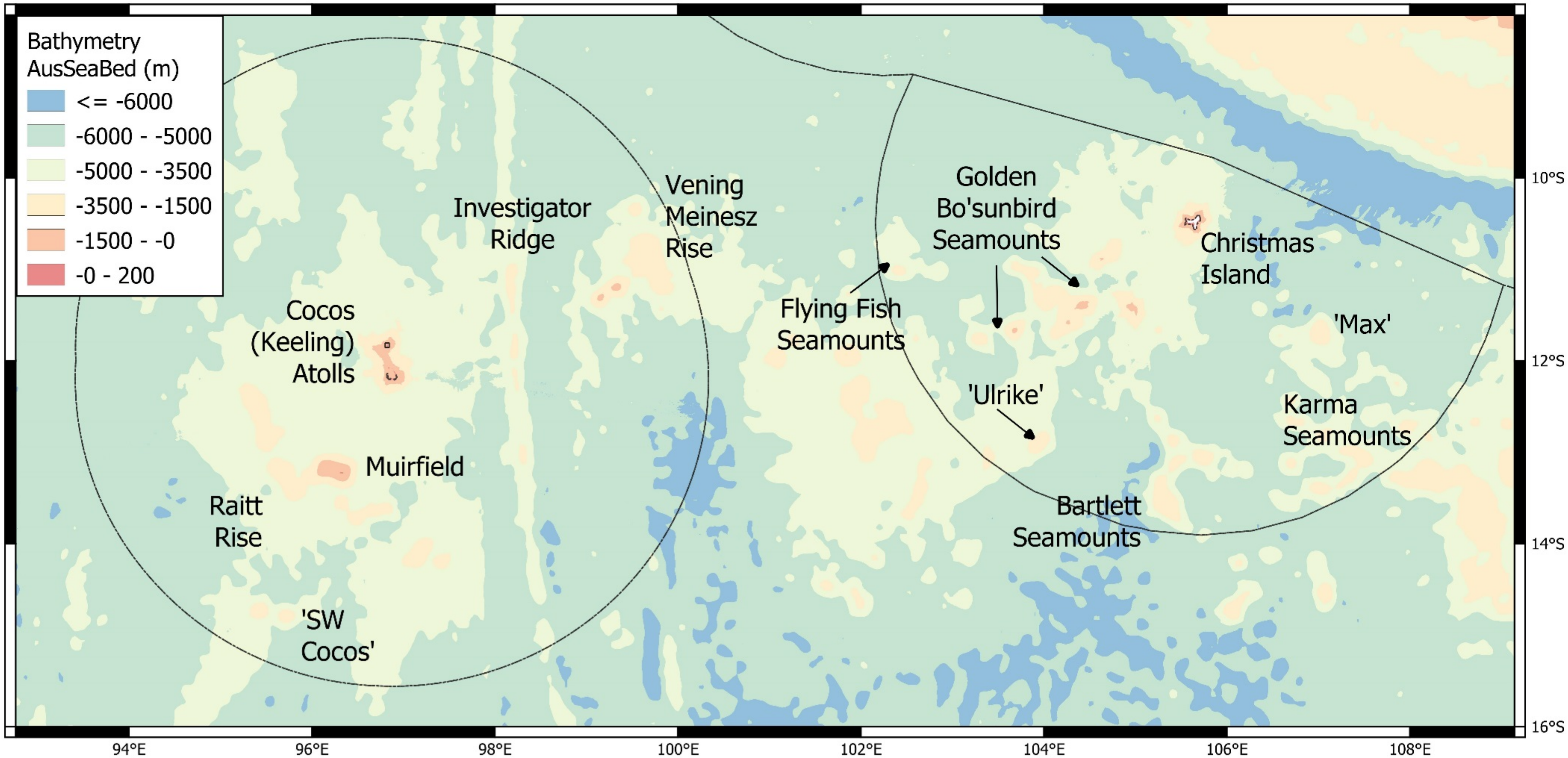

Figure 2 Seafloor bathymetry derived from the AusSeaBed dataset categorised into 6 depth layers. Topographical names follow the GEBCO gazetteer, informal names have single quotation marks

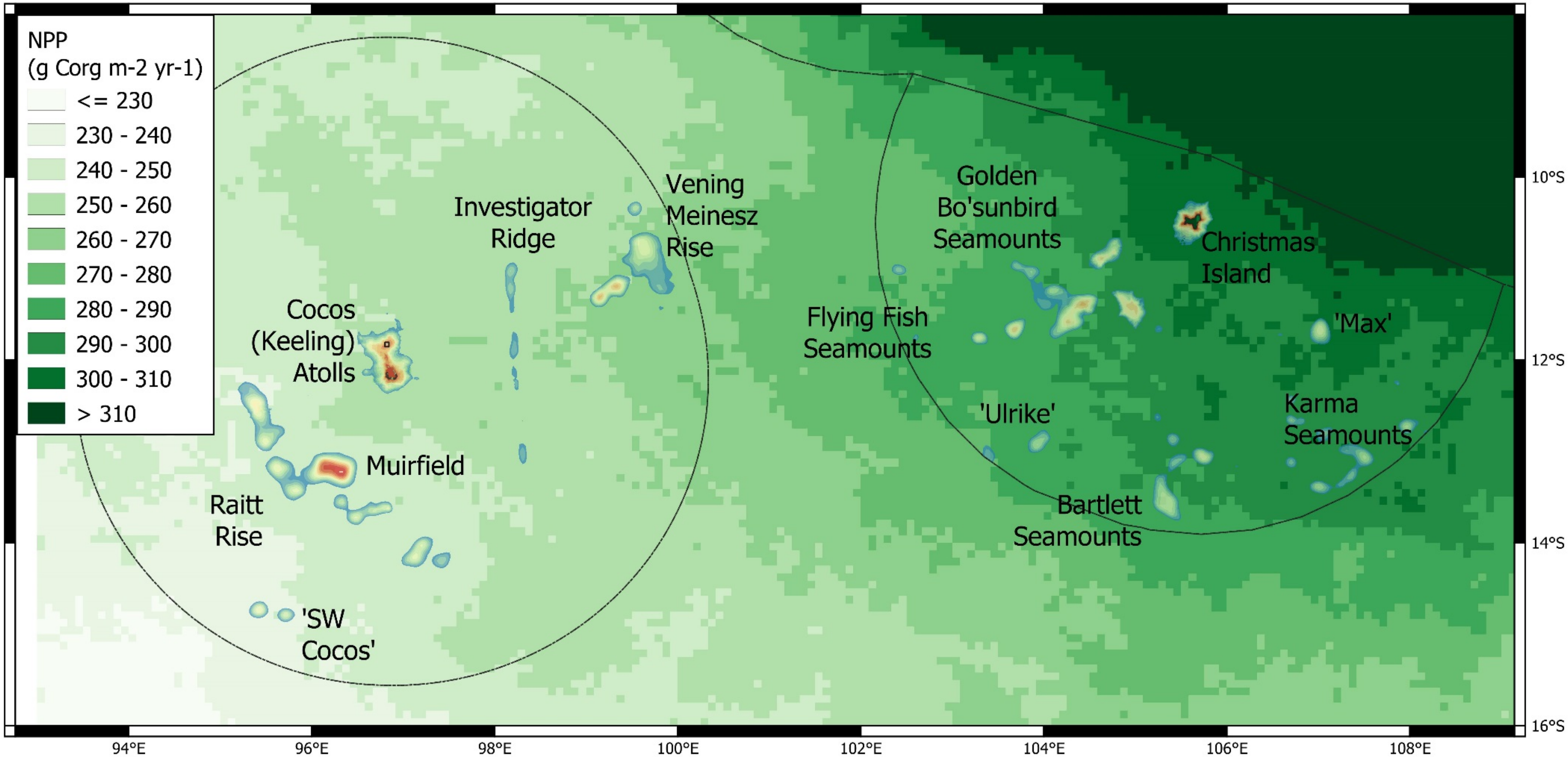

Figure 3. Annual Net primary productivity (NPP) as derived from a vertically generalized production model (VGPM) from 10 years of satellite-derived chlorophyll [23] showing a NE->SW gradient from a high near Indonesia (north of Christmas Island) to a low west of the Cocos EEZ. Seafloor bathymetry (3500-0 m, blue to red, from AusSeaBed) are superimposed over the NPP layer. Corg = organic particulate carbon. Topographical names follow the GEBCO gazetteer, informal names have single quotation marks.

The second anomaly affects seamounts in the Cocos EEZ. A magma plume to the SW [6] is hypothesised to be preventing the subsidence of the Muirfield seamount and slowing the subsidence of Cocos. The slowed rates of subsidence for Cocos has facilitated continuous coral growth and atoll development on the summit, and this seamount is now topped with 0.9-2.1 km of limestone [5]. The summit undergoes Karst development during the lowered sea-levels of glacial periods and the centre is dissolved by rainwater and reduced in height. With rising sea-levels, the rim forms an atoll and the centre forms a lagoon [7, 8]. Muirfield shows signs of relatively recent volcanism on its summit [9], although there is no record of active volcanic activity today.

Overlaying the oceanic crust and flatter areas on seamounts, are layers of carbonate sediment formed from the skeletal remains of pelagic organisms that are gradually compressed to form clays or oozes [4]. The oozes shift from being of calcareous to siliceous origin below 5000 m [10]. These sediment layers are relatively thin compared to other seafloors [11], as the overlying water column has been relatively unproductive, from 150 m of sediment to the west of the Cocos EEZ [12] to over 450 m west of Christmas Island [13] nearer the Sunda trench. The summit of Muirfield also has areas of coarse unconsolidated rippled sand implying strong currents [9]. The sediment aprons around the seamounts also include quantities of volcanic debris [14].

Manganese nodules are known to occur on the surface of siliceous clays (4780-5888 m) to the south-west of Christmas Island [10]. Ash from Indonesian volcanos may inhibit their formation further north [10]. Manganese crusts have formed on rocky seamount surfaces that are free of sediment [10]. Neither resource is economically valuable enough to extract [10].

3. Oceanography

The IOT are located in tropical latitudes in the eastern Indian Ocean. In winter the climate is dominated by SE monsoonal winds, and in summer by the western monsoon. Summer cyclones are common. The mixed-layer depth (the depth to which water turbulence blends oceanographic conditions) is between 40-80 m depending on how this is calculated.

The IOT sits in the path of the South Equatorial Current (SEC), a jet-like flow that contains low saline waters from the Pacific that has traversed across central Indonesia and out into the eastern Indian Ocean. It contains two separate water masses, one flowing at the surface (Indonesian Through Flow waters, ITW) and one at 500-1100 m (Indonesian Intermediate Water, IIW) [15, 16]. During summer, the monsoon winds drives the surface Java Current to the northern IOT from the NW, before it retroflexes and gets entrained by the SEC [17]. Some mixing between the ITW/IIW and Central Indian Water (to the south of the IOT) is also likely to occur [14].

Below 1000 m the currents tend to originate from the south. Antarctic Intermediate water (1800-1500 m, AAIW), originating at subantarctic latitudes flows along the western Australian coast. However, this water starts shoaling just (to 1200 m) to the south of the IOT (18-20˚S) as it gains salinity and it also gets entrained by the SEC and pushed west [14-16]. The AAIW and IIW possibly interleave with each other in finger-like extensions [15].

Both the Indian Deep Water (IDW, 2-3,800 m) and the Antarctic Bottom Water (AABW, or Lower Indian Deep Water, below 3,800 m) flow north along the Ninety East Ridge (which is more like 89°E at IOT latitudes) [18]. Indian Deep Water appears to mainly originate in the Atlantic Ocean via the circumpolar current south of Africa. However, the IDW would also include bottom waters that have gradually warmed, lost oxygen and upwelled in the northern Indian Ocean. There must be some southerly flows of IDW to offset the northerly flows but its location is unknown.

Annual water temperatures at the surface to 50 m are about 27˚C, falling to 10˚C by 350 m and 5˚C by 1000 m. Deep water varies from 2.5˚C at 2500, 1.2˚C at 3800 m and 1.1˚C at 5000m. Oxygen-levels reach a minimum (~80 µmol kg^{-1}) at depths of 550-750 m, but never reach the low levels experienced in a severe oxygen minimum zone (< 20 µmol kg^{-1}). Both surface waters and bottom waters are well oxygenated. Other oceanographic parameters such as salinity and silica also vary a little throughout the water column, but, although small differences in these values are used to characterise and track water masses, they are not likely to affect the function of benthic fauna.

Conversely, variation in Net Primary Productivity (NPP) has a marked effect on the biomass and richness of seafloor communities, from local [19, 20] to regional scales [21, 22]. The waters over the IOT are generally oligotrophic, except the nearest points to Indonesia (Fig. 3). Annual NPP declines in a gradient from the NE to the SW, however, phytoplankton production is seasonal. In winter (July-August) tongues of elevated phytoplankton extend to Christmas Island before being pushed westward by current over the northern half of the Cocos EEZ. However, in early summer (November-December) phytoplankton is slightly elevated in the southern Cocos EEZ [14].

4. Geomorphology and potential habitats

The fauna of the seafloor in the IOT is largely unknown. Previous faunal surveys have been focused almost exclusively on shallow water habitat (0-60 m) around Christmas and Cocos Islands. However, the vast majority of the IOT consists of deep-water habitats.

The biota will principally respond to depth (and environmental factors that correlate with it, such as light penetration, temperature, salinity, oxygen and nutrients), substrata (soft vs rocky seafloor surface), water flow, and primary productivity. Seafloor substrata (rock vs sediment) and water flow characteristics are very important in structuring marine faunas, but generally vary at too fine a scale to be mapped into bioregional units. The type of basement rock is often irrelevant unless it is exposed. There need only be a 10 cm covering of sediment over a rocky basement for the fauna to become a typical soft-sediment community.

Oxygen is not a limitation in the IOT as it is in other parts of the world where oxygen minimum zones (OMZ) occur. These form at upper bathyal depths where circulation is poor and shallow water productivity is high (the decomposition of which uses up available oxygen), and oxygen falls to less than 20 µmol kg^{-1}. The IOT is on the southern margin of the North Indian OMZ, however, the powerful currents from the deep Indonesian Through-Flow ensure oxygen levels remain above 75 µmol kg^{-1} and hence are not hypoxic or anoxic.

Consequently, this assessment categorises habitats along gradients of depth and net primary productivity (Table 1). Depth zones are based on water masses and typical faunal distributions. The evolutionary divergence between shallow (including the mesophotic zone, 0-150 m) and deep-sea animals can be in the order of hundreds of millions of years [24, 25]. To survive the cold, the immense pressures, the lack of light and limited food supply, deep-sea animal lineages may have to evolve a whole new biochemistry, physiology or anatomy. Change in community composition continues below 150 m, although this is not as dramatic as the change between shallow and deep. Ecologists have divided up the deep-sea into the bathyal (equivalent to continental slopes, 200-4000 m), the abyssal (plain, 4000-6000 m) and the hadal (trenches, below 6000 m) zones. Bathyal seafloors occur around continents, seamounts, ridges and volcanic plateaus. These zones are not uniform however, particularly the bathyal zone and there are very few organisms that can tolerate the range of conditions from 200 to 4000 m. It is convenient to divide the bathyal zone into upper (200-700 m), mid (700-2000 m) and lower (2000-4000 m) strata that reflect differing water masses (Table 1). However, these strata are just a convenient approximation. In reality, community composition changes continually through the bathyal region, with many species having overlapping bathymetric ranges [26]. Here, the boundary between upper and mid bathyal zones is set at 1000 m, the lower depth of the deep Indonesian ThroughFlow water.

The same depth layers on separate seamounts are linked by dispersal. Many organisms or their larvae/propagules can swim or be transported across the water to colonise similar depth ranges elsewhere. They don't descend, cross the abyssal plain, and re-climb the next seamount. The abyssal depths would kill them. A good way to visualise the connectivity of marine populations is to focus on colour similarities on a 3D topographic map (Fig. 4).

A major driver of community composition is food availability. The biomass, abundance and diversity of seafloor communities will differ between areas of high and low productivity [27]. Annual NPP is distributed in a continuous NE->SW gradient across the IOT, but patterns can vary with season. However, the geographic separation of the Christmas and Cocos EEZs provides a convenient break point in the gradient, dividing more productive waters in the Christmas EEZ from those of the more oligotrophic Cocos EEZ.

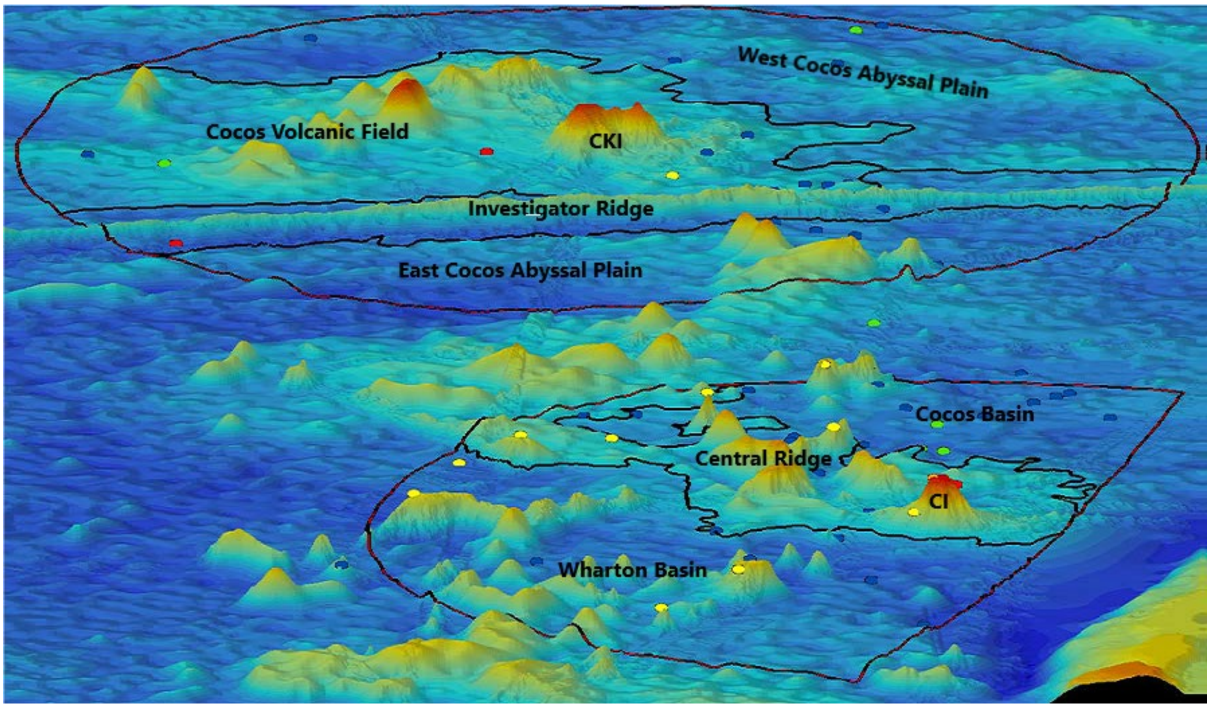

Figure 4. 3D visualisation of bathymetry from the IOT region – copied from Brewer et al. 2009. Each colour represents a separate but connected biological community. The named areas within the EEZs are sub-regions identified by Brewer – see 4.4. below.

Ecosystem	Water mass	Type	High Productivity Examples (Christmas EEZ)	Low Productivity Examples (Cocos EEZ)
Oceanic mesophotic coral reef (30-200 m)	Shallow Indonesian Through Flow	Island flanks	Christmas	Cocos (Keeling)
		Seamount	-	Muirfield
Upper bathyal reef and sediments (200-1000 m)	Deep Indonesian Through-Flow/Central Indian Water	Seamount flanks	Christmas	Cocos (Keeling), Muirfield
Mid bathyal reef and sediments (1000-2000 m)	Antarctic Intermediate Water	Seamount	Golden Bo'sunbird seamounts, 'Max', 'Bartlett', 'Lucia'	Vening Meinesz Rise and Raitt Rise seamounts
Lower bathyal reef and sediments (2000-4000 m)	Indian Deep Water	Seamount and ridge	Karma Seamounts, 'Clara Marie', 'Ulrike',	Investigator Ridge, SW Cocos.
Abyssal reef and sediments (4000-6000 m)	Antarctic Bottom Water	Carbonate sediments (above 5000 m)	Plateaus and hills between seamounts, particularly in the central Christmas EEZ.	Plateaus and hills between seamounts, particularly in the central Cocos EEZ.
		Siliceous sediments (below 5000 m)	Plain across Christmas EEZ	Plain across Cocos EEZ
		Gravel/ boulders	Seamount aprons, rises.	Seamount aprons, rises.
		Manganese nodule deposits	SW of Christmas EEZ	Unknown
Hadal sediments (below 6000 m)	Antarctic Bottom Water	Hadal plains and holes	East and south of Christmas EEZ	SE of Cocos EEZ

Table 1. List of proposed offshore benthic habitat classifications. Many habitats will have both exposed rock and soft sediment (sand, mud) communities depending on the slope of the feature. However, these are likely to vary at small spatial scales and cannot be mapped at present due to lack of multibeam backscatter data.

From a marine conservation perspective, it is important to protect several examples of each depth strata in each EEZ, and ensure that these examples contain a variety of substrata and water flow regimes. While the regional species pool is likely to be consistent across each EEZ (and perhaps across the IOT), there will be variation of assemblage structure within each of these habitats due to differences in colonisation history. Each seamount or feature will have a different subset of the regional species pool [28]. Any further subdivision of these EEZs for marine conservation purposes should be along a NE to SW axis that would reflect the distance from the Indonesian continental margin, from which pulses of high productivity originate and which is likely to be the source of much migration to the IOT.

4.1 Shallow and mesophotic reef and sediments (30-200 m)

There are three shallow-water (less than 200 m deep) features within the IOT and all are very different from each other.

4.1.1. Christmas Island

Christmas Island is an uplifted seamount with a Cretaceous (87.5 to 75.2 million years ago) basalt base capped with a thick layer of limestone (mostly Late Eocene and early Miocene reef deposits, 43 to 17 million years ago [29]), with a few volcanic extrusions (Eocene, 43 to 37, and Pliocene, 4.5 to 4.2 million years ago [2]) at the surface and a covering of phosphate deposits (guano from seabird colonies from 4.5 million years ago). Thus the initial volcanic seamount was above sea-level during the Late Cretaceous and early Cenozoic, submerging by the late Eocene (43.6-37.0 million years ago) to form an atoll, submerging again during the mid-Miocene climatic optimum (17-14.5 million years ago), before being uplifted by flexing of the oceanic crust to become an island again during the early Pliocene (5.66-4.49 million years ago) [30].

It is bounded by cliffs with a few beaches with calcareous (chalky) sand [14]. The maximum height is 361 m. The subtidal environment is rocky and very steep, rapidly descending to 1000 m within 500 m of the coastline, with few areas of coarse sand [14]. There are no estuaries, mangrove beds, or lagoons.

The main winter shallow current through the area is the east to west flowing South Equatorial Current. This can change to a flow coming from the NW during the summer monsoon. Annual Net primary productivity over the IOT is greatest near the Indonesian coast, north of Christmas Island (Fig. 3). In winter (July-August) tongues of elevated phytoplankton extend to Christmas Island.

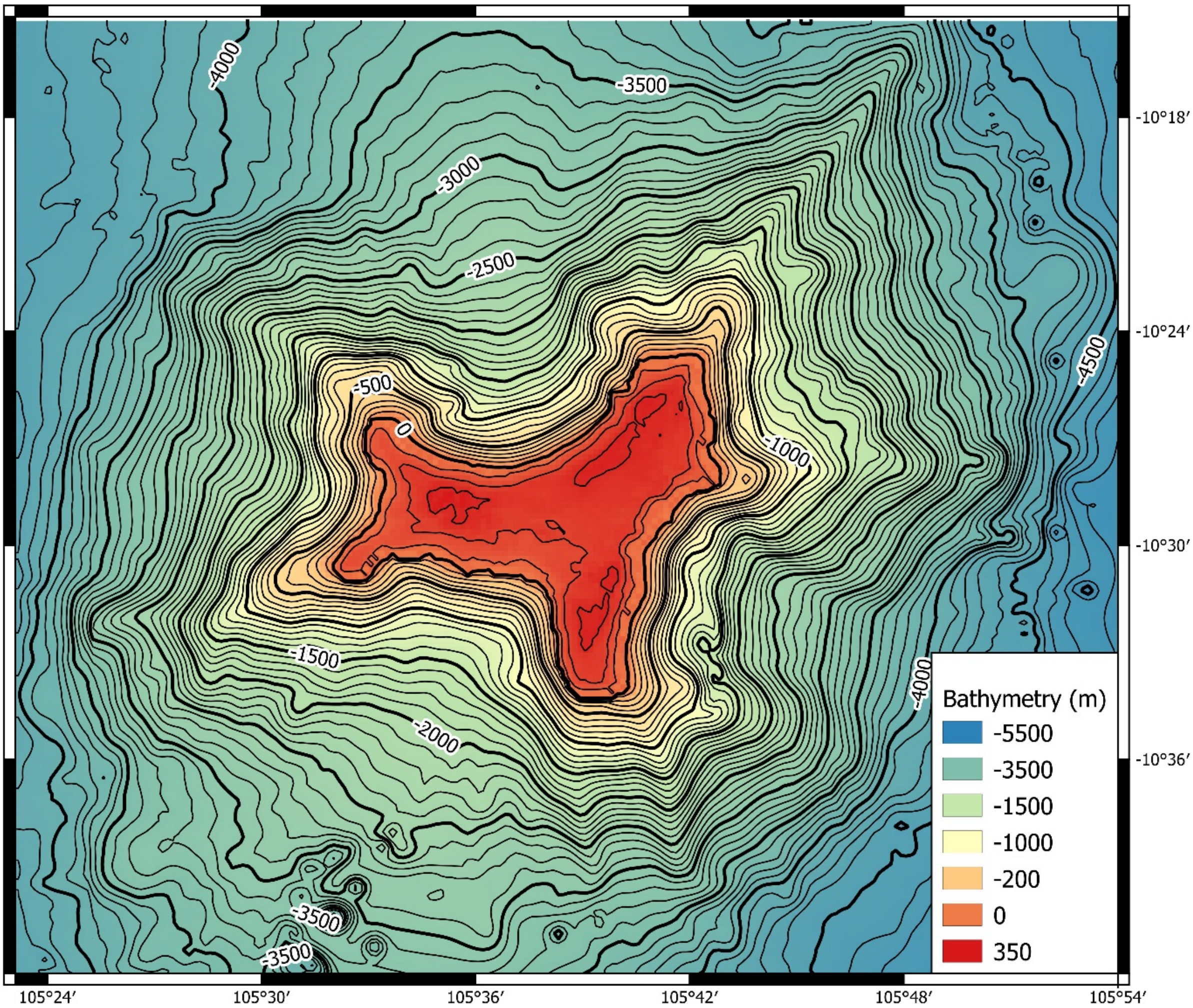

Figure 5. Bathymetric contours around Christmas Island from AusSeaBed. The embayment on the north may have arisen from slope failure, as there is strong evidence of associated sediment flows (convex contours) below 2500 m [3]. The same may have occurred off the SE and SW coasts.

4.1.2. Cocos (Keeling) Islands

The Cocos (Keeling) Islands form two groups of small sandy low-lying islands. To the south are 26 islands that form an atoll around a large shallow lagoon. North Keeling is one island, a micro-atoll with a semi-enclosed lagoon. These island groups sit on separate volcanic peaks of the underlying seamount that are capped in 900-2,100 m of limestone. Such atolls are likely to have developed on a flat Pliocene (5.3 to 2.8 million years ago) bank by seaward-growth of the outer rim during high-sea level interglacial periods and karst formation of the central lagoon-area during glacial low sea-level events [7]. Thus Cocos differs from Christmas in having areas of flat shallow-water seafloor with soft sediments and seagrass beds. There are no estuaries.

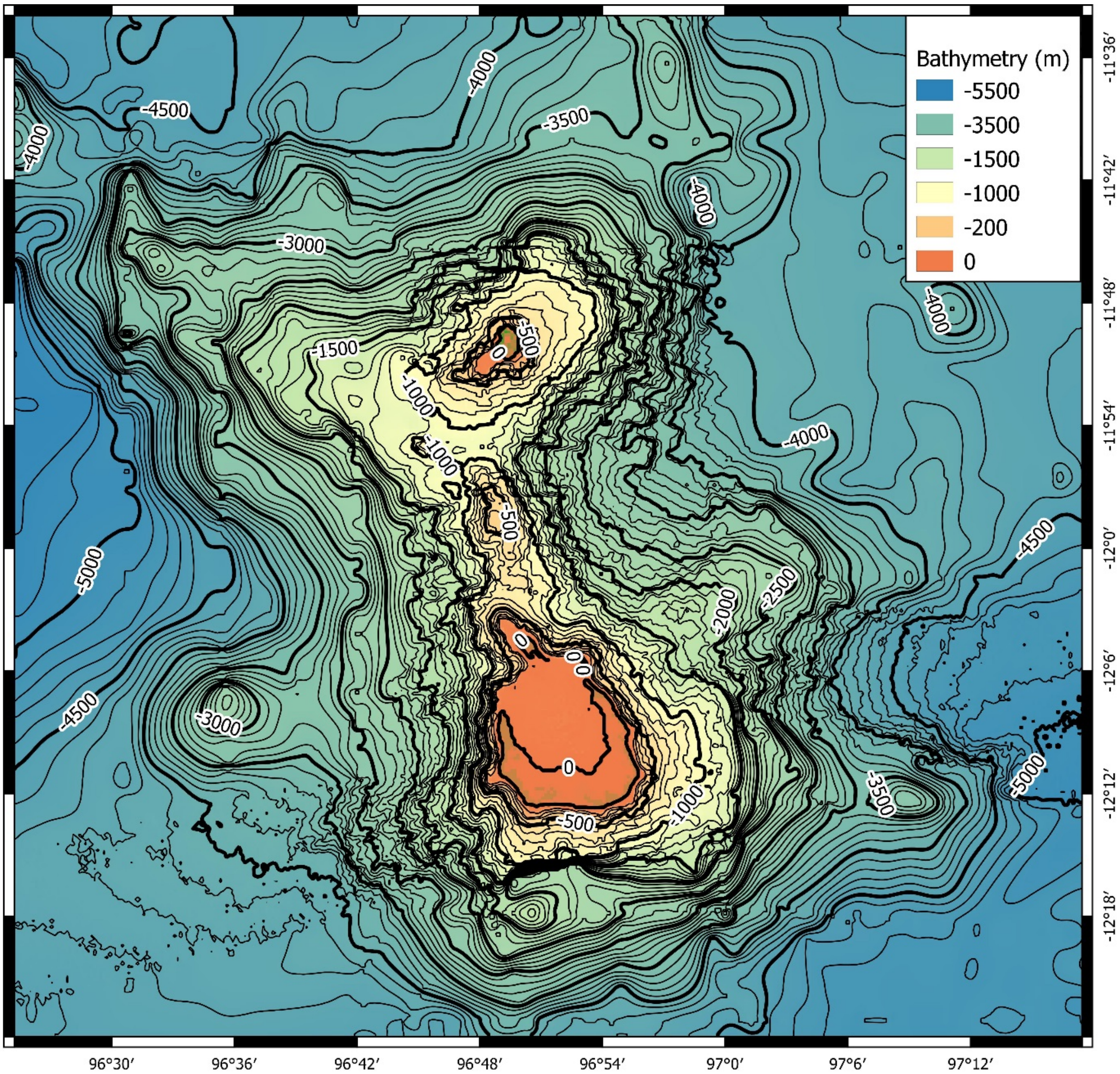

Figure 6. Complex bathymetric contours around Cocos (Keeling) Islands from AusSeaBed showing the north and south atolls, the presence of gentle slopes at ~1000 m around the SE and northern coasts, and a small peak at 350 m between the two main island groups.

Figure 7. Hard and soft coral in the Cocos (Keeling) Lagoon. Photo by Sally Watson.

4.1.3. Muirfield seamount

The Muirfield seamount has not been adequately mapped. Satellite gravity measurements (GEBCO 2019) show an elongate curved summit of 2 to 50 m depth extending 27 km in a west to southeast orientation. The AusSeabed bathymetry shows a shallow flat summit (under 20 m) to the east (96.316°E, 13.227°S) with a gently sloped ridge to 300 m extending to the west (Fig. 9). However, the depth soundings by the Franklin FR07/99 voyage found a seamount peak in the west (96.174°E, 13.178°S), with a 1km x 1km summit at 20 m, and a 500 m boundary at 96.214°E on its eastern side [9]. Consequently it is possible that Muirfield has two peaks, one in the west and one in the east with an intervening saddle of at least 500 m depth.

The FR07/99 data clearly shows that Muirfield is the shallowest seamount in the IOT, the only one (except the two islands) that is known to summit in less than 1000 m depth, and so potentially supports a unique shallow water environment. It may be the most recent of all IOT volcanos, with basalt visible near the summit. There is also hyaloclastite boulders and debris (from undersea eruptions), and areas of calcareous sand on the western summit and the upper seamount flanks (to at least 885 m) [9]. However, there are no reports of contemporary volcanic activity. The seamount summit experiences wave scour [9].

The FR07/99 expedition recorded sparse reef building corals above 25 m on the western summit and a band of gorgonian corals at 70 m [9]. Below that, sparse encrusting invertebrates and sea urchins were observed [9].

A dome of reduced particulate organic carbon has been recorded over the summits of some other shallow seamounts (e.g. Melville Bank on the SW Indian Ocean Ridge, summit at 120 m) [31], which has been attributed to the seamount penetrating the euphotic zone and disturbing primary production. It is unknown whether this occurs at Muirfield.

The main winter shallow current through the area is the east to west flowing South Equatorial Current. This can change to a flow coming from the NW during the summer monsoon. Annual Net primary productivity around Cocos is less than around Christmas Island although in early summer (November-December) phytoplankton can be slightly elevated in the southern Cocos EEZ [14].

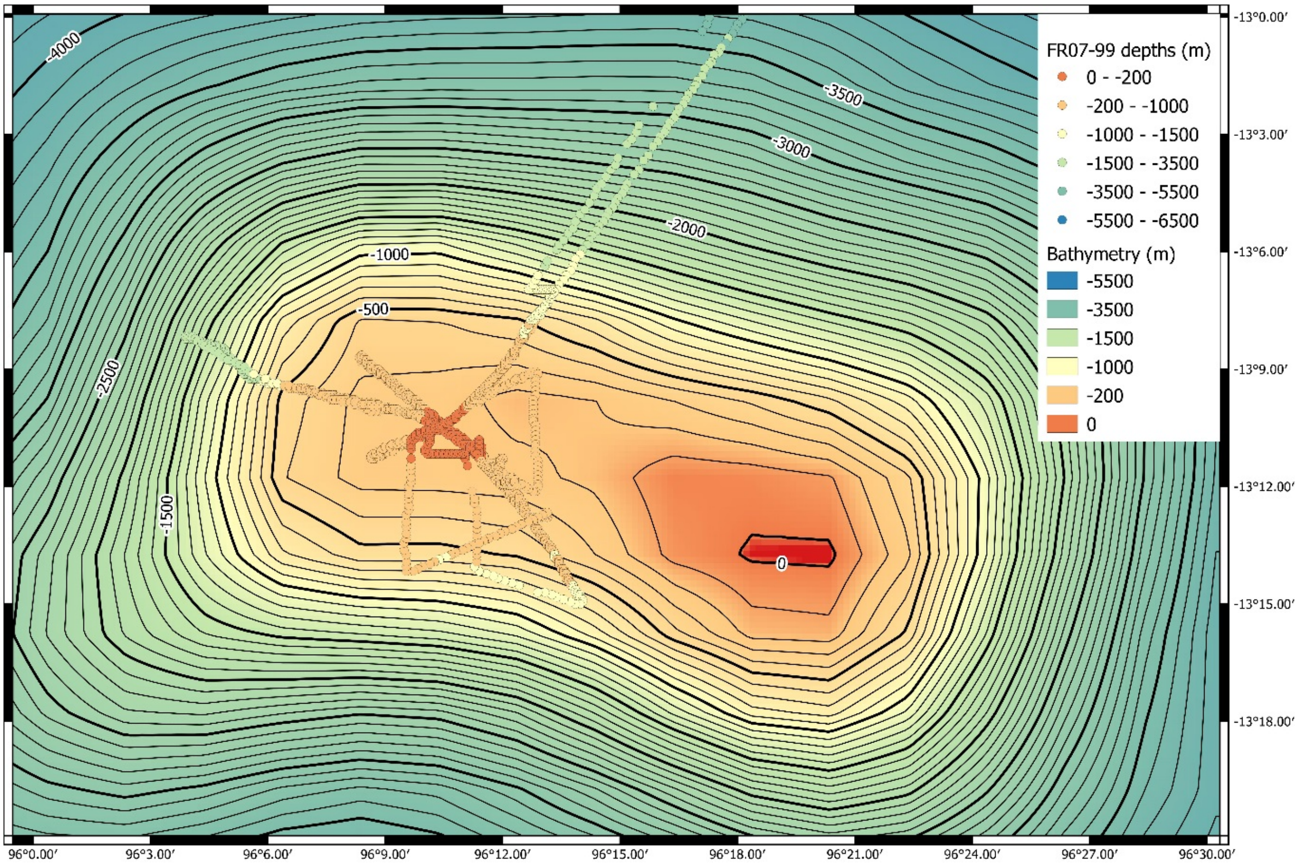

Figure 9. Estimated bathymetric contours around Muirfield seamount from AusSeaBed, overlain by depth soundings from the FR07/99 expedition showing the presence of a western summit.

4.2 Bathyal reef and sediments (200-4000 m)

4.2.1. Seamount reef and sediments (200-1000 m)

This depth layer only exists on the three shallow features listed in 4.1.

The seafloor around Christmas Island drops rapidly on all sides and is likely to be rocky with patches of sand.

The bathymetry around the Cocos atolls is more complex. The island groups are bordered by very steep drop-offs to 500 m which are likely to be exposed rock. Slopes between 500 and 1500 m on the south-eastern and northern sides are less steep and may be covered in pelagic sediments. A shallow (350-450 m) ridge like feature lies between the two island groups. It also may have soft sediments along the flattened ridge line.

Detailed bathymetry is lacking for Muirfield as described above. However, two video tows were performed by the FR07/99 expedition [9]. They show mostly unconsolidated sands, volcaniclastic detritus, breccia, and outcrops of basalt. Steep slopes (~18°) continued to about 300 m, followed by more gentle slopes (6-8°) from 300-885 m. The volcanic debris and outcrops were more common near the summit, and sands more common at lower depths. A strong downward current produces asymmetrical sand ripples at 500-800 m. Sediment slumping can occur on slopes as gentle as 2° and may be responsible for the down slope occurrence of volcanic debris [9].

Upper bathyal depths in the IOT are still strongly influenced by the east to west flowing South Equatorial Current with waters originating from the deep Indonesian Through-Flow [17]. However, seasonal flows from the NW can also be important [32].

Seafloors at upper bathyal depths can interact with diurnal vertical migrators. Some types of pelagic migrators (e.g. euphausid krill) will boost predator numbers [33], but others have learned to avoid seamount flanks and will locally reduce predator biodiversity [34]. Seamounts are also known to alter bottom currents, such as reported for Muirfield.

4.2.2. Seamount reef and sediments (1000-2000 m)

There are eight seamounts in the Golden Bo'sunbird seamount cluster that have summits between 1000-2000 m (including Shcherbakov, 'Apollo 8', 'Balthazar' (2 peaks), 'Halley', 'Glogg', 'Attention' and an unnamed seamount). 'Max' (east of Christmas Island), 'Bartlett' (south of Christmas Island), and 'Lucia' (Flyingfish seamount) also peak in just under 2000 m. In the Cocos EEZ, there are another six on the Raitt Rise ('Noel' and unnamed) and perhaps others on the Vening Meinesz Rise and to the SW of Cocos. The height of many of these seamounts are currently estimated from satellite gravity measurements and require confirmation from additional ship-based multibeam data.

The 1000-2000 m depth range typically contains rocky seafloors that are most likely to form thick manganese crusts [10] and support colonial cold-water coral communities [35]. Manganese crusts have been shown to influence benthic community composition on seamounts elsewhere [36, 37]. Flat seamount summits are likely to have areas of soft sediment and carbonate rocks. The rims, steep flanks and associated volcanic cones will likely be exposed rock. Two video tows of the SO199 expedition showed a rocky surface supporting gorgonians and crinoids on the flanks of Shcherbakov and 'Balthazar' (Fig. 12) at 1800-2000 m. The mid-bathyal flanks of Christmas, Cocos and Muirfield seamounts will also support hard-and soft substrata habitats depending on the slope. Gentle slopes can occur where there has been sediment failure and debris flows and are more likely to retain subsequent pelagic sedimentation.

Water masses at this depth would include a mixture of Indonesian Intermediate Water arriving from the east, Antarctic Intermediate Water from the SE, and Indian Central Water from the south [18]. All these waters get entrained by the South Equatorial Current and flow to the west. Muirfield and Cocos are in more oligotrophic surface waters which may reduce seafloor biomass.

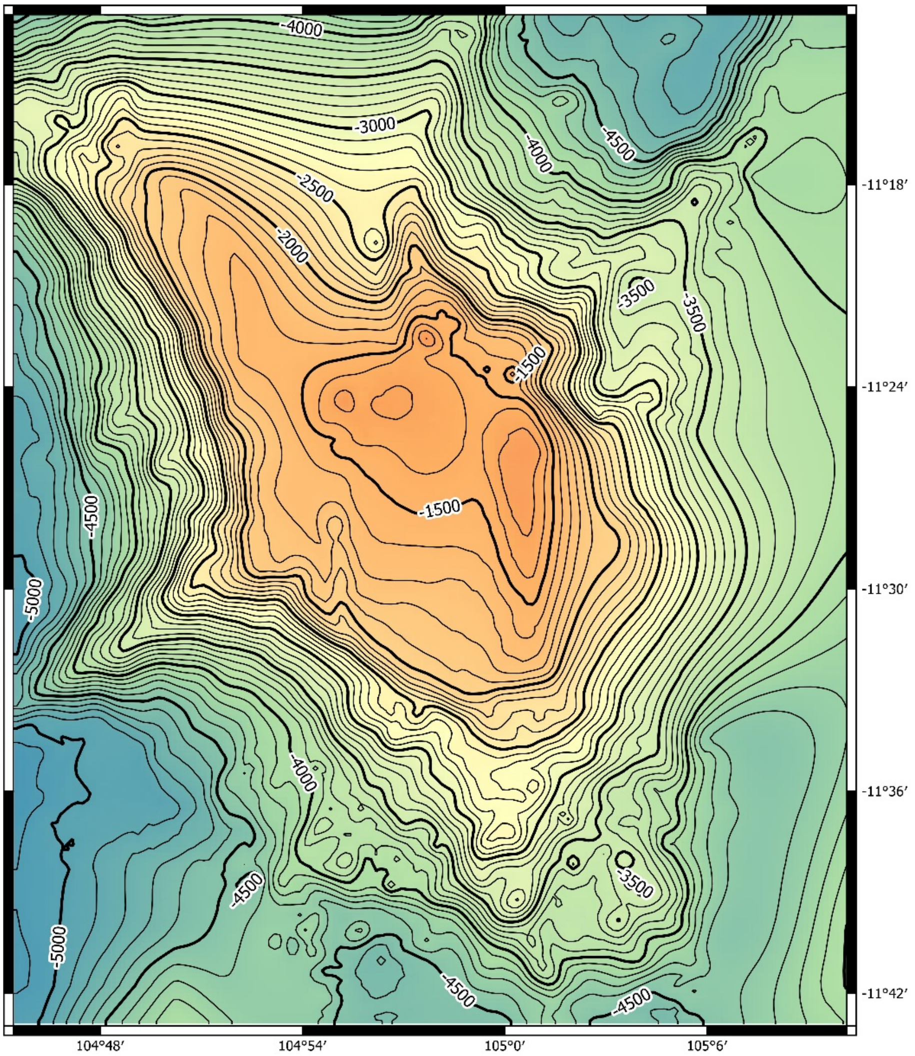

Figure 10. Estimated bathymetric contours around 'Apollo 8' Seamount from AusSeaBed showing a broad convex summit (1300-2000 m) and steep flanks.

4.2.3. Lower bathyal reef and sediments (2000-4000 m)

There are numerous seamounts that summit in 2000-4000 m spread around both Indian Ocean EEZs. Some have flat or gently convex summits (e.g. 'Clara Marie', Fig. 13) indicating that they may have once been above water [5], however, they can also be covered in smaller volcanic cones, which may have formed during later phases of volcanism [3]. Other seamounts have sharp peaks and may never have been emergent [5]. Steep flanks are likely to have exposed rocky surfaces and flatter surfaces will be covered in sediment.

A video tow from the SO199 expedition showed a muddy substratum on 'Max' at 2740 m [3]. Rocks obtained from the lower sides of seamounts across the IOT have been generally basaltic in origin, often with a thin manganese crust [3]. The Karma seamount cluster (SE of Christmas Island) contains some of the oldest seamounts in the IOT [2]. The central section of the Investigator Ridge also contains several elevated peaks as shallow as 2700 m (Fig. 14) [3]. The steep sides of the Ridge, and especially the western side, are probably covered in exposed rock.

The main water mass at lower bathyal depths is Indian Deep Water (temperature 2°C, salinity 35.85, oxygen 4.7 ml/l), which is an extension of North Atlantic Deep Water mixed with upwelled Antarctic Bottom Water [18]. It flows northwards along the Ninety-East Ridge (to the west of the Cocos EEZ. Some southward movement across the IOT is possible, to compensate for the northerly water flows further west [18].

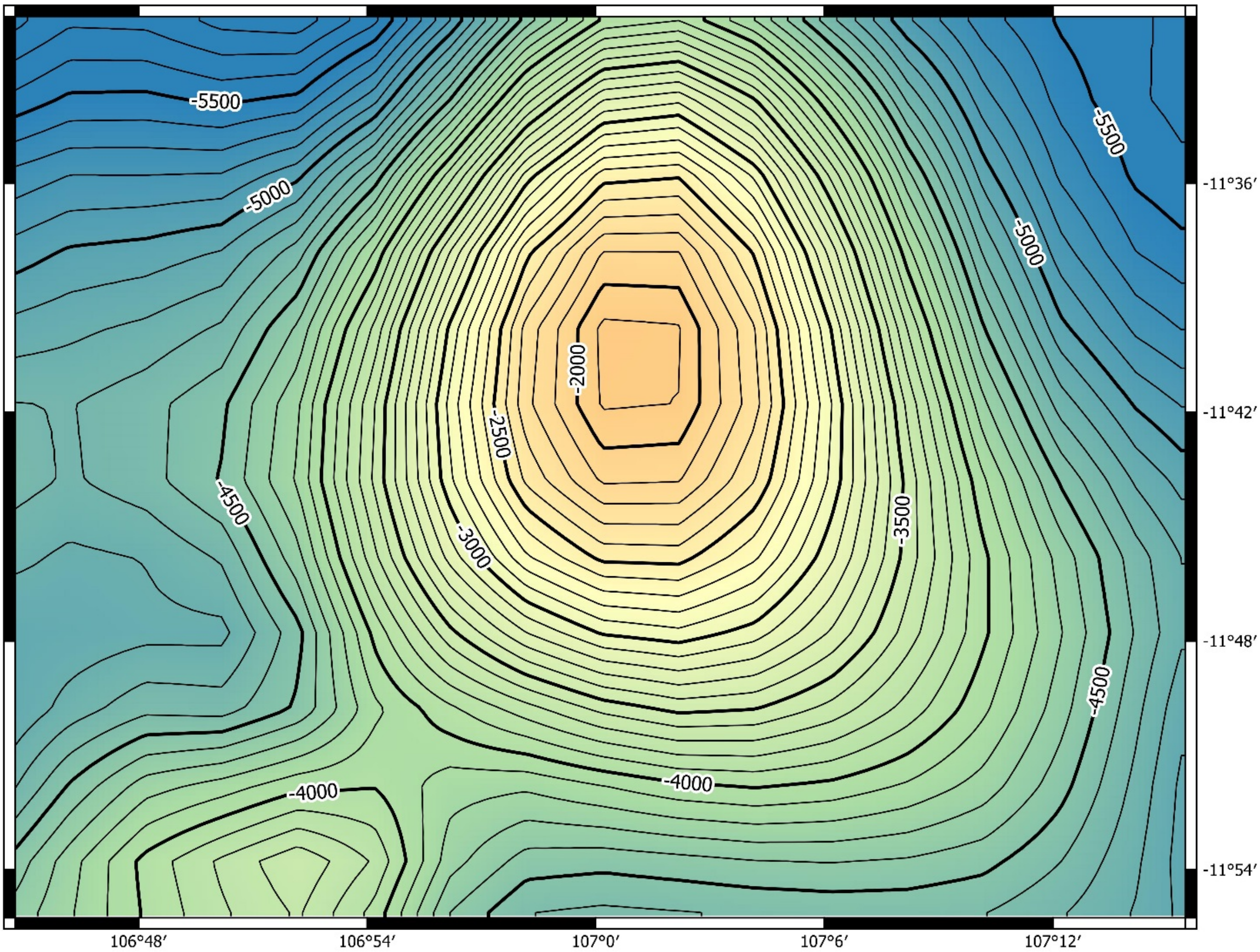

Figure 11. Estimated bathymetric contours around 'Max' Seamount from AusSeaBed showing a broad gently sloping conical feature with a small flat summit at 1800 m.

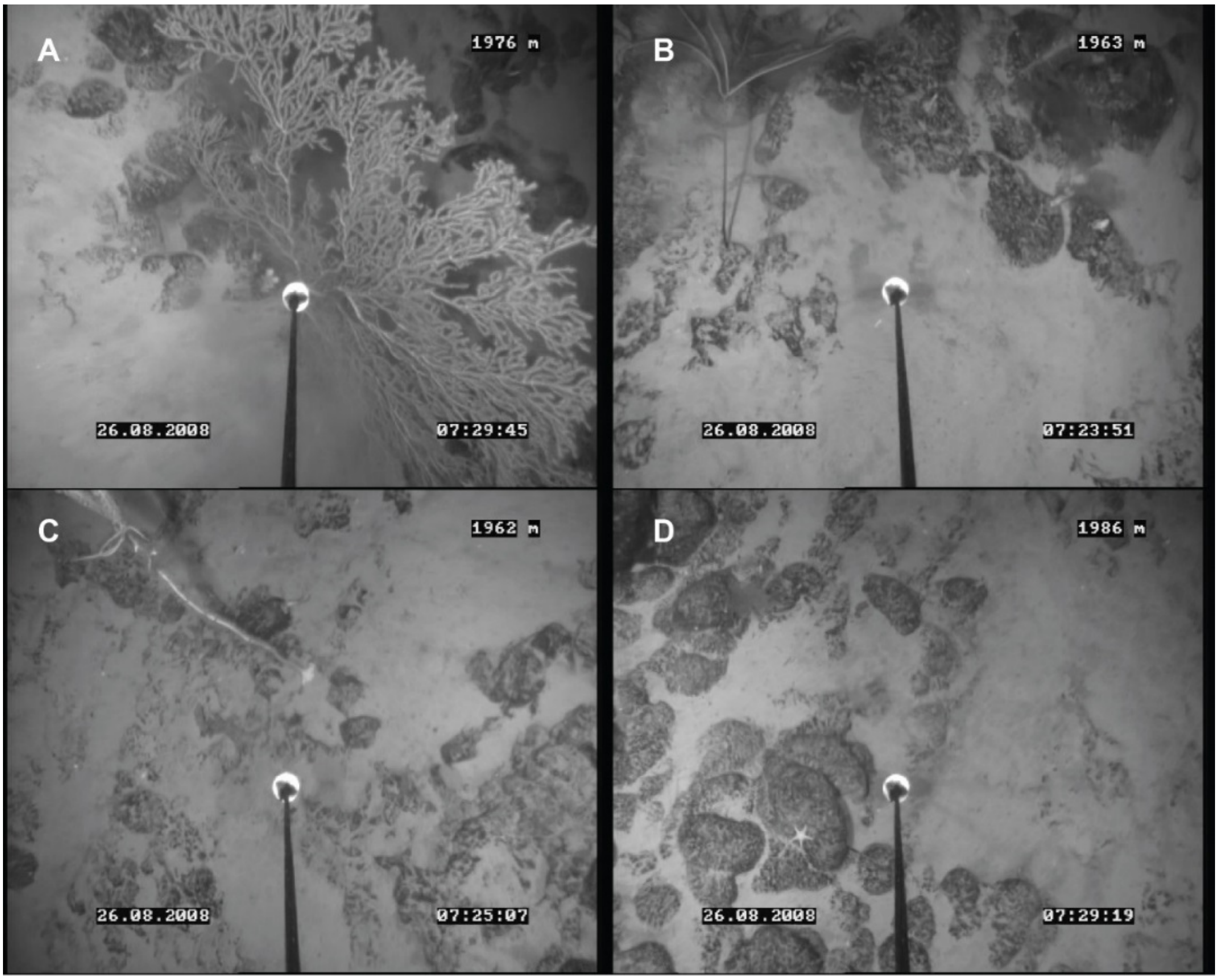

Figure 12. Video stills of a small volcanic cone on the NE flank of 'Balthazar' seamount in 1900-2000 m depth taken by the Sonne SO199 expedition (courtesy of Carsten Lüter, Berlin Museum of Natural History). A) Gorgonian coral, B) stalked crinoid, C) coral with epizoic brittle-star, D) seastar.

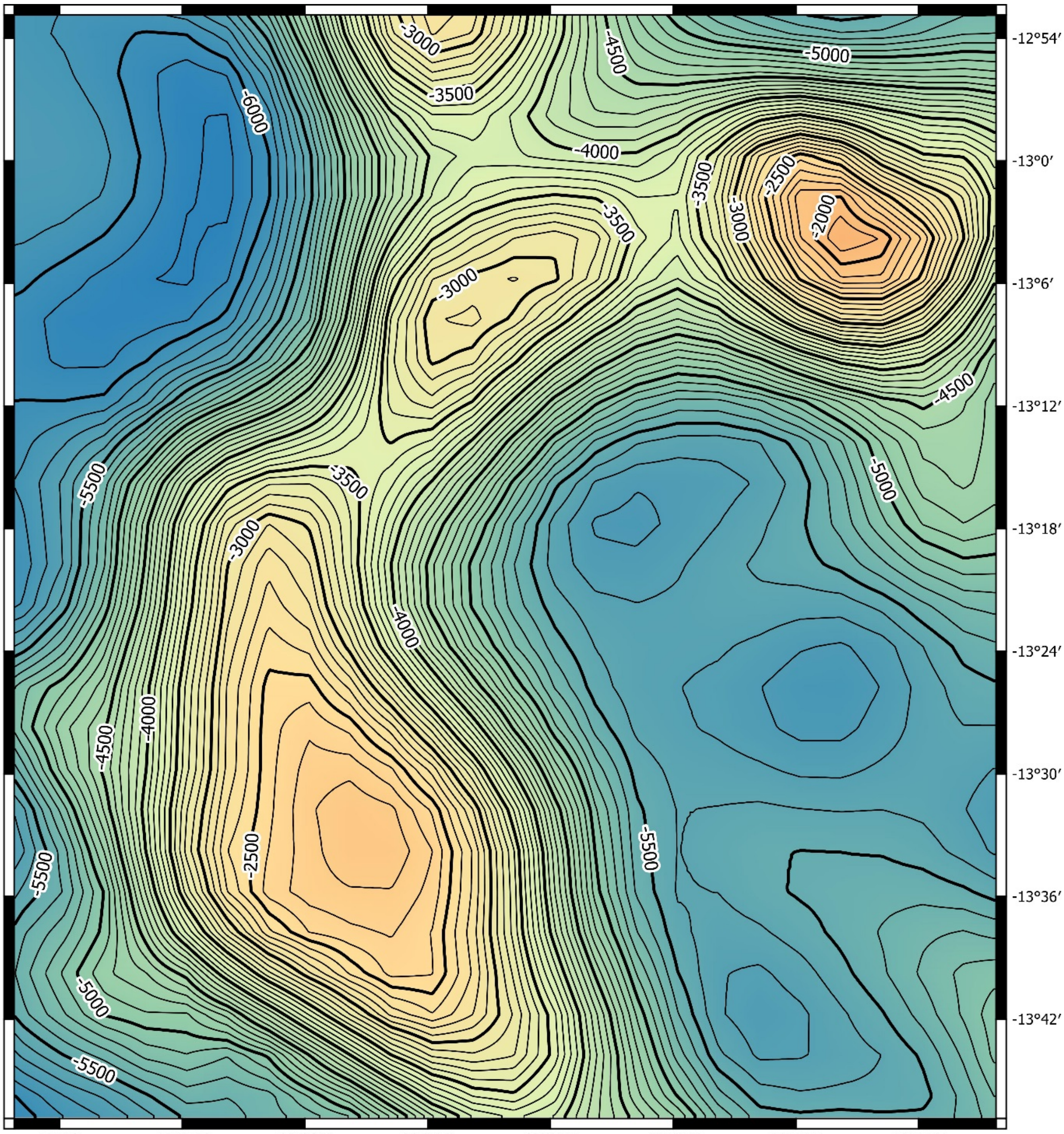

Figure 13. Estimated bathymetric contours for the Bartlett seamounts from AusSeaBed showing three peaks ('Clara Marie' to the SW) on a curved ridge.

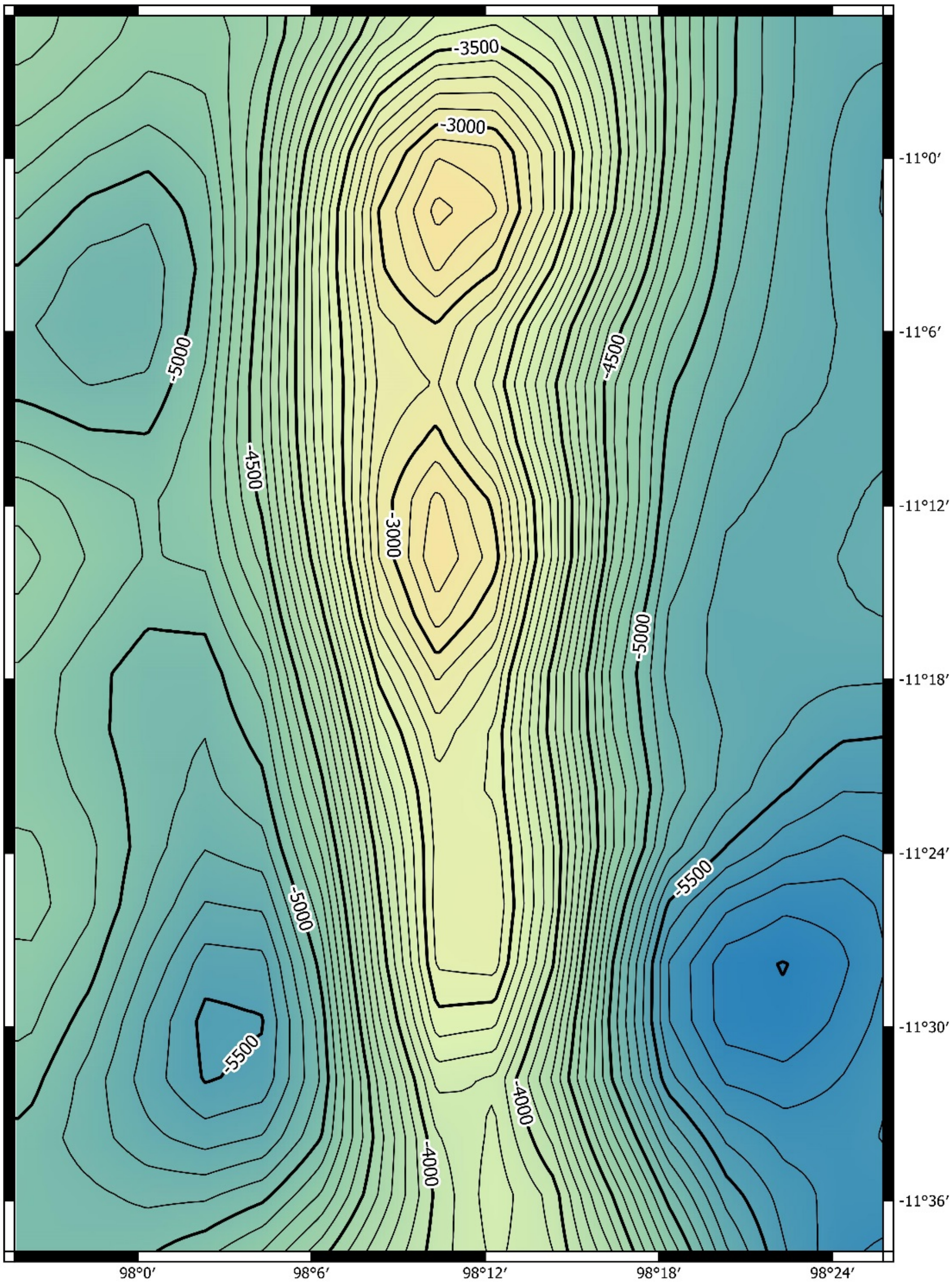

Figure 14. Estimated bathymetric contours around a central section of the Investigator Ridge from AusSeaBed showing two elongate peaks at 2700 m.

4.3 Abyssal (4000-6000 m) and hadal (>6000 m) reef and sediments

A thick layer of sedimentation will cover most abyssal and hadal seafloor habitats. Sediment thickness is greatest near the Sunda Trench along the northern boundary of the Christmas EEZ (~435 m) [13] and least to the W of Cocos EEZ (~154 m) [12] due to the decline in surface productivity. The sediment is generally compacted into clays/oozes, with calcareous sediments being replaced by siliceous ones below 3800 m [10].

Manganese nodules are known to occur at abyssal depths (4780 to 5888 m) to the SW of the Christmas EEZ, where they are most abundant in areas between seamounts [10]. The presence of nodules in the Cocos EEZ has not been quantitatively assessed [10]. Nodules form very slowly on the seafloor from a number of geochemical processes. Nodules influence the composition of the benthos as they provide hard substratum on a mainly sedimentary seafloor. The density of nodules will also affect community composition and biomass [38].

Multibeam sonar has revealed numerous abyssal hills across the IOT. It is unknown whether any of these have exposed rocky substrata. However, studies elsewhere have shown that the sediment covering abyssal hills (and the aprons around seamounts) generally has a greater gravel or boulder content from nearby volcanic activity (or drop stones from glaciers), which in turn alters epibenthic community composition [39].

The IOT also has abyssal troughs that mainly occur mainly in the SE and SW of the Cocos EEZ and NE and SW of the Christmas EEZ (Fig. 2). A comparison of ridges, plains and troughs in the Clarion-Clipperton Zone (NE Pacific, 3950-4250 m) found that although the nutrient content of the sediment was the same, the benthic assemblages in the troughs were different, in this case because of the increased density of manganese nodules [40].

The ecology of the abyssal seafloor depends almost entirely on the downward flux of organic detritus from the productive surface waters. The gradient of net primary productivity from a high in the north of the Christmas EEZ to a low to the SW of Cocos EEZ (Fig. 3) will influence biomass and diversity of the benthic organisms. Antarctic Bottom Water temperature (1.1°C, salinity 34.7) slowly moves northwards across the Wharton Basin, although the strongest flows are west of the IOT along the eastern side of the Ninety-East Ridge, and gradually upwells into the Indian Deep Water [18]. There is little variation across the IOT at abyssal depths in temperature, salinity or oxygen [18].

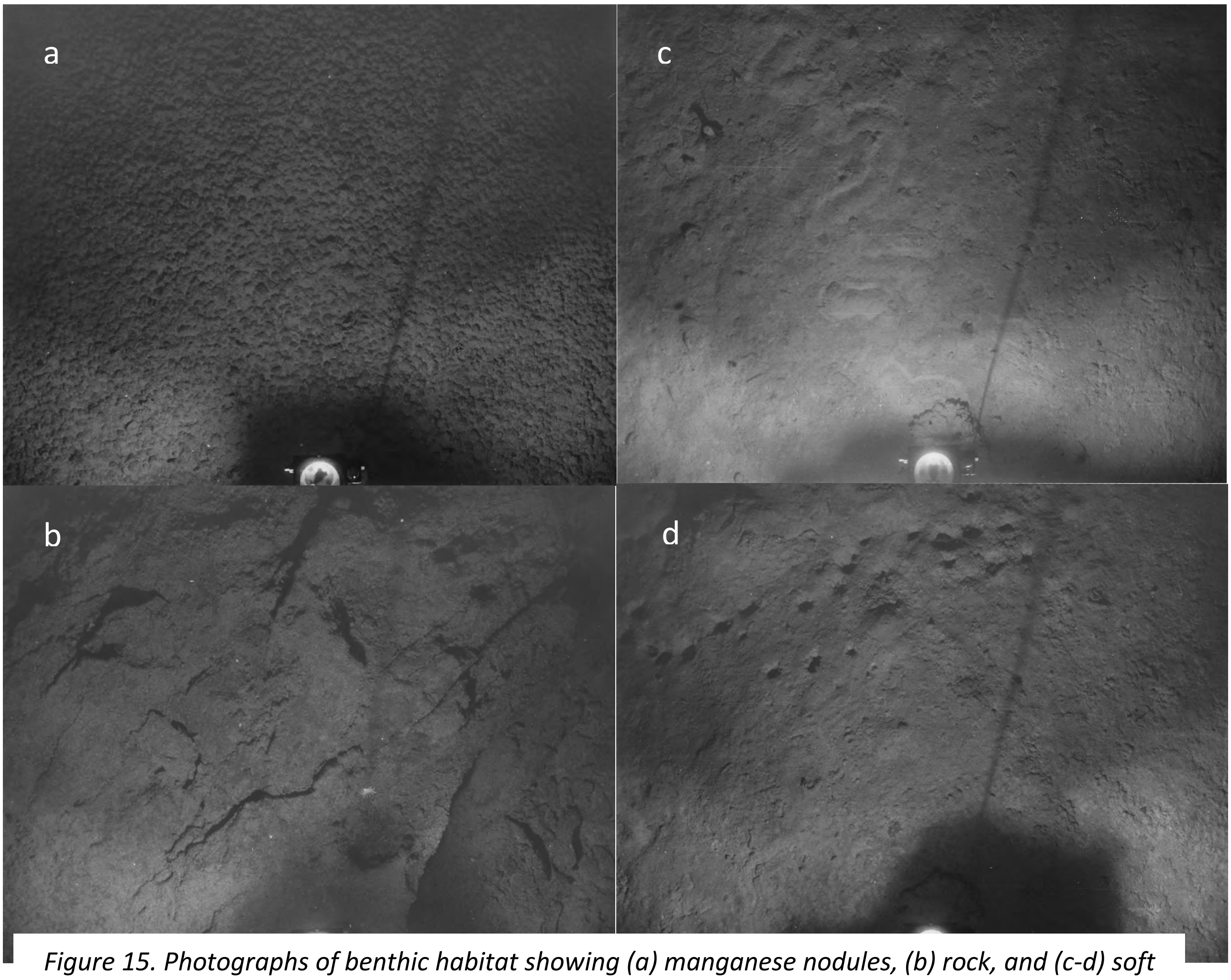

Figure 15. Photographs of benthic habitat showing (a) manganese nodules, (b) rock, and (c-d) soft sediment, at locations (a-b) VM33-005 (?2982 m, south Christmas EEZ) and (c-d) VM33-006 (3175 m, north Christmas EEZ), from Brewer et al (2009).

Oceanic depths below 6000 m are referred to as the hadal zone and animals require special adaptations to survive the extreme pressures, cold and lack of organic matter [41]. The deep seafloor (below 6000 m) of the Indian Ocean territories total 12,834 km^2 in area and represent 93.2% of this depth zone across the Australian EEZ [14]. The deepest point is 6,542 m (AusSeaBed 2020 bathymetric dataset) or 6,490 m (GEBCO 2019) east of Christmas Island. Other hadal areas occur to the south of the Christmas EEZ (to the NE of 'Clara Marie') and to the SE of the Cocos EEZ. These three areas may have different benthic communities based on differences in net primary productivity of overlying waters and proximity to the extensive Sunda Trench in Indonesia.

4.4. Comparison with the bioregionalisation in Brewer et al. (2009)

Brewer et al. [14] divide the IOT into seven bioregions, four in the Cocos EEZ and three in the Christmas EEZ. As biological data were lacking, the bioregionalsiation was based on a qualitative assessment of the geology and oceanography of the area. The seven bioregions are more or less placed east to west and so do capture the surface productivity gradient and predominant current flow of the IOT.

The area and boundaries of each of the Brewer bioregions reflect seafloor geomorphology, in particular the density and height of seamounts: 1) Wharton Basin has a sparse covering of deep old seamounts, 2) Christmas Central Ridge has a dense assemblage of seamounts on an 'uplifted block' , 3) Cocos Basin has relatively few seamounts and is mostly abyssal plain, 4) East Cocos Abyssal Plain is similar but in the Cocos EEZ, 5) Investigator Ridge includes a abyssal ridge and associated troughs, 6) Cocos Volcanic Field has a relatively dense covering of more recent seamounts, and 7) Western Cocos Abyssal Plain includes only abyssal habitat and has no seamounts of any size.

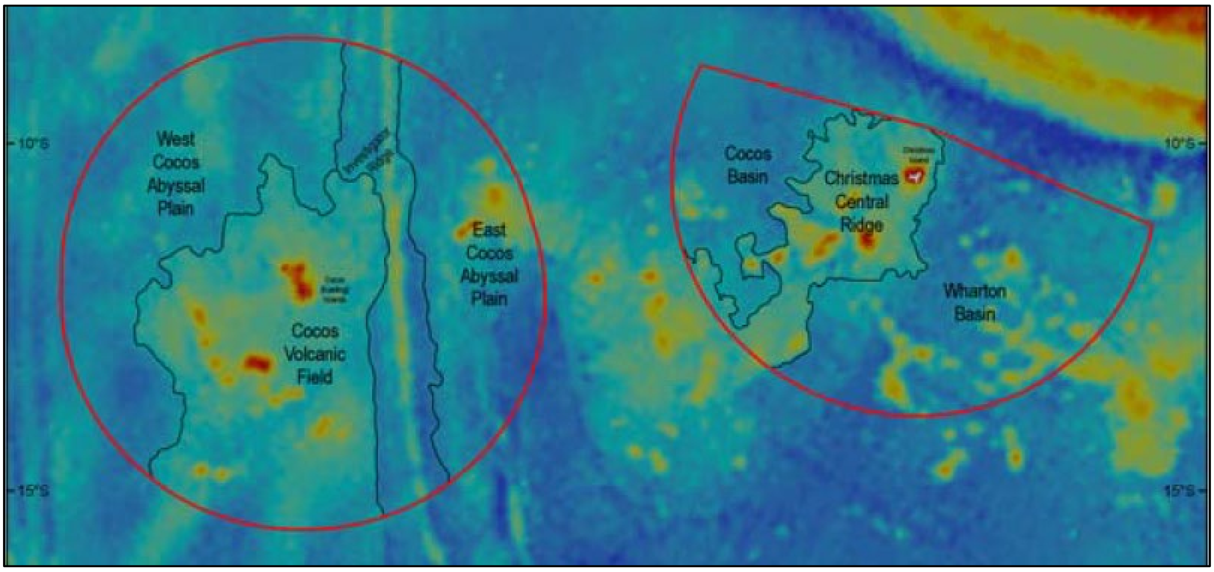

Figure 16. IOT bioregionalisation proposed by Brewer et al. [14].

The Brewer et al. report was written before the main geological findings of the Sonne SO199 expedition were published. Hoernle et al. [2] categorised the IOT seamounts into three volcanic provinces of different ages (Fig. 17) that have different boundaries than the Brewer bioregions. Their Vening Meinesz province extends from Christmas Island to the Investigator Ridge, thus includes Brewer's Christmas, Cocos Basin and East Cocos bioregions. The raised seafloor in the Christmas Central Ridge and Cocos Volcanic Field has also been interpreted differently, the former as a flexural bulge and the latter as a magma hotspot [5]. Moreover, seamounts are also surrounded by volcanic debris and sedimentary aprons, which can be consolidated into single rise-like systems if the seamounts are close enough together.

However, while the use of geomorphology is intuitive from a landscape perspective it is unclear why the benthic and pelagic fauna would be differentiated along these lines. The sub-region boundaries of the Brewer classification are unlikely to reflect faunal distribution and diversity, as the fauna would be unlikely to differ on either side of the boundaries at similar depths.

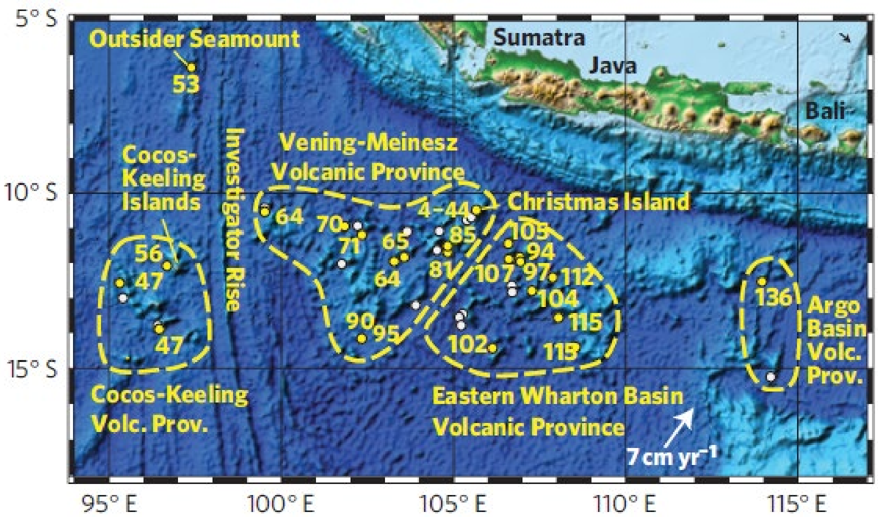

Figure 17. IOT volcanic provinces as figured by Hoernle et al. [2]. The numbers against each seamount are the estimated ages (millions of years) derived from ^{40}Ar / ^{39}Ar ratios in SO199 basalt samples.

5. The biogeographical significance of the area

The remoteness and location of the IOT, south-west of Indonesia in the eastern Indian Ocean, makes it unique within the Australian marine domain. The biogeography of the IOT benthic fauna is likely to be complex and differ between depth layers.

5.1. Shallow and mesophotic depths (0-200 m)

Surface waters of the IOT are part of the great Indo-West Pacific biogeographic province that stretches all the way from Africa to Easter Island. However, there is regional differentiation of fauna within the province. The islands of the IOT contain a mixture of species. Most are from 1) the Indonesian-N. Australian Archipelago (IAA) or coral triangle which contain the richest marine habitats on the planet, with some characteristic of 2) the western-northern Indian Ocean. The Cocos Islands are the westernmost distribution for many IAA species [42]. Sometimes both IAA and Indian Ocean species co-occur, especially around Christmas Island, leading to hybrids [43, 44]. The main (modern) migration routes for shallow water species would be via the South Equatorial Current from eastern Indonesia, or from the Indian Ocean coast of Sumatra via the South Java Current in summer [14]. For example, the seagrass (*Thalassia hemprichii*) appears to be genetically closer to populations in Eastern Indonesia than NW Australia or the Lesser Sunda Islands [45].

Our knowledge of the IOT's biogeography is likely to increase significantly as DNA is used to resolve the distribution of cryptic species (species that look very similar). For example, there are at least four Crown-Of-Thorns Seastar species with distinct regional distributions [46]. While the population off NW Australia is the Pacific species [46], the one at Christmas Island is the southernmost occurrence of a north Indian Ocean species, and the one at Cocos is the easternmost occurrence of a SW Indian Ocean species that also occurs at Chagos in the central Indian Ocean [47]. For fish, while Pacific and Indian Ocean sister species often overlap at Christmas Island, Cocos Islands can have both species [48] or just the Indian Ocean species [49, 50].

The remoteness of the islands has prevented many species from colonising from surrounding regions. For example, 160 coral species known from NW Australia are missing from Christmas Island but only eight species are known from Christmas Island but not Western Australia [51]. The fish fauna is described as a slightly impoverished Indo-Malay fauna with some notable absences [43, 52]. Equally, there are 50 fish species that do not occur elsewhere in Australia [14]. The species that do occur there tend to have pelagic adult or larval stages that can disperse over long distances [42]. Some species may have also arrived by rafting on debris or seaweeds.

The number of known endemic species is low, for example only 4 of 622 fish species are endemic to Christmas Island, and another three are shared with Cocos Islands [53]. Of the 602 fish recorded from the Cocos Islands, there are no endemic species [54]. There are five undescribed/unidentified coral species on Cocos that may turn out to be endemic or more widespread [55]. There are several mollusc populations from the IOT whose DNA differs from populations elsewhere and may be endemic species [56]. Endemic invertebrates have also been reported from marine and anchialine caves on Christmas Island [57-59] but other cave species have been found to be widespread, such as the patterned goby *Trimma fasciatum* [60]. The shallow water fauna on the Muirfield seamount is unknown [9].

Little is known about community composition at mesophotic depths.

5.2. Bathyal and abyssal depths (200-6500 m)

The bathyal and abyssal fauna of the IOT is completely unknown. Our best alternative is to rely on knowledge from elsewhere, in particular from Indonesia and NW Australia, as a biogeographical surrogate.

It is likely that the upper to mid bathyal (200-2000 m) fauna of the IOT is related to similar faunas elsewhere in the Indo-West Pacific region [25, 61]. This fauna is ancient, its high diversity related to its age rather than bursts of more recent speciation [25]. It is likely to have been a long term refuge for marine lineages, avoiding the glacial/interglacial temperature and sea-level fluctuations of shallow water, and the periodic anoxic conditions of the abyss [25].

Biogeographies of the deep-sea fauna have tended to view the Indian Ocean as a single unit [62]. However, as in shallow water, DNA analyses have indicated that the enormous distances between suitable upper bathyal habitat across the central-southern Indian Ocean can act as an biogeographic barrier with cryptic species divided into eastern and western lineages [63]. The potential for deep-water species to migrate between the Pacific and Indian Oceans may have also decreased over time. Australia/Papua New Guinea collided with Indonesia 25-17 million years ago, cutting off the deep water inter-oceanic connection [64]. Indonesian Through-Flow water now has to rise over sills as shallow as 600 m depth. The implication is that, unless they can survive conditions south of Australia or their pelagic stages can vertically migrate over the Indonesian sills, Pacific Ocean deep-sea species may have been isolated from their Indian Ocean counterparts for tens of millions of years. Thus we can speculate that upper bathyal populations in the IOT will be evolutionarily distinct from those in the Pacific Ocean and those in the western Indian Ocean.

The IOT lies at the boundary of the northward flowing Antarctic Intermediate Water, and the mid-bathyal fauna may reflect this and have components that are related to southern Indian Ocean faunas.

The amount of available mid-ocean habitat increases with depth. The SW, SE and Central Indian Ocean Ridges radiate out from the Rodrigues triple junction like spokes across the Indian Ocean, providing habitat typically as shallow as 2500 m deep. Other volcanic or tectonic features occur as ridges, plateaus or seamounts scattered across the ocean. Thus it becomes more feasible for lower bathyal (2000-4000 m) animals to migrate horizontally across the Indian Ocean and we would expect less regional differentiation. There will still be dispersal barriers for some species, as the ridges are not always continuous and can be intersected by strong currents or other oceanographic barriers [65]. Although hydrothermal vent animals at this depth generally have good dispersal abilities, they too can have distribution limits or regional population structure [66]. Conversely, the animals of the abyssal basins and hadal trenches (below 4000 m) may experience the ridges as a dispersal barrier, although these barriers are likely to only reduce rather than prevent cross-ridge dispersal [67, 68]. The extreme oligotrophic conditions at the centre of the Southern Indian Ocean Gyre maybe a resource limitation for many benthic species, although this would not prevent migration around its periphery. The predominant flow across the IOT at mid bathyal to abyssal depths appears to be from the south, and latitudinal temperature gradients are minor, so we can expect some relationship of IOT and SE Indian Ocean faunas at these depths.

6. The ecological significance of the area

6.1. Shallow and mesophotic benthic biota (0-200 m)

The three shallow water features are ecologically unique within the IOT. Christmas Island is an emergent seamount, bounded by steep sides (except the occasional beach and caves), and a rim of coral growth.

The south Cocos group of islands is an atoll of low lying sandy islands, with a shallow lagoon (including seagrass beds, a small area of mangroves, sand banks and coral reefs), and outer coral reefs (including an inner reef flat). North Keeling Island also has a shallow, largely closed, lagoon. There are no estuaries on any of the islands.

The lagoons host populations of Green and Hawksbill Turtles, which consume seagrass-algae and algae-sponge respectively [69]. Green turtles breed on both North Keeling and Christmas Island. Most of the green turtles foraging in the south Cocos lagoon appear to be from local brooding stock [70] although one tagged turtle originated at Ningaloo [71]. Five other tagged turtles only travelled on average 35.5 km (max. 66.5 km) after nesting at North Keeling [70]. The genetic diversity of nesting and foraging turtles is low compared to sites in NW Australia, with most sequenced green turtles belonging to widespread Indian Ocean or West Pacific lineages [72, 73]. Both the short foraging trips and low genetic diversity are indicative of an isolated population with the nearest alternative foraging area 1000s of km distant. The Hawksbill turtles also appear to be resident in South Cocos foraging grounds over multiple years at densities of 74-75 km^2 [74].

There is a high abundance (10 per Ha) of black-tip reef sharks (*Carcharhinus melanopterus*) and grey sharks (*C. amblyrhynchos*) in the lagoon at Cocos [75]. These animals are typically restricted to coastal habitats and bear live young [75]. There are numerous other fish and invertebrates typical of the reef and soft sediment habitats. Edible invertebrate species such as Beche-de-mer (*Holothuria* spp), giant clams (*Tridacna* spp), crabs, and Gong Gong gastropods (Common Spider Conch, *Lambis lambis*) are vulnerable to over-exploitation [75].

Muirfield is a submerged rocky seamount (summit at 16 m) with areas of exposed basalt, sparse coral cover, volcanic debris and coarse sand. While all three are in the path of the South Equatorial Current, the habitat nearest Indonesia (Christmas Island) experiences higher primary productivity and can be expected to support more abundant benthic and pelagic biota. The primary production over Muirfield may be even lower, as similar shallow seamounts elsewhere have been shown to have relatively low levels of dissolved particulate carbon [31].

Sometimes, the shallow water communities at Cocos and Christmas Islands have been described as slightly impoverished [52], however, for fish this has been attributed to reef area which is only 20 km^2 at Christmas and 110 km^2 at Cocos Islands [76], and coral species richness is similar to that at other offshore islands such as the Rowley Shoals [51].

There are fewer habitats at Christmas Island, but the exposed nature of the coastline reduces dominance by a few species and most species are rare [51]. Flying fish Cove was found to be the most sheltered and most diverse site for corals around the island [51]. The high diversity is around 20 m, below damaging waves but above the mesophotic zone [77]. The very exposed south coast is dominated by soft corals [51].

Each of these shallow water environments is also unique because of their isolation. Firstly, their biological communities have been assembled from long distance dispersal and so are biased to species that have reasonable dispersal capabilities [76]. Long distance dispersal always involves a degree of randomness and so every assemblage tends to be different. Five of the 169 species of shallow reef corals on Christmas Island have not been recorded anywhere else in Australia [51]. The currents arrive from both east and north-west directions, which ultimately has created a mixed fauna derived from both Pacific and Indian Oceans. This has facilitated hybridisation of closely related species, which is a key evolutionary process [43, 44].

The low rates of immigration to these isolated locations also mean that most species rely on self-recruitment of larvae. Larval self-recruitment can also facilitate the evolution of new endemic species. The number of endemic species on Christmas and Cocos is low (1.1 % and 0.4 % of fish species respectively), although their abundance can be relatively high [76].

Larval self-recruitment requires the on-going presence of an adult population. Recovery from long-distance dispersal is likely to be very slow after natural (e.g. cyclones) or anthropogenic (e.g. oil spill) disturbance events [75]. This could be catastrophic if it affected keystones species. In the Cocos lagoon, seagrass (mostly *Thalassia hemorichii*) is the basis of a food chain that includes nesting green turtles [69] and the odd dugong [78], mangroves (mostly the small-leaved mangrove *Pemphis acidula*) function as a fish nursery, and coral colonies shelter many animals [79].

There are marine and anchialine caves around the coast of Christmas Island. The anchialine caves are crustacean dominated with endemic species (and genera) below the halocline (and therefore derived from marine taxa) [80]. At least one new species has also been described from the marine caves [58]. However, these types of caves are typically occupied by widespread species [80] and subterranean caves generally are very under-sampled [81], so such species may be discovered elsewhere in the future.

6.2 Bathyal-Abyssal benthic fauna

The seamounts that lie under these shallow features are massive structures that rise up to 5 km from the deep-abyssal plain, making them some of the tallest seamounts in Australia. Seamounts are rare in the Australian marine domain. Equivalent-sized seamounts that arise from the abyssal plain otherwise only occur in the Tasmantid chain off eastern Australia. Mid-oceanic shallow seamounts and islands are also very rare in the eastern Indian Ocean. The nearest are located at the south of the Ninety-East Ridge (1,950 km from Cocos). The nearest islands to the east are Chagos (2,800 km from Cocos) and Amsterdam (3,600 km away).

As well as shallow water environments, Cocos, Christmas and Muirfield also support the only upper bathyal habitat (200-1000 m deep) of the IOT. The upper bathyal habitat of the IOT also experiences a strong South Equatorial Current, this time bringing intermediate water from Indonesia.

There are more IOT seamounts at mid to lower bathyal depths (1000-3500 m) that are likely to support cold-water coral and sponge communities on their summit rims and steep flanks, and infaunal communities on flat muddy seafloors [3]. However, although IOT seamounts at these depths possibly share the same regional fauna, each seamount assemblage is likely to be different, due to contrasting histories of dispersal, colonisation and persistence [28]. The age of the seamounts varies from east (oldest) to west (youngest), although it is unclear what effect, if any, this will have on the fauna [2]. Manganese crusts can form on exposed rock, particularly on shallower seamounts (1000-1500 m), which can shape epifaunal community composition [36].

The lower primary productivity in the Cocos EEZ may reduce biomass of the seafloor and bathypelagic fauna. Conversely, oceanographic anomalies like Taylor caps, tidal forcing or elevated currents can occur over seamounts and raise productivity. Other features such as Van Karman vortices can form in the lee of seamounts, which mix water masses, form eddies and also enhance productivity. This will be particularly true for seamounts that summit at depths traversed by the vertically migrating plankton (less than 1000m depth). Seamounts have been called the “stirring rods” of the ocean [82].

The Investigator Ridge has been proposed as a barrier to dispersal [14]. However, most of the ridge crests in 3,500 to 4,500 m of water, so it is only likely to affect the dispersal of the abyssal fauna. Moreover, bottom currents flow parallel to the ridge axis and some gaps exist in the south which would allow for some cross-ridge dispersal. The shallower peaks on the ridge (shallowest is 2,408 m) would function as elongated seamounts.

The steep western sides of the Investigator Ridge may provide rare exposed rock habitat at abyssal depths. Other rock habitat at abyssal depths is provided by the development of manganese nodules, particularly at very deep depths (4780-5888 m) in the southern sections of the Christmas EEZ (the Cocos EEZ is largely unexplored for nodules). Other hard substrata may occur near seamounts as recent volcanic debris or reworked flank slumps. However, most of the abyssal seafloor is covered in a thick layer of sediment. This sediment changes from being principally of calcareous origin above the calcite saturation horizon (~3800 m [83]) to being of siliceous origin below, including sediments below 6000 m.

6.3. Pelagic seabirds

Four species of booby breed in the IOT, Abbott’s booby (*Papasula abbotti*), Red-footed booby (*Sula sula*), Brown booby (*Sula leucogaster plotus*), and Masked booby (*Sula dactylatra*). The first is endemic, as it breeds only on Christmas Island (2500 breeding pairs), the second two breed both on Christmas and North Keeling [84], and a few pairs of the last species have started to breed on North Keeling [85]. Abbott’s booby used to breed on other western Indian Ocean islands but ceased by the early 20th century. The breeding colony of the Red-footed booby is one of the largest in the world [85]. Both Abbott’s and Red-footed booby tend to forage during the day and return to the nesting or roosting site at night. A tracking study of *P. abbotti* found that nesting birds tend to forage either to the NW or SE of Christmas Island, aligned with the prevailing wind (in August to October), and directly out to sea from the two nesting grounds [86]. Most foraging trips were less than 60 km out, with one as far as 550 km [86]. The foraging behaviour of *Sula sula* has also been tracked from Christmas Island, with an average maximum range of 164 km of up to 4 days in duration [87]. Most foraging trips were to the east, but longer trips tended to be to the NW or SE, and trips were correlated with chlorophyll α concentration rather than prevailing wind direction [87]. There has been no equivalent study of *S. sula* around North Keeling. This species probably identifies aggregated prey by tracking subsurface predators [88]. Breeding Brown booby at Swains Reef off the Great Barrier Reef foraged in relatively short trips (14.5±10.1 km range over 6.8±2.8 hours), with two-thirds of the trips during daylight hours [89].

Three frigatebirds breed in the IOT, the Christmas Island frigatebird (*Fregata andrewsi*), the Greater frigatebird (*F. minor*) and the Lesser frigatebird (*F. ariel*). The former species is endemic, as it only breeds at Christmas Island, and the latter breeds almost exclusively at North Keeling where it forms the second largest breeding colony in the Indian Ocean [85]. Frigatebirds are special amongst seabirds in not being able to land on the sea as their plumage is not waterproof [90]. However, they expend little energy while flying and can remain in the air for up two months at a time, travelling 1000s km between roosting sites [90]. When not nesting, the Christmas Island frigatebird ranges across the Indian Ocean and South East Asia. Genetic analyses indicate that birds tend to return to the same nesting location. They predominantly feed on flying fish or by kleptoparasitism (robbing other seabirds of their food) or rarely scavenging on land. From breeding or roosting sites, such as on North Keeling or Christmas Islands, they forage shorter distances, up to 240 km. Consequently, although there are no data for foraging activities of frigate birds in the IOT, it is likely that the most important foraging area is nearby to each island.

Two tropic birds also breed both on Christmas and North Keeling, the Red-tailed tropic bird (*Phaethon rubricauda*) and an endemic subspecies of the White-tailed trophic bird (*P. lepturus fulvus*, known locally as the Golden Bosun). They are plunge divers, catching flying fish and squid, to a depth of 25.6 m [91]. Red-tailed tropic birds with chicks at Christmas Island have been recorded taking alternate short (3±4 hr) and long (57±41 hr) trips, with those incubating going on longer trips (153±47 hr) [91].

The Common noddy (*Anous stolidus*) breeds on both islands (550 pairs on Christmas Island) and the Lesser noddy (*Anous tenuirostris*) and Sooty tern (*Onychoprion fuscata*) on North Keeling [84, 85, 92]. The White tern (*Gygis alba*) breeds on a number of islands in the Cocos group [92]. A number of other petrels, gulls, terns and shearwaters are vagrants throughout the IOT [84, 92].

The IOT is part of one of four areas that are foraged by Sooty terns that breed on a small island in the Seychelles in the western Indian Ocean [93]. Non-breeding birds can forage up to 50,000 km on a single trip and the bird appears to sleep in flight. This species is the largest bird consumer of marine resources in the tropics. It forages in flocks by following tuna and mackerel, eating small fish and squid by ‘dipping’ and not settling on waters. The practice of ‘facilitated foraging’ by eating small fish chased to the surface by predatory fish is likely to be important for many seabirds [94].

Conversely, Lesser noddys and White terns do not stray that far from breeding colonies [95, 96]. The White tern’s diet matches that of tuna and mackerel off Hawaii [96] suggesting that they too rely on facilitated foraging.

Only one bird (a Wedge-tailed shearwater) was sighted on the last survey around the Muirfield seamount [9].

6.4 Pelagic mammals

Little is known about whale and dolphin activity in the IOT. Several whale species have been sighted around the islands or from marine observers, including Fin, Humpback, Blue and Sei whales, but many of these observations require validation [14].

Three dolphins are known to occur, Spinner (*Stenella longirostris*) and Short-beaked common dolphins (*Delphinus delphis*) around Christmas Island, and Bottlenose (*Tursiops truncates*) and Common dolphins around the Cocos Islands [14]. A pod of Common dolphins are occasionally seen around the south eastern corner of Christmas Island and an indented bay on the north coast of Christmas Island supports a population of approximately 200 resident Spinner dolphins [14].

Various dolphins and whales are known to associate with schools of tuna, particularly Yellowfin and Bigeye tuna, as they follow schools of bait fish. This was originally reported from the eastern Pacific but also occurs in the western and central Indian Ocean [97]. Fishers have used this association to locate Yellowfin schools and set nets under feeding dolphins resulting in cetacean casualties [97]. Other cetaceans, such as false killer whales, have been recorded removing bait from tuna longlines [97].

A single male dugong ('Kat') has been reported from the north of the lagoon at the southern Cocos Islands, where it appears to seek the company of divers [78, 98].

6.5 Pelagic sharks and rays

Two species of manta rays have been recorded from the IOT, the Reef manta ray (*Mobula alfredi*) in and around the lagoon between the southern Cocos Islands, and the Oceanic mantra ray (*M. birostris*) around Christmas Island [99]. Reef manta rays appear to have long term affinity to foraging sites off Western Australia [100], with migrations generally less than 500 km and rarely up to 1150 km [99], so the population of this species at Cocos may be more or less resident to the IOT.

Whale sharks (*Rhincodon typus*) are regularly sighted along the north and east coasts of Christmas Island [14], including rarely seen juveniles [101]. They are seen mostly from December to April but can occur at the Island all year round [14]. Some animals have been tracked arriving from Ningaloo [14] and one animal tagged at Christmas Island swam past Timor into the Banda Sea [102]. The animals arrive at Christmas Island at the same time as the spawning of the Red-land crab (*Gecarcoidea natalis*) [101] and genetic evidence shows that the whale sharks consume a large amount of crab larvae [103]. However, Whale sharks regularly dive to 1000 m, and would consume other plankton in the deep water surrounding the island [14].

Pelagic sharks would also traverse the IOT but little information is available [14].

6.6 Pelagic fin fish.

Southern bluefin tuna (SBT, *Thunnus maccoyii*) is a single stock and the only known spawning ground is located between Java and NW Australia, including the Christmas Island EEZ. Adults (10-40 years old) arrive in September-October and February-March to spawn [104]. Spawning is largely late in the evening or early in the morning and occurs near the water surface [105]. Fish then regularly dive into deeper water to thermoregulate. SBT is a cold-water fish and cannot tolerate the warm waters of the spawning ground (24-30˚C) for extended periods. The location of a spawning ground outside its foraging range may reduce the risk of larval predation in the relatively oligotrophic waters [106] or because the larvae are endothermic [104].The timing of the spawning season occurs during the NW Monsoon which brings higher productivity and SE flowing currents to the region [14]. Females may have several spawning events and then rapidly migrate south again [106].

The larvae drift passively before becoming entrained in the southwards flowing South Java and Leeuwin Currents and carried down the coast of Western Australia [106]. One to two-year old juveniles then head east to the Great Australian Bight, or west to the waters off South Africa. They probably migrate by following older fish ('adopted' migration) [107] which decreases the chance of population recovery after over-fishing of adult fish. Historically, SBT was fished by Japanese longline fishers in waters now encompassed by the IOT, however, the meat of spawning fish is of poor quality [105] and from the 1960s fishing effort gradually moved southwards into the Southern Ocean [107].

Other pelagic fish also use IOT waters as a foraging or spawning ground. Tuna at equatorial latitudes are mainly Yellowfin (*Thunnus albacares*) and Bigeye (*Thunnus obesus*) [14, 108]. Yellowfin migrate through the IOT in the cooler months where they are caught by recreational fishers from the Islands [14]. Conversely Sailfish (*Istiophorus platypterus*) are caught mainly when waters begin to warm. Some pelagic species are commonly found associated with shallower reef and slope structures around the islands, such as Bluefin trevally (*Caranx melampygus*), Small-toothed jobfish (*Aphareus rutlians*) and Wahoo (*Acanthocybium solandri*), whose prey include demersal and benthic seamount species [14]. Wahoo appears to breed all year round [14]. Although, there is no genetic differentiation [109] across Wahoo's global range, its morphology and parasite load shows regional differentiation [110], and it is likely to remain in a home range and be semi-resident [75]. Flying fish and small pelagic fish and squid are an important component of the pelagic food web in the IOT, especially during the spring upwelling when the water temperatures decrease [14].

7. Conclusion

The IOT contains a diverse range of benthic habitats ranging in depth from island coastal assemblages to hadal plains below 6000 m. There is a NE to SW gradient in sea-surface primary productivity that will influence benthic community composition and abundance. There is also a relatively high proportion of rocky substrata compared with the Australian continental margin.

The oceanic seamount and island communities (30-2000 m) in the IOT are rare examples of these habitats in the eastern tropical Indian Ocean and are of national to international conservation significance. Each of these seamounts is likely to have a distinct migration and environmental history leading to relatively unique combinations of the regional fauna at each location.

The presence of rocky substrata at lower bathyal depths, manganese nodules at abyssal depths, and seafloor at hadal depths are significant in a more regional context.

Appendix 1: IOT Seamount names

A number of names have been applied to seamounts, clusters of seamounts, rises and volcanic provinces within the IOT regions. The names in international gazetteers (eg GEBCO, Marine Regions) originated from discovery voyages of the International Indian Ocean Expeditions (IIOE, 1959-1965) or survey expeditions in the 1960-1980s when mapping technology was rudimentary. Consequently, many of these names refer to seamount clusters, rather than individual features (Fig. 1), and their geographic limits are unclear. These include the Raitt Rise to the SW of Cocos, the Vening Meinesz Rise to the east of the Investigator Ridge, the Flying Fish seamounts at the far NW of the Christmas EEZ, the Golden Bo'sunbird Seamounts to the SW of Christmas Island, the Bartlett Seamounts to the south of Christmas Island, and the Karma Seamounts to the SE. Confusingly, the name 'Vening Meinesz Seamounts' has also been given to 1) an overlapping group of northern Golden Bo'sunbird and Flying Fish Seamounts (but excluding Shcherbakov, 'Glogg' and 'Attention'), and to 2) a large volcanic province that stretches from Christmas Island all the way to the Investigator Ridge. The name 'Karma' was originally used for an "ill-defined tract of seafloor" before it was known to include seamounts. The utility of these names is debatable.

Hoernle et al. [2] divided the IOT seamounts into three volcanic provinces (Fig. 1): East Wharton Basin (south and southeast of Christmas Island), Vening Meinesz (Christmas Is and southwest to the Investigator Ridge) and Cocos (west of the Investigator Ridge) [2], although it is unclear on what basis this was done as the seamounts form a broad age gradient from east (oldest) to west [2].

Apart from the two island groups, the only individual features with official names are the Muirfield Seamount to the SW of Cocos islands and Shcherbakov Seamount (often misspelt Sherbakov or Scherbakov) to the west of Christmas Island. The voyage report by Werner et al. [3] of a geological expedition (SO199) of the RV Sonne in 2008 partially rectified this situation by unofficially naming numerous IOT seamounts that they discovered using multibeam sonar. However, these names have not been lodged in marine gazetteers or used in scientific literature. Instead Taneja & O'Neill [5] reused the seamount group names (listed above) to refer to a single seamount, including Golden Bo'sunbird for both Werner's 'Apollo 8' (their Fig. 1) and 'Balthazar' seamount (their Table 4), Flying Fish for 'Melchior', Vening Meinesz for 'Lucia', and Bartlett for a seamount NE of 'Clara Marie'.

To avoid further confusion, this assessment uses the unofficial names of Werner et al. [3] placed in quotation marks (Fig. 1) as they refer to single identifiable features. However, many seamounts are still unnamed.

References

1. Zahirovic, S., et al., *Tectonic evolution and deep mantle structure of the eastern Tethys since the latest Jurassic.* Earth-Science Reviews, 2016. **162**: p. 293-337.
2. Hoernle, K., et al., *Origin of Indian Ocean Seamount Province by shallow recycling of continental lithosphere.* Nature Geoscience, 2011. **4**: p. 883–887.
3. Werner, R., F. Hauff, and K. Hoernle, *RV Sonne Fahrtbericht / Cruise Report SO 199 CHRISP. Christmas Island Seamount Province and the Investigator Ridge: Age and Causes of Intraplate Volcanism and Geodynamic Evolution of the south-eastern Indian Ocean*. 2009, IFM-GEOMAR: Leibniz. p. 210 pp.
4. Chaproniere, G.C., S. Shafik, and P.J. Coleman, *Biostratigraphy of Rig Seismic samples from Vening Meinesz seamounts, Christmas Island area, northeastern Indian Ocean.* AGSO Journal of Australian Geology & Geophysics, 1997. **16**(5): p. 677-699.
5. Taneja, R. and C. O'Neill, *Constraining the age and origin of the seamount province in the Northeast Indian Ocean using geophysical techniques.* Marine Geophysical Research, 2014. **35**(4): p. 395-417.
6. Montelli, R., et al., *Finite-Frequency Tomography Reveals a Variety of Plumes in the Mantle.* Science, 2004. **303**(5656): p. 338-343.
7. Droxler, A.W. and S.J. Jorry, *The Origin of Modern Atolls: Challenging Darwin's Deeply Ingrained Theory.* Annual Review of Marine Science, 2021. **13**(1): p. null.
8. Woodroffe, C.D., R.F. McLean, and E. Wallensky, *Geomorphology of the Cocos (Keeling) Islands.* Atoll Research Bulletin (Chapter 4), 1994. **402**(1-33).
9. Williams, A., et al., *A preliminary survey of the Muirfield Seamount seabed. A report by CSIRO Marine Research to Environment Australia*. 2000. p. 1-38.
10. Exon, N.F., et al., *BMR Cruise 107: Seabed Morphology and Offshore Resources around Christmas Island, Indian Ocean.* Australian Geological Survey Organisation Record 1993. **1993/6**: p. v+87+appendices.
11. Straume, E.O., et al., *GlobSed: Updated Total Sediment Thickness in the World's Oceans.* Geochemistry, Geophysics, Geosystems, 2019. **20**(4): p. 1756-1772.
12. von der Borch, C.C., et al., *Site 213.* Initial reports of the Deep Sea Drilling Project, covering Leg 22 of the cruises of the drilling vessel Glomar Challenger; Darwin, Australia to Colombo, Ceylon, January-March 1972, 1974. **22**: p. 85.
13. von der Borch, C.C., et al., *Site 211*, in *Initial reports of the Deep Sea Drilling Project, covering Leg 22 of the cruises of the drilling vessel Glomar Challenger; Darwin, Australia to Colombo, Ceylon, January-March 1972*. 1974. p. 13.
14. Brewer, D.T., et al., *Conservation values in Commonwealth waters of the Christmas and Cocos (Keeling) Island remote Australian Territories. Report to Department of Environment and Water Resources*. 2009, CSIRO: Cleveland. p. 216 pp.
15. Talley, L.D. and J. Sprintall, *Deep expression of the Indonesian Throughflow: Indonesian Intermediate Water in the South Equatorial Current.* Journal of Geophysical Research: Oceans, 2005. **110**(C10).

16. Wijffels, S., et al., *The JADE and WOCE I10/IR6 Throughflow sections in the southeast Indian Ocean. Part 1: water mass distribution and variability.* Deep Sea Research Part II: Topical Studies in Oceanography, 2002. **49**(7): p. 1341-1362.
17. Wijeratne, S., C. Pattiaratchi, and R. Proctor, *Estimates of Surface and Subsurface Boundary Current Transport Around Australia.* Journal of Geophysical Research: Oceans, 2018. **123**(5): p. 3444-3466.
18. Tomczak, M. and J.S. Godfrey, *Regional Oceanography: An Introduction*. 2nd improved edition ed. 2003, Delhi: Daya Publishing House. 390.
19. Smith, C.R., et al., *Abyssal food limitation, ecosystem structure and climate change.* Trends in Ecology and Evolution, 2008. **23**: p. 518-528.
20. Wolff, G.A., et al., *The Effects of Natural Iron Fertilisation on Deep-Sea Ecology: The Crozet Plateau, Southern Indian Ocean.* PLOS ONE, 2011. **6**(6): p. e20697.
21. O'Hara, T.D., et al., *Deep-sea temperate-tropical faunal transition across uniform environmental gradients.* Deep Sea Research Part I: Oceanographic Research Papers, 2020. **161**: p. 103283.
22. Woolley, S.N.C., et al., *Deep-sea diversity patterns are shaped by energy availability.* Nature, 2016. **533**: p. 393–396.
23. Behrenfeld, M.J. and P.G. Falkowski, *Photosynthetic rates derived from satellite-based chlorophyll concentration.* Limnology and Oceanography, 1997. **42**: p. 1-20.
24. Bribiesca-Contreras, G., et al., *The importance of offshore origination revealed through ophiuroid phylogenomics.* Proceedings of the Royal Society B: Biological Sciences, 2017. **284**(1858): p. 20170160.
25. O'Hara, T.D., et al., *Contrasting processes drive ophiuroid phylodiversity across shallow and deep seafloors.* Nature, 2019. **565**(7741): p. 636–639.
26. Carney, R.S., *Zonation of deep biota on continental margins.* Oceanography and Marine Biology: An Annual Review, 2005. **43**: p. 211-278.
27. O'Hara, T.D., et al., *Regional-scale patterns of deep seafloor biodiversity for conservation assessment.* Diversity and Distributions, 2020. **26**: p. 479-494.
28. Tracey, D.M., et al., *Deep-Sea Fish Distribution Varies between Seamounts: Results from a Seamount Complex off New Zealand.* PLOS ONE, 2012. **7**(6): p. e36897.
29. Ludbrook, N.H., *Tertiary fossils from Christmas Island (Indian Ocean).* Journal of the Geological Society of Australia, 1965. **12**(2): p. 285-294.
30. Ali, J.R. and J.C. Aitchison, *Time of re-emergence of Christmas Island and its biogeographical significance.* Palaeogeography, Palaeoclimatology, Palaeoecology, 2020. **537**: p. 109396.
31. Djurhuus, A., J.F. Read, and A.D. Rogers, *The spatial distribution of particulate organic carbon and microorganisms on seamounts of the South West Indian Ridge.* Deep Sea Research Part II: Topical Studies in Oceanography, 2017. **136**: p. 73-84.

32. Davis, R.E., *Intermediate-depth circulation of the Indian and South Pacific Oceans Measured by autonomous floats.* Journal of Physical Oceanography, 2005. **35**: p. 683-707.
33. Letessier, T.B., et al., *Seamount influences on mid-water shrimps (Decapoda) and gnathophausiids (Lophogastridea) of the South-West Indian Ridge.* Deep Sea Research Part II: Topical Studies in Oceanography, 2017. **136**: p. 85-97.
34. Laptikhovsky, V., et al., *Cephalopods of the Southwest Indian OceanRidge: A hotspot of biological diversity and absence of endemism.* Deep Sea Research Part II: Topical Studies in Oceanography, 2017. **136**: p. 98-107.
35. Cordes, E.E., et al., *Chapter 42: Cold-Water Corals*, in *The First Global Integrated Marine Assessment: World Ocean Assessment I.* , L. Inniss and A. Simcock, Editors. 2016, Under the auspices of the United Nations General Assembly.
36. Delavenne, J., et al., *Deep-sea benthic communities in the largest oceanic desert are structured by the presence of polymetallic crust.* Scientific Reports, 2019. **9**(1): p. 6977.
37. Schlacher, T.S., et al., *Seamount benthos in a cobalt-rich crust region of the Central Pacific: implications for conservation challenges posed by future seabed mining.* Diversity and Distributions, 2014. **20**: p. 491–502.
38. Simon-Lledó, E., et al., *Ecology of a polymetallic nodule occurrence gradient: Implications for deep-sea mining.* Limnology and Oceanography, 2019. **64**(5): p. 1883-1894.
39. Durden, J.M., et al., *Abyssal hills – hidden source of increased habitat heterogeneity, benthic megafaunal biomass and diversity in the deep sea.* Progress in Oceanography, 2015. **137**: p. 209-218.
40. Simon-Lledó, E., et al., *Megafaunal variation in the abyssal landscape of the Clarion Clipperton Zone.* Progress in Oceanography, 2019. **170**: p. 119-133.
41. Jamieson, A.J., et al., *Hadal trenches: the ecology of the deepest places on Earth.* Trends in Ecology & Evolution, 2010. **25**(3): p. 190-197.
42. Woodroffe, C.D. and P.F. Berry, *Scientific studies in the Cocos (Keeling) Islands: An introduction.* Atoll Research Bulletin (Chapter 1), 1994. **399**: p. 1-16.
43. Hobbs, J.P.A., et al., *Marine hybrid hotspot at Indo-Pacific biogeographic border.* Biology Letters, 2009. **5**: p. 258-261.
44. Hobbs, J.P.A. and G.R. Allen, *Hybridisation among coral reef fishes at Christmas Island and the Cocos (Keeling) Islands.* Raffles Bulletin of Zoology, 2014. **Supplement 30**: p. 220-226.
45. Hernawan, U.E., et al., *Historical processes and contemporary ocean currents drive genetic structure in the seagrass Thalassia hemprichii in the Indo-Australian Archipelago.* Molecular Ecology, 2017. **26**(4): p. 1008-1021.
46. Vogler, C., et al., *A threat to coral reefs multiplied? Four species of crown-of-thorns starfish.* Biology Letters, 2008. **4**: p. 696-699.
47. Vogler, C., et al., *Phylogeography of the Crown-of-Thorns Starfish in the Indian Ocean.* PLoS ONE, 2012. **7**(8): p. e43499.

48. DiBattista, J.D., et al., *Indo-Pacific Butterflyfishes Reveals Divergent Evolutionary Histories and Discordant Results from mtDNA and Microsatellites.* Journal of Heredity, 2012. **105**(5): p. 617-629.
49. Ahti, P.A., et al., *Phylogeography of Indo-Pacific reef fishes: sister wrasses Coris gaimard and C. cuvieri in the Red Sea, Indian Ocean and Pacific Ocean.* Journal of Biogeography, 2016. **43**(6): p. 1103-1115.
50. Waldrop, E., et al., *Phylogeography, population structure and evolution of coral-eating butterflyfishes (Family Chaetodontidae, genus Chaetodon, subgenus Corallochaetodon).* Journal of Biogeography, 2016. **43**: p. 1116-1129.
51. Richards, Z.T. and J.-P.A. Hobbs, *The status of hard coral diversity at Christmas Island and Cocos (Keeling) Islands.* Raffles Bulletin of Zoology, 2014. **Supplement 30**: p. 376-398.
52. Allen, G.R., R.C. Steene, and M. Orchard, *Fishes of Christmas Island. 2nd Edition*. 2007, Christmas Island, Australia: Christmas Island Natural History Association. 284.
53. Hobbs, J.-P.A., et al., *Checklist and new records of Christmas Island fishes: the influence of isolation, biogeography and habitat availability on species abundance and community composition.* Raffles Bulletin of Zoology, 2014. **Supplement 30**: p. 184-202.
54. Hobbs, J.-P.A., et al., *Fishes of the Cocos (Keeling) Islands: new records, community composition and biogeographic significance.* Raffles Bulletin of Zoology, 2014. **Supplement 30**: p. 203-219.
55. Veron, J.E.N., *Hermatypic corals of the Cocos (Keeling) Islands.* Atoll Research Bulletin (Chapter 11), 1994. **409**: p. 1-21.
56. Tan, S.K. and M.E.Y. Low, *Checklist of the Mollusca of Cocos (Keeling) / Christmas Island ecoregion.* Raffles Bulletin of Zoology, 2014. **Supplement 30**: p. 313-375.
57. Hui, T.H., et al., *Observations on the fauna from submarine and associated anchialine caves in Christmas Island, Indian Ocean Territory, Australia.* Raffles Bulletin of Zoology, 2004. **Supplement No. 30**: p. 406-418.
58. Okanishi, M., Y. Oba, and Y. Fujita, *Brittle stars from a submarine cave of Christmas Island, northwestern Australia, with description of a new bioluminescent species Ophiopsila xmasilluminans (Echinodermata: Ophiuroidea) and notes on its behaviour.* The Raffles Bulletin of Zoology, 2019. **67**: p. 421-439
59. Ng, P.K.L. and T. Naruse, *A new family, genus and species of cavernicolous crab (Crustacea: Decapoda: Brachura: Pseudozioidea) from Christmas Island, Australia.* Raffles Bulletin of Zoology, 2014. **Supplement 30**: p. 263-273.
60. Hui, T.H., *A new record of Trimma fasciatum Suzuki, Sakaue & Senou, 2012 (Perciformes: Gobiidae) from Christmas Island, Indian Ocean, Australia.* Raffles Bulletin of Zoology, 2014. **Supplement 30**: p. 227-229.
61. O'Hara, T.D., A.A. Rowden, and N.J. Bax, *A southern hemisphere bathyal fauna is distributed in latitudinal bands.* Current Biology, 2011. **21**: p. 226-230.

62. Watling, L., et al., *A Proposed Biogeography of the Deep Ocean Floor.* Progress in Oceanography, 2013. **111**: p. 91-112.
63. O'Hara, T.D., et al., *Limited phylogeographic structure for five bathyal ophiuroids at continental scales.* Deep Sea Research Part I: Oceanographic Research Papers, 2014. **84**: p. 18-28.
64. Kuhnt, W., et al., *Neogene History of the Indonesian Throughflow*, in *Continent-Ocean Interactions Within East Asian Marginal Seas*, P. Clift, et al., Editors. 2004. p. 299-320.
65. Yearsley, J.M., et al., *Biophysical models of persistent connectivity and barriers on the northern Mid-Atlantic Ridge.* Deep Sea Research Part II: Topical Studies in Oceanography, 2020. **180**: p. 104819.
66. Won, Y., et al., *Dispersal barriers and isolation among deep-sea mussel populations (Mytilidae: Bathymodiolus) from eastern Pacific hydrothermal vents.* Mol Ecol, 2003. **12**(1): p. 169-84.
67. Riehl, T., L. Lins, and A. Brandt, *The effects of depth, distance, and the Mid-Atlantic Ridge on genetic differentiation of abyssal and hadal isopods (Macrostylidae).* Deep Sea Research Part II: Topical Studies in Oceanography, 2018. **148**: p. 74-90.
68. Bober, S., et al., *Does the Mid-Atlantic Ridge affect the distribution of abyssal benthic crustaceans across the Atlantic Ocean?* Deep Sea Research Part II: Topical Studies in Oceanography, 2018. **148**: p. 91-104.
69. Whiting, S.D., et al., *Sea turtles of the Cocos (Keeling) Islands, Indian Ocean.* Raffles Bulletin of Zoology, 2014. **Supplement 30**: p. 168–183.
70. Whiting, S.D., et al., *Non-migratory breeding by isolated green sea turtles (Chelonia mydas) in the Indian Ocean: biological and conservation implications.* Naturwissenschaften, 2008. **95**(4): p. 355-60.
71. Jensen, M.P., *Assessing the composition of green turtle (Chelonia mydas) foraging grounds in Australasia using mixed stock analyses*, in *Institute for Applied Ecology, Faculty of Applied Science*. 2010, University of Canberra: Canberra. p. 132.
72. Dethmers, K.E.M., et al., *Migration of green turtles (<i>Chelonia mydas</i>) from Australasian feeding grounds inferred from genetic analyses.* Marine and Freshwater Research, 2010. **61**(12): p. 1376-1387.
73. Jensen, M.P., et al., *The evolutionary history and global phylogeography of the green turtle (Chelonia mydas).* Journal of Biogeography, 2019. **46**(5): p. 860-870.
74. Whiting, S.D., *The Sea Turtle Resources of Cocos (Keeling) Islands, Indian Ocean. Year 9 Jan 2008, Year 10 Jan 2009, Year 11 Jan 2010*. 2010, Biomarine International, Charles Darwin University: Darwin, NT. p. 34.
75. Hourston, M., *Review of the exploitation of marine resources of the Australian Indian Ocean Territories: the implications of biogeographic isolation for tropical island fisheries. Fisheries Research Report No. 208*. 2010, Department of Fisheries, Western Australia. p. 49.

76. Hobbs, J.-P.A., et al., *Biogeography and the structure of coral reef fish communities on isolated islands.* Journal of Biogeography, 2012. **39**(130-139).
77. Richards, Z.T., et al., *Diversity on the edge: non-linear patterns of coral community structure at an isolated oceanic island.* Marine Ecology Progress Series, 2016. **546**: p. 61-74.
78. Hobbs, J.-P.A., et al., *Long-distance oceanic movement of a solitary dugong (Dugong dugon) to the Cocos (Keeling) Islands.* Aquatic Mammals 2007. **33**: p. 175-178.
79. Bellchambers, L.M. and S.N. Evans, *A Summary of The Department of Fisheries, Western Australia Invertebrate Research at Cocos (Keeling) Islands 2006 – 2011, Fisheries Research Report No. 239*. 2013, Department of Fisheries, Western Australia. p. 72.
80. Humphreys, W.F., *Subterranean fauna of Christmas Island: habitats and salient features.* Raffles Bulletin of Zoology, 2014. **Supplement 30**: p. 29-44.
81. West, K.M., et al., *Under the karst: detecting hidden subterranean assemblages using eDNA metabarcoding in the caves of Christmas Island, Australia.* Scientific Reports, 2020. **10**: p. 21479.
82. Perfect, B., N. Kumar, and J.J. Riley, *Vortex Structures in the Wake of an Idealized Seamount in Rotating, Stratified Flow.* Geophysical Research Letters, 2018. **45**(17): p. 9098-9105.
83. Peterson, L.C. and W.L. Prell, *Carbonate dissolution in Recent sediments of the eastern equatorial Indian Ocean: Preservation patterns and carbonate loss above the lysocline.* Marine Geology, 1985. **64**(3): p. 259-290.
84. James, D.J. and I.A.W. McAllan, *The birds of Christmas Island, Indian Ocean: A review.* Australian Field Ornithology, 2014. **31 (Supplement)**: p. S1-S175.
85. Department of Environment and Heritage (DEH), *Pulu Keeling National Park Management Plan 2015-2025*. 2015, Department of the Environment and Heritage: Canberra, Australia. p. 131 pp.
86. Hennicke, J.C. and H. Weimerskirch, *Foraging movements of Abbott's Boobies during early chick-rearing and implications for a marine Important Bird Area in Christmas Island waters.* Raffles Bulletin of Zoology, 2014. **Supplement 30**: p. 60-64.
87. Mendez, L., et al., *Geographical variation in the foraging behaviour of the pantropical red-fotted booby.* Marine Ecology Progress Series, 2017. **568**: p. 217-230.
88. Weimerskirch, H., et al., *Foraging strategy of a tropical seabird, the red-footed booby, in a dynamic marine environment.* Marine Ecology Progress Series, 2005. **288**: p. 251-261.
89. Bunce, A., *Foraging behaviour of a declining population of Brown Boobies (Sula leucogaster) breeding in the Swain Reefs, Great Barrier Reef.* Emu - Austral Ornithology, 2015. **115**(4).
90. Weimerskirch, H., et al., *Diversity of migration strategies among great frigatebirds populations.* Journal of Avian Biology, 2017. **48**: p. 103-113.

91. Sommerfeld, J. and J.C. Hennicke, *Comparison of trip duration, activity pattern and diving behaviour by Red-tailed Tropicbirds (Phaethon rubricauda) during incubation and chick-rearing.* Emu - Austral Ornithology, 2010. **110**: p. 78-86.
92. Island Explorer Holidays, *Christmas and Cocos Keeling Islands Birding Guide*. 2008. p. 30 pp.
93. Jaeger, A., et al., *Geolocation Reveals Year-Round at-Sea Distribution and Activity of a Superabundant Tropical Seabird, the Sooty Tern Onychoprion fuscatus.* Frontiers in Marine Science, 2017. **4**(394): p. 1-10.
94. Maxwell, S.M. and L.E. Morgan, *Foraging of seabirds on pelagic fishes: implications for management of pelagic marine protected areas.* Marine Ecology Progress Series, 2013. **481**: p. 289-303.
95. Surman, C.A., L.W. Nicholson, and S. Ayling, *Foraging behaviour of the Lesser Noddy Anous tenuirostris melanops from the eastern Indian Ocean: insights from micro-geologging.* Marine Ornithology, 2017. **45**: p. 123-128.
96. Yeung, N.W., D.C. Duffy, and S. Conant, *Characterizing isotopic variation of a tropical seabird, the White Tern Gygis alba.* Marine Ornithology, 2014. **42**: p. 113-117.
97. Anderson, R.C., *Cetaceans and Tuna Fisheries in the Western and Central Indian Ocean.* . 2014, International Pole and Line Foundation: London. p. 133 pp.
98. Hobbs, J.-P.A. and K. Willshaw, *Unusual behavior and habitat use of a solitary male dugong inhabiting coral reefs at the Cocos (Keeling) Islands.* Marine Biodiversity, 2016. **46**(1): p. 31-32.
99. Armstrong, A.J., et al., *The geographic distribution of reef and oceanic manta rays in Australian coastal waters.* Journal of Fish Biology, 2020. **96**(3).
100. Armstrong, A.J., et al., *Satellite tagging and photographic identification reveal connectivity between two UNESCO World Heritage Areas for Reef Manta Rays.* Frontiers in Marine Science, 2020. **7**.
101. Hobbs, J.P.A., et al., *Seasonal aggregation of juvenile whale sharks (Rhincodon typus) at Christmas Island, Indian Ocean.* Coral Reefs, 2009. **28**: p. 577.
102. Meekan, M. and B. Radford, *Migration Patterns of Whale Sharks; A summary of 15 satellite tag tracks from 2005 to 2008. Report to the Browse Joint Venture Partners.* . 2010, Australian Institute of Marine Science: Perth. p. 21.
103. Meekan, M.G., et al., *DNA evidence of whale sharks (Rhincodon typus) feeding on red crab (Gecarcoidea natalis) larvae at Christmas Island, Australia.* Marine and Freshwater Research, 2009. **60**(6): p. 607-609.
104. Evans, K., et al., *Reproductive Schedules in Southern Bluefin Tuna: Are Current Assumptions Appropriate?* PLOS ONE, 2012. **7**(4): p. e34550.
105. Farley, J.H., et al., *Spawning Dynamics and Size Related Trends in Reproductive Parameters of Southern Bluefin Tuna, Thunnus maccoyii.* PLOS ONE, 2015. **10**(5): p. e0125744.
106. Hobday, A., et al., *Distribution and Migration—Southern Bluefin Tuna (Thunnus maccoyii)*, in *Biology and Ecology of Bluefin Tuna*, T. Kitagawa and S. Kimura, Editors. 2015, CRC Press. p. 189-210.

107. Chambers, M.S., et al., *Evidence of separate subgroups of juvenile southern bluefin tuna.* Ecology and Evolution, 2017. **7**(22): p. 9818-9844.
108. Reygondeau, G., et al., *Biogeography of tuna and billfish communities.* Journal of Biogeography, 2012. **39**: p. 114-129.
109. Theisen, T.C., et al., *High connectivity on a global scale in the pelagic wahoo, Acanthocybium solandri (tuna family Scombridae).* Molecular Ecology, 2008. **17**(19): p. 4233-4247.
110. Zischke, M.T., et al., *Stock identification of wahoo (Acanthocybium solandri) in the Pacific and Indian Oceans using morphometrics and parasites.* ICES Journal of Marine Science, 2012. **70**(1): p. 164-172.