Characteristics of shallow and mesophotic environments of the Pemba Channel, Tanzania: Implications for management and conservation

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A B S T R A C T

Information on the spatial distribution of habitats and vulnerable species is important for conservation planning. In particular, detailed knowledge on connectivity of marine ecosystems in relation to depth and seafloor characteristics is crucial for any proposed conservation and management actions. Yet, the bulk of the seafloor remains under-sampled, unstudied and unmapped, thereby limiting our understanding of connections between shallow and deep-water communities. Recent studies on mesophotic coral ecosystems (MCEs) have highlighted the Western Indian Ocean as a particularly understudied marine region. Here we utilise an autonomous underwater vehicle (AUV) to collect in-situ temperature, oxygen concentration, bathymetry, acoustic backscatter and photographic data on benthic communities from shallow (<30 m) and mesophotic (30–150 m) depths at selected sites in the Greater Pemba Channel, Tanzania. Further, we use generalised additive models (GAMs) to determine useful predictors of substratum (hard and sand) and benthic community type (coral, turf algae, fleshy algae, fish). Our results revealed the presence of a complex seafloor characterised by pockmarks, steep slopes, submarine walls, and large boulders. Photographs confirmed the presence of MCE composed of corals, algae and fishes on the eastern margins of the Pemba Channel. The GAMs on the presence and absence of benthic community explained 35%–91% of the deviance in fish and fleshy algae assemblages, respectively. Key predictors of the distribution of hard substrata and the coral reef communities were depth, showing the upper boundary of MCEs present at 30–40 m, and seafloor slope that showed more occurrences on steep slopes. The upper 100 m of water column had stable temperatures (25–26 °C) and oxygen concentrations (220–235 μmol/l). We noted the presence of submarine walls, steeply inclined bedrock, which appeared to support a highly bio-diverse community that may be worthy of particular conservation measures. Our results also highlight the capability of using marine robotics, particularly autonomous vehicles, to fill the knowledge gap for areas not readily accessible by divers or with surface vessels, and their potential application for the initial survey and subsequent monitoring of Marine Protected Areas.

1. Introduction

Coral reef ecosystems are characterised by a light dependent biotic community comprising corals, sponges, and algae, with associated fish species that are distributed from shallow (0–30 m) to mesophotic (30–150 m) depths. In the latter depth range they are typically referred to as Mesophotic Coral Ecosystems (MCEs) (Laverick et al., 2018; Pyle and Copus, 2019). MCEs are considered distinct from their shallow counterparts due to a decrease in light attenuation and temperature with increasing depth, resulting in a vertical zonation of community structure (Kahng et al., 2019). As such, MCEs can provide, to a variety of species, a refuge against high temperature (Kahng et al., 2019), which has significant impacts on shallow coral reef systems by causing massive coral bleaching and mortality, as evidenced in different Western Indian Ocean (WIO) locations (Obura et al., 2017; Gudka et al., 2019). MCEs are also important for the maintenance of biodiversity and, in some places the

provision of fisheries resources, or as a refuge from high fishing pressure in shallow waters (Tyler et al., 2009; Bongaerts et al., 2010; Pinheiro et al., 2016). As such, understanding distribution of organisms and habitat use is critical towards ensuring effective sustainable management of marine areas.

Nearly 10% of the global ocean floor is unmapped (Wölfl et al., 2019). This is especially the case in the WIO region where water column and seafloor characteristics are under-sampled (Groeneveld et al., 2017). In particular, MCEs in the WIO are amongst the most under-studied marine ecosystems of the world (Laverick et al., 2018; Pyle and Copus, 2019). This contrasts with the shallow coral ecosystems that in general have been adequately surveyed. The dichotomy in sampling effort stems from logistical and capacity challenges associated with accessing these ecosystems. Shallow coral ecosystems are easily accessible by SCUBA divers and have benefited from long-term monitoring programmes, particularly those set up after the 1998 El Niño event (Souter et al., 2000; Muhando, 2009). Data acquisition in deep areas is associated with high ship-based costs related to time and human resources (Wölfl et al., 2019), and a lack or limited access to technology. For instance, since the 1970s, there have been less than ten ship-based deep-sea surveys in Tanzania (Kaehler et al., 2008; Groeneveld and Koranteng 2017; see also Gates et al., this issue). In part, these surveys involved the deployment of remotely operated vehicles aimed at locating and filming coelacanths (*Latimeria chalumnae*) and their habitats. Nevertheless, information on the existence and spatial distribution of MCEs is underreported or non-existent, limiting any efforts in conservation planning especially in this era of increasing ocean temperatures (Bridge et al., 2012; Hoegh-Guldberg et al., 2018). The potential importance of the WIO's mesophotic depths is indicated by the high fish biomass (1100 kg/ha) recorded on ocean-exposed fringing reefs that occur at the boundary between shallow and upper mesophotic depths (Samoilys et al., 2019; Osuka et al., 2020). However, given the limited number of surveys in the WIO, the extent and overall linkages between shallow and mesophotic systems remains unknown.

Unmanned, autonomous vehicles offer an alternative option for reducing the high operational costs and logistical challenges associated with surveying deeper waters (Wynn et al., 2014; Benoist et al., 2019). They can provide an improved mission safety and can undertake distant operations beyond the detection ranges of human observers (Verfuss et al., 2019). Water column vehicles, such as autonomous underwater vehicles (AUVs), have the ability to: survey greater depths (some being full ocean depth capable; see e.g. Durden et al., 2020), provide high spatial resolution data (0.1–0.5 m) on seabed properties and simultaneously collect data on water column properties, bathymetry, acoustic backscatter, and benthic habitats and species (Wynn et al., 2014; Huvenne et al., 2018). For these reasons, application of unmanned vehicles has increased rapidly in recent years and is now widely applied in remote seabed mapping and oceanography studies (Simon-Lledó et al., 2019), and the monitoring of Marine Protected Areas (MPAs) and wildlife (Verfuss et al., 2019; Benoist et al., 2019; Zelada Leon et al., 2020).

Seafloor and water column characteristics can help to predict the occurrence of biotic communities such as those comprised of coral and algae (Sterne et al., 2019; Pörtner 2010). Abiotic predictors, such as water depth, seabed slope, rugosity, and aspect, influence the distribution of benthic communities and habitats (Wilson et al., 2007). Water depth has distinctive, and occasionally contrasting, associations with benthic communities. For example, scleractinian zooxanthellate corals are anticipated to reduce in abundance with increasing water depth (Stefanoudis et al., 2019). However, at greater depths (e.g. >30 m), the coral community (e.g. octocorals and antipatharians) can show a positive relationship with depth (Schmahl et al., 2008; Stefanoudis et al., 2019). Benthic communities also show well-established relationships with seafloor slope, rugosity, and plan curvature (Wedding and Friedlander, 2008). Slope is defined as steepness of seafloor surface and is useful in calculating slope of slope i.e. the rate of change in steepness,

while rugosity describes the ruggedness of seafloor surface. Plan curvature refers to how sloping surfaces are shaped, whether concave, convex or linear, this influences the convergence and divergence of flow (Sterne et al., 2019). Aspect denotes the direction a surface faces and can determine the direction of water flow over the seafloor as well as influence both the distribution of substratum types and benthic communities (Sterne et al., 2019). Thus, particular benthic community and substratum may occur where prevailing currents are low or high. Water column temperature and oxygen concentrations frequently show distinct relationships with water depth (Kahng et al., 2019). Both water temperature and oxygen concentration have significant physiological impacts on the organisms present (Pörtner, 2010), such that both absolute values and variability in these parameters can be critical in determining distribution and survival of organisms.

For the present study, we deployed a comparatively low-logistics autonomous underwater vehicle (AUV) (Hiller et al., 2012) at multiple sites in the Pemba Channel to collect baseline information on water column characteristics (temperature and oxygen), marine habitats and benthic communities from 5 to 150 m depths. Our aim was to increase the understanding of the distribution of habitats and benthic communities, and hence inform about their vulnerability and long-term sustainability. We hypothesised that substrata and benthic communities in the Greater Pemba Channel are structured according to water column and seafloor characteristics. These characteristics have either linear or non-linear effects on the availability of key substrata and broad taxa groups. We identify main substrata and benthic communities from AUV photographs and use bathymetry and acoustic backscatter data to model their distribution based on a set of predictive factors (water depth, acoustic backscatter, slope, slope of slope, plan curvature, rugosity and aspect). We further delineate the probable boundary of shallow and MCEs in the Pemba Channel.

2. Materials and methods

2.1. Study area

Pemba Island is part of the Zanzibar Archipelago, and is located about 50 km from mainland Tanzania. It is isolated from the mainland Tanzania by a deep-water channel and is classified as a true oceanic island (Archer and Turner, 1993). It is also surrounded by fringing reefs that cover an area of 222 km^2, representing ca. 9% of Tanzania's coral reefs (Klaus, 2014; Levin et al., 2018). The shallow reefs of Pemba Island show a broad range of reef conditions, with some reefs in healthy states and dominated by hard coral cover, while others are in a degraded state with low coral cover (Grimsditch et al., 2009). The western side of the island contains 60% of the islands' fringing reefs, which drop off rapidly into the deep water of the Pemba Channel. Previous surveys have estimated that the coral cover averages 23% and ranges from 3% to 86%, with the highest coral cover and greatest diversity, 42 coral genera, occurring at Misali Island on the western fringe of the Pemba Archipelago (Grimsditch et al., 2009).

Sites were selected based variously on a preliminary towed side-scan survey, previous research of the shallow coral reef ecosystem (Grimsditch et al., 2009), information from key local knowledge on management and fishing pressure, and the prevailing sea state. The AUV was deployed at three sites located in the south west of Pemba Island (West Misali, South Misali, and Mkoani) and one site in the northwest sector of Unguja Island (Tumbatu Shoal) (Fig. 1). The Pemba Island sites are all located within the Pemba Channel Conservation Area (PECCA) while Tumbatu Shoal is not subject to any form of management, although it neighbours the Tumbatu Island Marine Conservation Area (TUMCA).

3. Methods

A Teledyne Gavia Offshore Surveyor AUV 'Freya' was used to survey seafloor and water column properties in depths between 5 and 150 m.
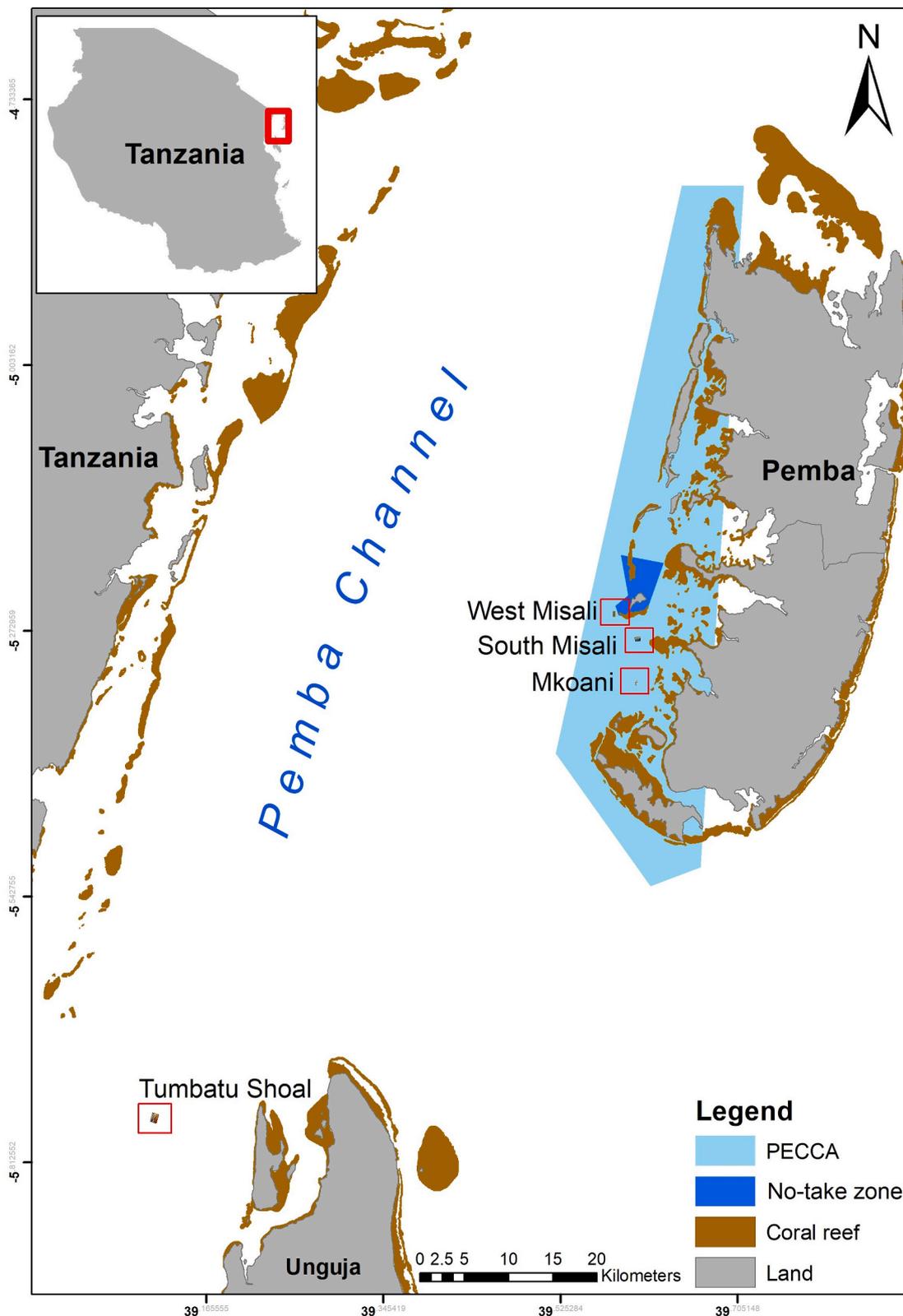
Fig. 1. Greater Pemba Channel area, showing where the autonomous underwater vehicle (AUV) was deployed: West Misali, South Misali, Mkoani, and Tumbatu Shoal. PECCA: Pemba Channel Conservation Area, a Marine Protected Area. (Geographic Coordinate System: GCS_WGS_1984, Datum: D_WGS_1984). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

The AUV was a modular vehicle consisting of camera, geoswath, control and command centre, and science bay (Table 1). It collected data on bathymetry, backscatter and benthic communities following methods described in Howe et al. (2019). Bathymetry provided information on water depth, backscatter indicated sediment grain-size and seafloor roughness, while benthic community was assessed from photographs captured by the AUV.

The AUV was variously operated in three primary modes: (a) for seafloor mapping, the vehicle was programmed to survey from 10 m above the seafloor for ca. 2-hours, giving a 30 m swath width and a resolution of 0.1 m; (b) for detailed seabed photography, the vehicle was programmed to survey from 2 m above the seafloor for ca. 1-hour; (c) for an oceanographic survey, the vehicle was programmed to profile the water column between 5 and 150 m (Table 2). The surveys were conducted over three days in July 2019, covering a total distance of 75 km, with a total underwater duration of 13 h. All operations were carried out from the RV *Angra Pequena*. During AUV missions, a SonTek [YSI] CastAway-CTD was used to collect additional water column conductivity, temperature, and depth (CTD) profiles (Supplementary Material Table S1). These measurements, together with the AUV's on-board sound velocity probe, were used to calculate the speed of sound in water. Progress of the AUV missions was closely checked using Ultra-Short Base line pinger, which received signals up to 2 km away from the surface vessel.

2.3. Data analysis

2.3.1. Bathymetry and acoustic backscatter

Tidal and sound velocity corrections were undertaken to process the raw bathymetry and backscatter data (Howe et al., 2019). Tidal corrections involved applying a synthetic 'zero-tide' in order to reduce survey depths to a common datum (lowest astronomical tide), while sound velocity correction was done by removing sound artefacts using in-situ sound velocity measurements to correct for water column density, salinity, and temperature.

The GeoAcoustic data (bathymetry and side-scan sonar) were filtered and cleaned using the learning algorithm in GeoAcoustics GS4 software (www.kongsberg.com) and Sonarwiz (www.chesapeaketech.com). This produced flagged .rdf files that were imported into Caris HIPS and SIPS v.11 (www.teledynecaris.com). The data were then further cleaned using Side Scan editor and Swath sub-editors, and a Combined Uncertainty Bathymetric Estimator (CUBE) surface produced which had a resolution of 0.5 m (bathymetry) and 0.1–0.5 m (acoustic backscatter), dependent on data density and quality.

These surfaces were exported as geo-corrected rasters into ArcMap v.10 (Environmental Systems Research Institute). The focal statistic function was applied to ensure acoustic backscatter and bathymetry raster layers matched the AUV's image spatial footprint of 54 m². The focal statistic tool used the median operation to compute an output

Table 1

Autonomous underwater vehicle configuration characteristics.

Module	Function	Data type
Nosecone (camera)	Camera (FLIR [Point Grey] Grasshopper, Sony ICX285 CCD sensor) with a strobe, providing seabed images.	.jpg
GeoSwath Plus Sonar	500 kHz interferometric sonar (Kongsberg GeoAcoustics), providing bathymetric and acoustic backscatter data.	.rdf
Control and Command Centre	Provide commands and storage of data.	KML, KMZ, Log
Science Bay	Conductivity (salinity), temperature, and depth (CTD; Seabird SBE-49) sensors, and dissolved oxygen sensor (Aanderaa oxygen optode 4831) to provide oceanographic data.	.raw

Table 2

Autonomous underwater vehicle missions in the Greater Pemba Channel.

Site	Mission Number	Total distance (km)	Duration (hours)	Vehicle altitude (m)	Depth range (m)
Mkoani	2	8.6	1.4	10	13.1–25.1
	3	10	2.7	Variable	5.0–150.0
	4	4.2	0.7	2	11.0–25.0
West Misali	5	9.9	1.7	10	21.1–150.0
	7	4.6	0.8	2	20.6–51.3
South Misali	6	10.0	1.6	10	18.5–24.9
Tumbatu Shoal	10	27.3	4.2	10	35.5–66.2

Missions 8 and 9 were aborted due to bad weather.

raster of backscatter and bathymetry layers in a 9 x 9 neighbourhood window. These data were used to calculate several bathymetric derivatives: slope, slope of slope, plan curvature, and aspect. Additionally, an extension Remote Sensing Object Based Image Analysis (RSOBIA) was applied to calculate ruggedness (Le Bas, 2016).

2.3.2. Image processing

Images from each AUV mission were geo-referenced by extracting their latitude and longitude information using open source BR ExIF software (www.br-software.com). Correction of illumination and colour representation was performed followed by identification of key substratum and benthic community characteristics in every 20th image recorded by the AUV. This represented an inter-image distance of ca. 20 m between photos.

Species-level identification of benthic community routinely requires high-resolution imagery, which depends on the height of the camera. For this reason, benthic organisms photographed during the AUV's seafloor mapping survey, were identified and placed in broad taxa groups of: corals, fleshy algae, turf algae, and fish. Corals were composed of habitat-forming taxa of Scleractinia (hard coral), Octocorallia (octocorals/soft corals) and Antipatharia (black corals) (Stefanoudis et al., 2018). Other invertebrates such as molluscs and crustaceans were observed but were not analysed further. Turf algae encompassed filamentous algae, while fleshy algae were macro algae (Littler and Littler, 2011; Stefanoudis et al., 2018). Fish were defined as vertebrate organisms either cartilaginous or bony species identified from fish manuals (Lieske and Myers 2002).

A primary substratum type was identified based on majority area of the image (≥50%) following definitions given in Benoist et al. (2019): "hard", "coarse", and "sand". A secondary substratum was recorded when it covered ≥10% of the seafloor. Combination of primary and secondary substratum yielded mixed substrata (Supplementary Material Table S2). The image geo-reference data were used to attribute corresponding data on acoustic backscatter, bathymetry, slope, slope of slope, plan curvature, aspect and ruggedness.

2.3.3. Temperature and oxygen profile

To simplify the presentation and interpretation of data, and to acknowledge sensor (time) lag during vehicle ascend and descend, temperature and oxygen data were binned at 10 m depth interval and summarised as box plots.

2.3.4. Modelling

Presence and absence data on substrata and key benthic community types were derived from seabed images from the seafloor-mapping missions conducted at West Misali (n = 377) and South Misali (n = 458), and Tumbatu Shoal (n = 792). The photographs from Mkoani were excluded from modelling because of high turbidity at the site that limited taxa identification. Generalised additive models (GAMs) were

fitted on presence and absence data using the *mgcv* package in R (Woods, 2012, www.r-project.org). Substrata and benthic community types were predicted using acoustic backscatter, bathymetry, slope, slope of slope, plan curvature, aspect, and ruggedness. Site based GAM analyses were first performed to determine key seafloor predictors (Supplementary Material Figs. S1–5). The site data were thereafter pooled, and the dataset partitioned into training (70%) and testing (30%) data (Platts et al., 2008). Slope of slope and ruggedness were removed from the GAM analyses as they showed substantial correlations (r > 0.5) with slope and plan curvature respectively. GAM assessments were run using the restricted maximum likelihood criterion (Wood, 2011), to predict the probabilities of presence of hard and sand substratum, corals, turf algae, fleshy algae, and fish. Contribution of the predictors to the GAM model was assessed from effective degrees of freedom (edf), which represents the complexity of the smoothing term. An edf of 1 represented a straight line or a linear effect while an edf of $\geq$2 described a non-linear effect with quadratic or wiggly curves. The accuracy of GAMs was assessed firstly by calculating area under the receiver operating curve (AUC ROC), and secondly by determining the number of times presence was categorised into either present or absent using a threshold probability value (Deleo, 1993). AUC ROC refers to the probability that the model correctly predicts a randomly chosen positive observation and a randomly chosen negative observation. A threshold probability value was determined for each independent variable by iteratively searching for the optimal cut-off probability. Application of thresholds is recommended where the data contains more absences than presences (Sigler et al., 2015; Hosmer and Lemeshow, 2004) in order to balance the number of false positives and false negatives.

3. Results

3.1. Site bathymetry and acoustic backscatter

The AUV was deployed at sites showing varying gradients of water depths and benthic community as detailed below.
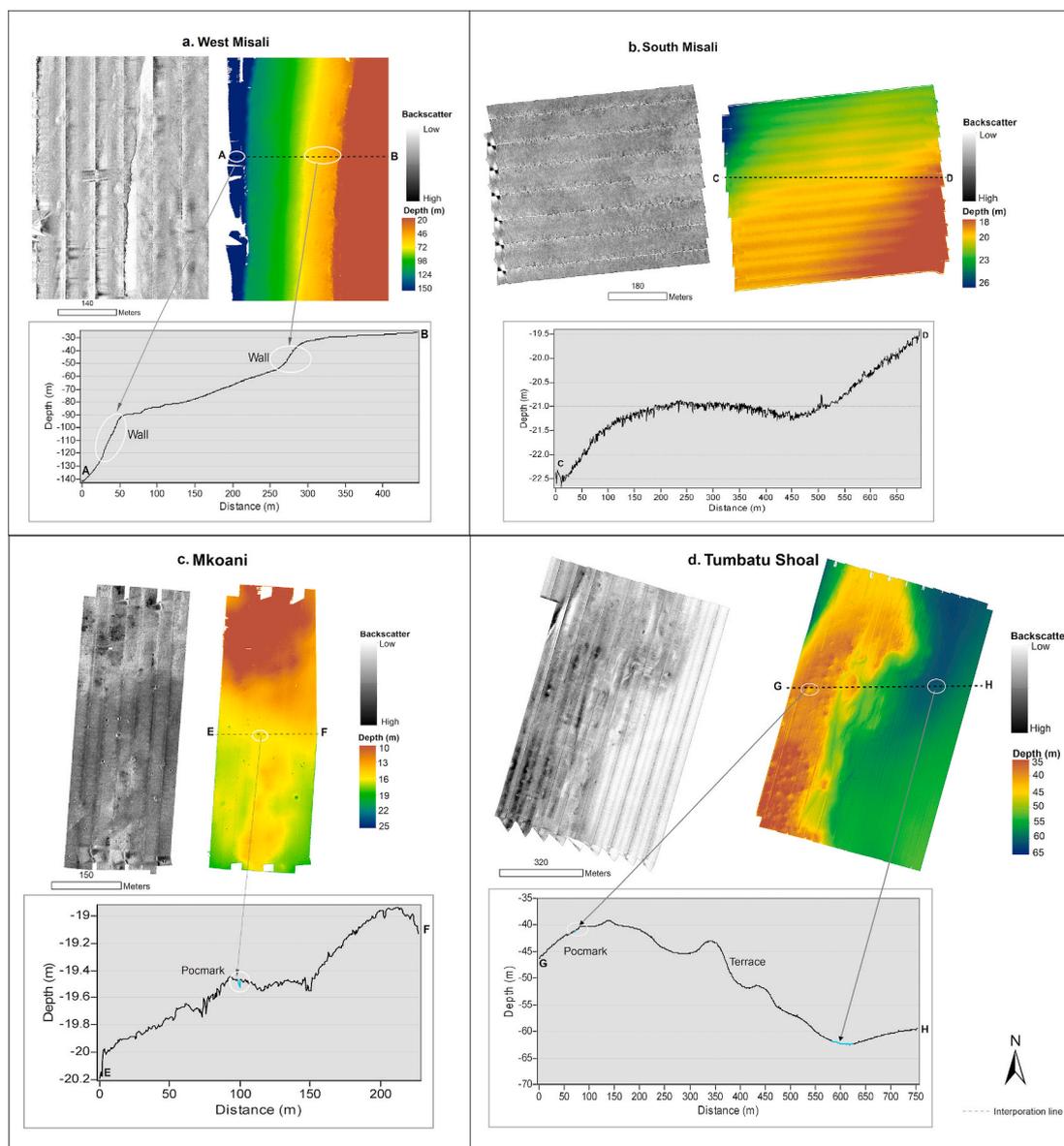
Fig. 2. Seafloor survey detail of the four Greater Pemba Channel sites. Each panel illustrates (i) acoustic backscatter (greyscale), (ii) bathymetry (colour scale), and (iii) example bathymetric profile (line plot). Refer to Fig. 1 for a, b, c and d. Artefact due to AUV roll error was noted in South Misali. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.1.1. West Misali

The AUV surveys at West Misali extended from shallow to mesophotic water depths and mapped the reef transition from 20 to 150 m, including the terraced margins (Fig. 2a). The water depths increased westwards with two rock walls of slopes >70° evident from the reef crest at ca. 40–50 m and 90–110 m. The walls formed staircase structures that were separated by a gentle west-oriented slope (ca. 20°) with sparse corals and large boulders (>1 m) (Fig. 2a). The shallow areas <25 m were dominated by healthy hard corals as evidenced from the high acoustic backscatter (Fig. 2a; Fig. S2) and photographs (Fig. 3b). Beyond 25 m depth the seafloor showed decreasing availability of hard substrata and increasing sandy substrata (Fig. S1). The sandy substrata occurred on platforms with low slopes (<30°) and low backscatter signals. Deeper areas (>100 m) were characterised by the presence of octocorals (Fig. 3 f, h, i). Fish occurred from shallow to lower mesophotic depths. However, due to differences in the capture angle and resolution of the photographs, it was not always possible to identify fish to the lowest taxonomic unit. Nevertheless, of note was the observation of soldier fish (Holocentridae) found at 117 m (Fig. 3g).

3.1.2. South Misali

The AUV survey at south Misali was conducted in an east-west lawnmower pattern and in depths ranging from 18 to 25 m (Fig. 2b). Sand mixed with hard substrata characterised the seafloor, which had a low slope of <10° (Fig. S3). The relief was generally featureless except for one depression. Fleshy and turf algae were the dominant benthic community type (Fig. 3c).

3.1.3. Mkoani

The AUV surveys at Mkoani covered water depths from 13 to 25 m with acoustic backscatter data showing mixed sediments and a diversity of submarine landform features in a north-south orientation (Fig. 2c). The seafloor features included coral heads, rubble and depressions or pockmarks exclusively occurring in sandy substrata. The coral heads occurred in the north and in shallow waters of <15 m and were characterised by a darker acoustic backscatter resulting from a high reflectance signal. Mixed substrata, composed of patchy corals, sand and rubble, showed moderate backscatter and occurred on the seafloor south of the coral heads. Numerous seafloor pockmarks were noted during a preliminary towed side-scan survey in water depths of ca. 20 m. The
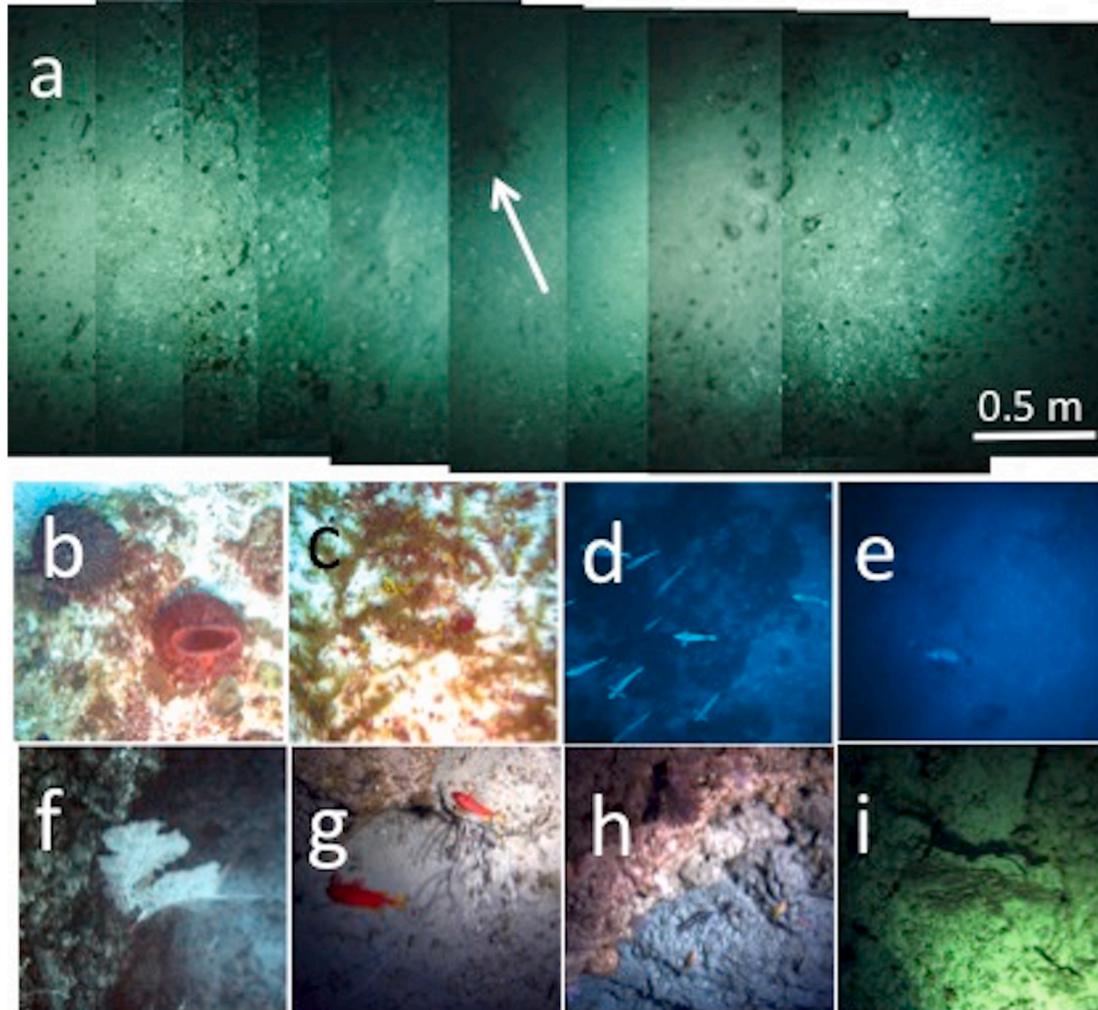
Fig. 3. Example images of substrata and benthic community types from shallow and mesophotic environments in the Greater Pemba Channel, as captured from ca. 2 m altitude (a, b, f-i) and ca. 10 m altitude (c–e). a) by autonomous underwater vehicle. a) Mosaicked images of pockmark (arrow shows the centre), 22 m water depth, Mkoani. b) Healthy hard coral and sponge, 15 m, West Misali. c) Turf and fleshy algae, 23 m, South Misali. d) Hard coral and surgeon fish (Acanthuridae), 35 m, Tumbatu Shoal, e) Snapper (Lutjanidae) on mixed sand hard substrata, 42 m, Tumbatu Shoal. f) Octocorals, 39 m, West Misali. g) Soldier fish (Holocentridae), 117 m, West Misali. h) Hard substrata with octocorals and small fish, 117 m, West Misali. i) Octocorals 118 m, West Misali. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

AUV surveyed more than 30 pockmarks that occurred in the south and in water depths of 18–21 m. The rims of the pockmarks had a moderate lighter backscatter in comparison to the centre of the depression that had darker backscatter. Photographs revealed pockmarks varied in diameter from 5 to 10 m and in depth from 3 to 5 m (Fig. 3a).

3.1.4. Tumbatu Shoal

The AUV surveys were conducted in a northeast orientation and in upper mesophotic water depths ranging from 36 to 66 m (Fig. 2d). The site had a relatively low slope of <40°, with the seafloor either of sand or sand mixed with hard substrata (Fig. S4). These were noticeable in acoustic backscatter as indicated by darker and lighter backscatter signals for hard and sand substrata respectively (Fig. 2d). Pockmark features were conspicuous in water depths >40 m. Availability of hard substrata decreased with increasing depth and decreasing slope (Fig. S4). Patchy corals were found on the western margin in depths <45 m and where seafloor surface was concavely shaped and extended from south to north (Fig. S5). School of surgeonfish (Acanthuridae) and snappers (Lutjanidae) were photographed at upper mesophotic depths at 31 m and 42 m respectively (Fig. 3d–e).

3.2. Temperature and oxygen profiles

The water column temperature increased from <18 °C in lower mesophotic depths (150 m) to 26 °C in surface waters (<10 m) (Fig. 4). The greatest change in temperature occurred below 100 m. Oxygen concentrations increased from 180 μmol/l at 150 m to 220 μmol/l in surface waters.
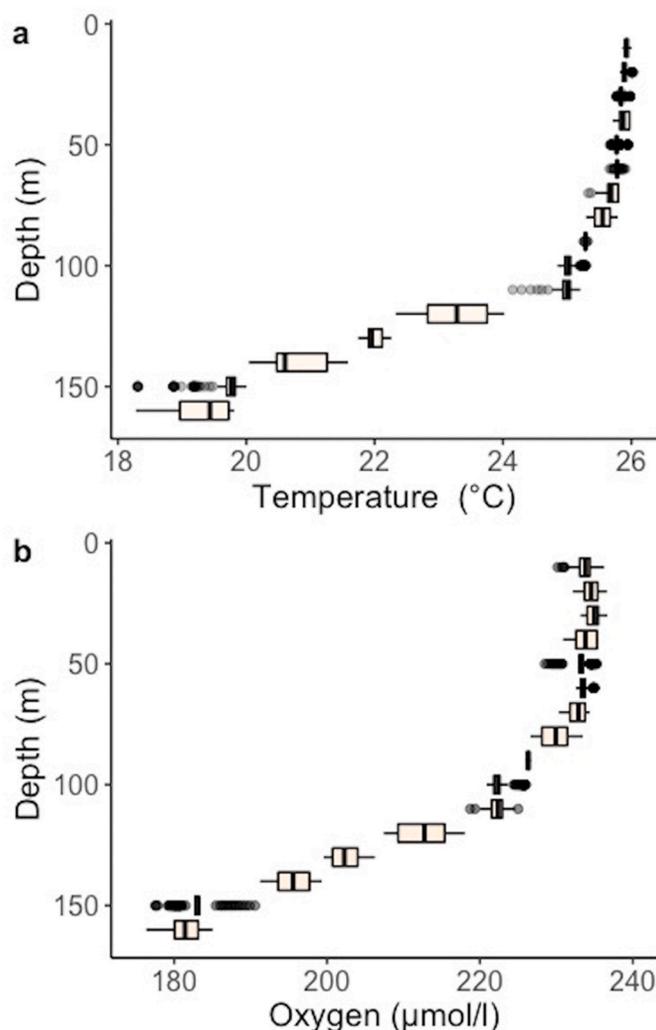
3.3. Prediction of substrata and benthic community

The AUC ROC of training and test data indicated good (>0.80) model results that ranged from 0.85 for fish to 0.99 for fleshy algae (Table 3). GAMs on the two primary substrata explained 64% and 60% of the deviance for hard and sand substrata respectively (Table 3). The significant explanatory variables were depth and slope. Presence-absence of hard substrata was correctly predicted 95% and 91% of the times on training and test data respectively, based on threshold probabilities of 0.07. In reference to effective degrees of freedom (edf), depth had a non-linear effect (edf = 8.1) on presence of hard substrata with greater probabilities occurring in shallow areas (20–30 m; Fig. 5). As expected, the presence of hard substrata was increasingly probable on steeper slopes (30°–70°) and walls (>70°). Opposing patterns, with respect to depth and slope were found for sand substrata.

The GAMs on presence-absence of coral, turf algae, fleshy algae and fish explained 35–91% of the deviance (Table 3). The significant predictors were acoustic backscatter (coral, turf algae), depth (coral, fleshy algae, turf algae), slope (coral, fleshy algae, turf algae, fish), and aspect (fleshy algae). Curvature did not show any significant contribution to the models. The greatest model accuracy was predicted for fleshy algae at 98% and 91% of the times on training and test data respectively, based on threshold probabilities of 0.04 (Table 3). The model accuracy for corals was 80% on training data and 73% on test data based on threshold of 0.15. Higher probabilities of occurrence of corals were found where acoustic backscatter was high. Depth had a non-linear effect (edf = 7.7) on the presence of corals with greater probabilities (>0.5) at depths between shallow (25 m) and upper mesophotic (55 m) (Fig. 5). Presence of coral was greater on steep slopes (30°–70°) particularly found at 30 m, and walls (>70°) occurring in ca. 40–50 m depths, compared to low slopes. Depth, backscatter and slope had a non-linear effect (edf >2) on presence of turf algae (Table 3). High probabilities of >0.5 occurred at around 30 and 80 m water depth and on steep slopes. Marginally higher probabilities of presence of turf algae were found where acoustic backscatter was mid-range (Fig. 5).

Depth and slope affected the presence of fleshy algae, with greater probabilities in shallow areas (ca. 20 m) and low slopes (<30°) respectively (Fig. 5). Aspect had significant but minimal influence on the presence of fleshy algae, with greater probabilities at south facing areas.

Presence of fish increased rapidly from a seafloor slope of 25°–45° where maximum probability was evident, and then declined more gradually on steep slopes of 70° to similar probabilities to those at 20–25° (Fig. 5). Other predictors showed non-significant contribution to the model.

4. Discussion

4.1. General observations

This study presents a first attempt to document mesophotic coral ecosystems (MCEs) in the understudied Western Indian Ocean (WIO) using an autonomous underwater vehicle (AUV), which collected in-situ data on bathymetry (water depth), acoustic backscatter (substratum) and benthic community types (seabed images) from selected sites in the Greater Pemba Channel. The bathymetry and acoustic backscatter data showed the presence of a complex seafloor variously characterised by pockmarks, steep slopes, 'staircase walls', and large boulders. These landscape features may have been formed through geological processes and over time have become ecologically important in sustaining the coral reef ecosystems in the Greater Pemba Channel (Sherman et al., 2019). Additionally, the AUV photographs confirmed presence of MCE

Fig. 4. Summary boxplots of water temperature (°C) and oxygen concentrations (μmol/l) in water column in Mkoani in the Greater Pemba Channel.

Table 3
Generalised additive model results for substrata (hard and sand) and benthic community types (coral, turf algae, fleshy algae, fish) showing significant predictors (p < 0.05), effective degrees of freedom (edf), deviance explained by the model, area under the receiver operating curve (AUC ROC), threshold probability used to test model accuracy, and total percentage occurrence correctly predicted.

Substratum or community type	Significant predictors (edf)	Deviance explained (%)	AUC ROC		Threshold	Correct predictions (%)	
			Training	Test		Training	Test
Hard substratum	Depth (8.1), Slope (3.2)	63.8	0.97	0.95	0.07	95	91
Sand substratum	Depth (8.2), Slope (3.6)	60.0	0.96	0.92	0.06	95	93
Coral	Backscatter (1.0), Depth (7.7), Slope (1.0)	38.6	0.88	0.91	0.15	80	73
Turf algae	Backscatter (3.0), Depth (8.2), Slope (3.6)	38.1	0.90	0.87	0.07	87	88
Fleshy algae	Depth (5.2), Slope (4.7), Aspect (1.0)	90.5	0.99	0.99	0.04	98	91
Fish	Slope (4.6)	35.2	0.93	0.85	0.09	99	96
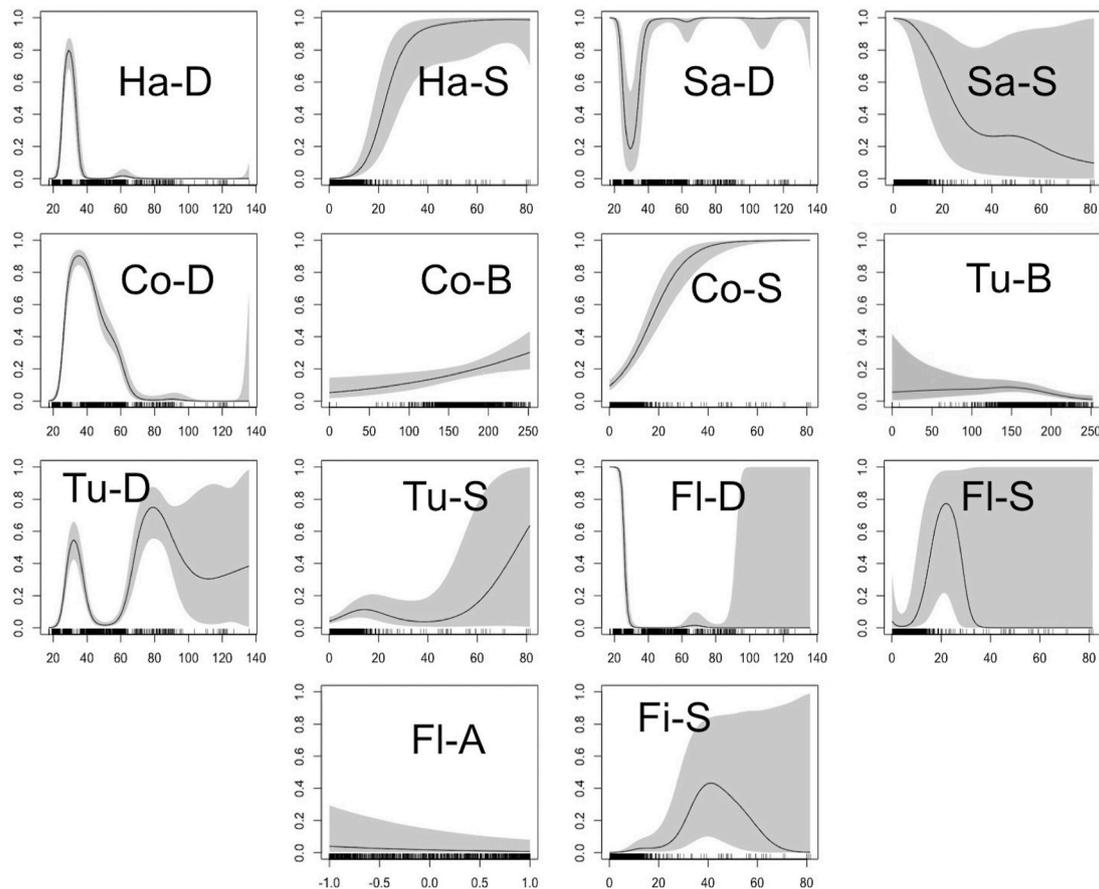
Fig. 5. Generalised additive model plots for substrata (Ha, hard; Sa, sand) and benthic community types (Co, coral; Tu, turf algae; Fl, fleshy algae; Fi, fish), for significant predictor variables (B, acoustic backscatter; D, depth (m); S, slope (°); A, aspect (cosine transformed)), shaded areas represent 95% confidence intervals. Plots are identified by Yy-X letter coding where Yy codes the dependant variable and X the independent variable.

composed of corals, algal and fish communities on the continental margins of Pemba and Unguja islands. Corals and fleshy algae were typically present in the shallow (<30 m) and upper mesophotic depths (30–45 m), while turf algae and fish occurred at different depths from shallow to lower mesophotic depths (60–150 m). The modeled occurrence of substrata and benthic community showed peak probabilities for hard substrata, corals, turf algae and fleshy algae to occur at ca. 30–40 m. This indicates that the boundary between shallow and mesophotic coral ecosystems in the Greater Pemba Channel was located at ca. 30–40 m, which concurs with other studies around the world (Bridge et al., 2012; Laverick et al., 2018; Pyle and Copus, 2019). Given the complexity of the seafloor environments encountered, and the study being constrained to only four sites, two of which were less than 25 m in depth, there will certainly be other features of MCE such as species distribution of corals, fleshy algae, sponges, and fish that warrant further study. This study serves to highlight the potential distribution of broad

taxa groups of the MCE in the Greater Pemba Channel and provides an interpretation based on available data.

Of particular note was the occurrence of pockmarks that were widespread in 20–40 m water depths. The origin of these pockmarks remains unknown, although previous observations of pockmarks on other continental shelves describe their origin as being bio-erosional, methane gas, or other fluid, escape related (Sumida et al., 2004; Audsley et al., 2019). Surveys using baited remote underwater videos (BRUVs) deployed in Mkoani recorded a high abundance of sea urchins around these pockmarks (Osuka, unpubl. data). Apparent aggregations of sea urchins have previously been noted in association with fluid escape structures in the Gulf of Cadiz (Cunha et al., 2002) and with large hydrocarbon-related pockmarks offshore of Angola (Hughes and Bett, 2007). Therefore, the pockmarks that we surveyed in Mkoani and Tumbatu Shoal sites may be of fluid-escape origin rather than bio-erosional. Further studies are needed to establish their distribution

more completely and ascertain their particular origins.

4.2. Modeling efforts

Modelling using generalised additive models gave relatively high prediction accuracies but low threshold levels, suggesting threshold probabilities were trading off sensitivity and specificity to result in high area under the curve (AUC ROC) values. Of note were the large proportion of absences in some taxa, such as fleshy algae and fish, which could have led to low thresholds (Sigler et al., 2015). Absences can result from low image resolution in greater water depths, further hindering full quantitative assessment of benthic community types (Armstrong et al., 2019). Indeed, this reduction in image resolution prompted this study to use broad morphotype groups, rather than more specific taxonomic groups, which are likely to mask the specific habitat requirements of individual species associated with the group. For instance, low numbers of fish were observed in the randomly selected AUV photographs, despite the complexity of seafloor in Misali and Tumbatu Shoal. The low abundance of fish in AUV photographs suggests that the vehicle may be scaring away fish causing biased and unreliable estimates (Hagen et al., 1999). This may also be exacerbated by the low sampling effort in mesophotic depths, which were halted by rough southeast monsoon winds of up to 30 knots that peaked during the survey, even leading to cancellation of two missions (Table 2). The variables selected and scales at which the data were collected thus limit generalisability of our results. However, even with four sites, the models provide some satisfactory performance for predicting the presence of substrata and benthic community types from shallow to mesophotic depths.

4.3. Distribution of habitats and communities

4.3.1. Hard and sand substrata

Hard substrata were widespread in shallow and upper mesophotic depths, while sand dominated the lower mesophotic depths. Hard substrata in tropical marine environments provide an important attachment platform for organisms, especially those in mesophotic depths, to colonise and grow (Sherman et al., 2019). They can support more than twice the number of species compared to mixed or sandy substrata (Ruiz et al., 2009). The high level of diversity on hard substrata relates to their ability to provide stable basal structures and high topographical complexity, which are both essential for the successful larval development of sessile and sub-adult mobile species. The hard substrata in the upper mesophotic depths may therefore be key to the presence of MCEs found in the Greater Pemba Channel.

Hard substrata were predominantly found on steep slopes and walls rather than flat or low slopes. The most biodiverse MCEs in Hawaii have been linked with either hard substrata with discontinuous features such as limestone outcrops and ledges, or walls with complex structures (Pyle and Copus, 2019; Sherman et al., 2019). The MCEs in the Greater Pemba Channel may therefore sustain a highly biodiverse community. Indeed, walls are widespread along the western side of Pemba Island, stretch from north to south, interspersed by several reef passes (Grimsditch et al., 2009). These walls were formed through geological processes involving tectonic movements (Baker and McConnell, 1970; Sherman et al., 2019), and over time strong physical erosion from the north flowing East African Coastal Current (EACC) has had a pronounced effect on their complexity (Klaus, 2014). The EACC is also particularly important in increasing and maintaining connectivity between coral reef ecosystems (Obura 2012; Gamoyo et al., 2019; Sekadende et al., 2020). The current coupled with a changing seasonal monsoon winds, and the proximity of the walls to the shoreline (ca. 2 km) implies the water column is well mixed. The stable temperature and oxygen concentrations recorded in the upper 100 m of the water column in the Greater Pemba Channel (Fig. 4) also provide some evidence of a well-mixed water column, which may help promote the survival of fish and benthic communities in the area. The walls of the Pemba Channel may

therefore be of particular conservation interest, suggesting the need for a careful management against anthropogenic pressures such as fishing.

4.3.2. Coral, fleshy and turf algae

Water depth was a significant predictor of the presence of coral, fleshy, and turf algae. Vertical zonation of community structure is influenced by light and temperature and both are key factors restricting the distribution of MCEs (Kahng et al., 2010, 2019). Light provides energy to photosynthesising communities such as scleractinian zooxanthellate corals and algae, while water temperature is essential in setting the thermal tolerance for physiological processes. The mid-water AUV surveys revealed stable temperature in the upper 100 m of water column, providing some indication that light was a limiting abiotic factor (Kirk 2011; Kahng et al., 2019). Very low light levels experienced in deep walls can limit occurrence of corals, particularly Scleractinia zooxanthellate. Therefore, changes in temperature and light intensity with depth are not only associated with changes in the occurrence of coral and algal community types, but also taxon composition (Pyle and Copus, 2019). Similar changes in species composition are expected for algal and sponge community types. To establish this will require high-resolution photography across the entire mesophotic depth, which can be achieved by flying the AUV close to the seafloor at ca. 2 m. However, drawing on studies from Bermuda (Stefanoudis et al., 2019), a turnover in coral taxa can be expected in the Greater Pemba Channel for instance, scleractinians (hard corals) can occur in the shallow water depths (15–30 m), and overlap at the upper MCE boundary (30–40) with octocorals. The octocorals can extend to 60 m below which the antiparians (black corals) become more abundant. Algae will occur in all water depths although the turnover in taxa groups will reflect the decrease in temperature and primary productivity.

Occurrence of corals was higher on steep slopes or walls than low slopes, consistent with findings from the Caribbean (Sherman et al., 2010) but different from results from the Great Barrier Reef MCEs (Bridge et al., 2011a, 2011b), which showed corals were concentrated and most diverse on the flatter surfaces of submerged reefs at depths <60 m. Occurrence of MCEs in the Caribbean were influenced by the downslope sediment transport and water clarity, such that steeper slopes easily shed off accumulated sediments while low relief slopes accumulate sediments, which can suppress coral recruitment and growth (Sherman et al., 2010). Erosional rates coupled with sediment retention are therefore important factors influencing the occurrence and distribution of MCEs in the Greater Pemba Channel. Fleshy algae were highly restricted to the shallow reef depth transition (ca. 20 m), low slopes and south facing seafloor. While an increase in the coverage of shallow fleshy algae can outcompete corals and lead to phase shifts (Hughes et al., 2007), the presence of mesophotic fleshy algae is regarded an important refugium habitat for other organism providing protection against environmental stress (Spalding et al., 2019). Fleshy algae are versatile marine plants able to grow in depths greater than 200 m and on both hard and soft substrata. It is therefore likely that the presence of fleshy algae is more widespread than found in this study. Our findings also contrast with reports from American Samoa, where fleshy algae were more pronounced in the upper mesophotic water depth from 50 to 70 m (Bare et al., 2010). That depth range, however, was similar to the peak depths for turf algae, which this study found to be in the shallow (30 m) and upper mesophotic depths (80 m). Turf algae were also associated with seafloor areas having mid-range acoustic backscatter and slopes, suggesting their preference or ability to grow on mixed hard and sandy substrata that are characterised by varying slopes (Spalding et al., 2019). In contrast to fleshy algae, turf algae showed non-significant predictions with aspect suggesting they are not constrained by current. These findings underscore the ability of algae to change with increasing depth as well as colonise different forms of substrata.

4.3.3. Fish

Fish were more abundant in areas with steep slopes rather than on

platforms or flat seafloor. High fish abundance on steep slopes and walls is expected (Jankowski et al., 2015) because of their exposure to currents and waves, which are also essential in maintaining high levels of suspended food resources (McLachlan and Defeo, 2017). The presence of suspended food drives the abundance of fish, especially planktivores and omnivores (Pinheiro et al., 2016; Goodbody-Gringley et al., 2019), which subsequently serve as prey for higher trophic level predatory species (Stewart and Jones, 2001). These trophic groups are more likely to be abundant in lower mesophotic depths than shallow and upper mesophotic depths where a high abundance of herbivorous fish is expected (Jankowski et al., 2015; Medeiros et al., 2010). Thus, it was surprising for water depth to be a non-significant predictor of fish occurrence in the present study. Furthermore, due to threats of overfishing and destructive fishing practices in the Pemba Island area (Grimsditch et al., 2009), we expected fish to be more abundant in greater depths, including walls where rapid changes in water depth would help in escaping from fishing pressure. Moreover, local fishing gears are less adapted to deep environments (Tyler et al., 2009; Samoilys et al., 2011). In Bermuda, fish population metrics (abundance, biomass and species richness) were found to increase with water depth, supporting the deep reef refugia hypothesis – where more fish move to deeper areas to escape from high fishing pressure (Pinheiro et al., 2016; Stefanoudis et al., 2019). Such fish movements affect the overall productivity of shallow areas and can have negative impacts on the livelihoods that dependent on them. Taken at face value, our results might suggest that fish abundance was low. However, based on the findings of similar studies (Bongaerts et al., 2010; Pinheiro et al., 2016), a more probable explanation is the limited ability of the AUV to photograph fish at mesophotic depths and in regions of steep slopes and crevices. As fish communities are partitioned according to abiotic factors (Jankowski et al., 2015), Pemba's Channel fish communities are likely to be dissimilar at different water depths and over different seabed slopes. This, together with the distribution of shallow species on steep slopes, requires further research. Nevertheless, the modelling results for fish occurrence contribute to a better understanding of the importance of walls in offering natural protection from fishing and, therefore, their consideration as important in conservation planning.

4.4. Conservation and management

There are few conservation efforts directed towards deep environments such as MCE, yet they sustain distinct biodiversity and are probably acting as refugia for shallow reefs (Pyle and Copus, 2019; Turner et al., 2019). Conservation efforts for MCEs in Pemba Island area would require targeted detailed monitoring surveys across the mesophotic depth range to assess the effectiveness of any management measures. At present, the logistical challenges in gathering such data and the high costs associated with monitoring MCEs may be the greatest bottleneck (Wölfl et al., 2019). Despite these challenges, the development and investment in low-cost marine robotics, such as low-logistics AUVs like the Gavia vehicle used in the present study, clearly offers opportunities to reduce monitoring costs to within the budget range of most management agencies. These costs are expected to be comparatively low in the Pemba Island case as a result of the proximity of the MCEs to the shore, particularly those found on walls. Another important consideration is to encourage the involvement of local communities in the management of MCE. A first step towards this realisation will require building awareness of the existence of MCEs and their importance as depth refugia (Tyler et al., 2009; Turner et al., 2019). As such, awareness raising through stakeholder engagement should also involve discussions regarding the conservation of mesophotic depths and walls. A second potential step would involve the amendment of fisheries and conservation policies to include MCEs in the management plans for various forms of conservation areas, notably Marine Protected Areas (MPAs) and Locally Managed Marine Areas (LMMAs) (Turner et al., 2019). A potential intermediate option for studying the Western Indian Ocean's

MCEs could involve using divers equipped with closed-circuit rebreathers (Pyle, 2019). Other tools such as mid-water remote camera systems may also be considered when surveying fish communities. Application of multiple techniques will enable accurate measurement of fish community composition (Goodbody-Gringley et al., 2019). Whether achieved through marine robotics or technical diving teams, the initial costs for acquiring the technology and the training of technical personnel would need support.

AUVs will likely play two important roles in conservation and marine management operations: (i) initial baseline data acquisition, and (ii) routine monitoring programmes. They may have particular value in conducting initial surveys and collecting baseline data in areas that are not easily accessible and/or where staff may otherwise be limited (Wynn et al., 2014; Huvenne et al., 2018; Wölfl et al., 2019). Their use might therefore be encouraged in regions such as the WIO, where survey and monitoring costs appear to be the biggest challenge. The multiple data streams that can be derived from AUV operations, as demonstrated in the present study, can be used to inform managers on location and status of MCEs and other features and species of conservation interest. Such AUV-derived data may also be of particular value in informing and planning more targeted vessel-based surveys where unexpected or high interest features are detected. AUVs also have clear value in the repeat or routine monitoring of habitats and species of interest (see e.g. Benoist et al., 2019; Zelada Leon et al., 2020). Other possible monitoring applications may include studies of topographical complexity, invasive species, and fish diversity (Ferrari et al., 2016; Ling et al., 2016; James et al., 2017). Such operations can be likely be launched from locally available platforms and make use of low-logistics AUVs to enable cost-effective implementations of marine robotics in the future.

5. Conclusions

Application of a low-logistics AUV showed great potential for mapping the photic and mesophotic coral ecosystems of the Greater Pemba Channel. This was due to their ability to follow a pre-designed track, map deep areas down to 500 m and beyond, and to collect high-resolution data of both the water column and the seabed. Therefore, AUVs should certainly be considered for the collection of baseline and routine monitoring data, not least for tackling under-researched ecosystems such as the MCEs of the WIO. This study has indicated that wall areas are potential hotspots of MCE biodiversity, such that they and should be considered as priority areas for management and conservation.

Authors' contributions

K.E.O., D.O., M.S. conceived the study. K.E.O., B.J.B., T.L., J.H. designed the study. C.A. and J.H. directed the AUV and all technical operations. K.E.O., B.J.B. and S.Y. were involved in deployment and retrieval of the AUV. K.E.O. processed the seabed images with the help of B.J.B., M.S., S.Y. and J.H. Backscatter and bathymetry datasets were processed by C.A., K.E.O., T.L. and J.H. Statistical analysis were performed by K.E.O. with support from C.M. and B.S. Drafting of the original manuscript was by K.E.O. with the supervision from C.M., B.S. M.S. and B.J.B. All authors made significant edits to the manuscript.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ocecoaman.2020.105463.

References

Archer, A., Turner, D., 1993. Notes on the endemic species and some additional new birds occurring on Pemba Island. Tanzania. Scopus 16, 94–98.

Armstrong, R.A., Pizarro, O., Roman, C., 2019. Underwater robotic technology for imaging mesophotic coral ecosystems. In: Loya, Y., Puglise, K.A., Bridge, T.C.L. (Eds.), Mesophotic Coral Ecosystems. Springer, Cham, pp. 973–988.

Audsley, A., Bradwell, T., Howe, J.A., Baxter, J., 2019. Distribution and classification of pockmarks on the seabed around western Scotland. J. Maps 15, 807–817. https://doi.org/10.1080/17445647.2019.1676320.

Baker, B.H., McConnell, R.B., 1970. The structural pattern of the Afro-Arabian rift system in relation to plate tectonics. Phil. Trans. Roy. Soc. Lond. 267, 383–391. https://www.jstor.org/stable/73628.

Bare, A.Y., Grimshaw, K.L., Rooney, J.J., Sabater, M.G., Fenner, D., Carroll, B., 2010. Mesophotic communities of the insular shelf at Tutuila, American Samoa. Coral Reefs 29, 369–377. https://doi.org/10.1007/s00338-010-0600-y.

Benoist, N.M., Morris, K.J., Bett, B.J., Durden, J.M., Huvenne, V.A., Le Bas, T.P., Wynn, R.B., Ware, S.J., Ruhl, H.A., 2019. Monitoring mosaic biotopes in a marine conservation zone by autonomous underwater vehicle. Conserv. Biol. 33, 1174–1186. https://doi.org/10.1111/cobi.13312.

Bongaerts, P., Ridgway, T., Sampayo, E.M., Hoegh-Guldberg, O., 2010. Assessing the 'deep reef refugia' hypothesis: focus on Caribbean reefs. Coral Reefs 29, 309–327. https://doi.org/10.1007/s00338-009-0581-x.

Bridge, T., Done, T., Beaman, R., Friedman, A., Williams, S., Pizarro, O., Webster, J., 2011a. Topography, substratum and benthic macrofaunal relationships on a tropical mesophotic shelf margin, central Great Barrier Reef, Australia. Coral Reefs 30, 143–153. https://doi.org/10.1007/s00338-010-0677-3.

Bridge, T.C.L., Done, T.J., Friedman, A., Beaman, R.J., Williams, S.B., Pizarro, O., Webster, J.M., 2011b. Variability in mesophotic coral reef communities along the Great Barrier Reef, Australia. Mar. Ecol. Prog. Ser. 428, 63–75. https://doi.org/10.3354/meps09046.

Bridge, T., Beaman, R., Done, T., Webster, J., 2012. Predicting the location and spatial extent of submerged coral reef habitat in the Great Barrier Reef world heritage area, Australia. PLoS One 7, e48203. https://doi.org/10.1371/journal.pone.0048203.

Cunha, M.R., Subida, M.D., Vandendriessche, S., Lima, I., Ravara, A., 2002. TTR 11 Scientific Party, Macrofaunal communities associated to the carbonate chimneys from the Gulf of Ca'diz. Preliminary results from the video imagery and dredge sampling obtained during the TTR-11 Cruise. In: Final Proceedings of the International Conference on Fluid Escape Structures and Tectonics at Continental Margins and Ocean Ridges. Aveiro, Portugal, pp. 77–78.

Deleo, F.J., 1993. Receiver operating characteristic laboratory (ROCLAB): software for developing decision strategies that account for uncertainty. In: Proceedings 2nd International Symposium on Uncertainty Modelling and Analysis, pp. 318–325.

Durden, J.M., Bett, B.J., Ruhl, H.A., 2020. Subtle variation in abyssal terrain induces significant change in benthic megafaunal abundance, diversity, and community structure. Prog. Oceanogr. 186, 102395. https://doi.org/10.1016/j.pocean.2020.102395.

Ferrari, R., Bryson, M., Bridge, T., Hustache, J., Williams, S.B., Byrne, M., Figueira, W., 2016. Quantifying the response of structural complexity and community composition to environmental change in marine communities. Global Change Biol. 22, 1965–1975. https://doi.org/10.1111/gcb.13197.

Gamoyo, M., Obura, D., Reason, C.J., 2019. Estimating connectivity through larval dispersal in the Western Indian Ocean. J. Geophys. Res. Biogeosci. 124, 2446–2459. https://doi.org/10.1029/2019JG005128.

Gates, A.R., Durden, J.M., Richmond, M.D., Muhando, C.A., Khamis, Z.A., Jones, D.O.B. (this issue, submitted). Ecological considerations for marine spatial management in deep-water Tanzania. Ocean Coast Manag.

Goodbody-Gringley, G., Noyes, T., Smith, S.R., 2019. In: Loya, Y., Puglise, K.A., Bridge, T.C.L. (Eds.), Mesophotic Coral Ecosystems. Springer, Cham, pp. 31–45. Bermuda.

Grimsditch, G.D., Tamelander, J., Mwaura, J., Zavagli, M., Takata, Y., Gomez, T., 2009. Coral reef resilience assessment of the Pemba Channel conservation area, Tanzania. IUCN, gland.

Groeneveld, J.C., Koranteng, K.A., 2017. RV Dr Fridtjof Nansen in the Western Indian Ocean: Voyages of Marine Research and Capacity Development. 1975-2016. FAO, Rome, p. 174.

Groeneveld, J., Koranteng, K., Francis, J., Bianchi, G., 2017. The nansen programme in the western Indian ocean–a synthesis of results. In: Groeneveld, J., Koranteng, K.A. (Eds.), The RV Dr Fridtjof Nansen in the Western Indian Ocean: Voyages of Marine Research and Capacity Development. 1975-2016. FAO, Rome, pp. 143–159.

Gudka, M., Obura, D., Mbugua, J., Ahamada, S., Kloiber, U., Holter, T., 2019. Participatory reporting of the 2016 bleaching event in the Western Indian Ocean. Coral Reefs 39, 1–11. https://doi.org/10.1007/s00338-019-01851-3.

Hagen, P.E., Storkersen, N.J., Vestgard, K., 1999. HUGIN-use of UUV technology in marine applications. Oceans '99. MTS/IEEE. In: Riding the Crest into the 21st Century. Conference and Exhibition. Conference Proceedings (IEEE Cat. No.99CH37008). https://doi.org/10.1109/OCEANS.1999.805003.

Hiller, T., Steingrimsson, A., Melvin, R., 2012. Expanding the Small AUV Mission Envelope; Longer, Deeper & More Accurate. In: 2012 IEEE/OES Autonomous Underwater Vehicles (AUV). IEEE, pp. 1–4. https://doi.org/10.1109/AUV.2012.6380725.

Hoegh-Guldberg, O, Kennedy, EV, Beyer, HL, McClennen, C, Possingham, HP, 2018. Securing a long-term future for coral reefs. Trends Ecol. Evol. 33 (12), 936–944. https://doi.org/10.1016/j.tree.2018.09.006.

Hosmer, D.W., Lemeshow, S., 2004. Applied Logistic Regression, second ed. John Wiley & Sons, Hoboken.

Howe, J.A., Husum, K., Inall, M.E., Coogan, J., Luckman, A., Arosio, R., Abernethy, C., Verchili, D., 2019. Autonomous underwater vehicle (AUV) observations of recent tidewater glacier retreat, western Svalbard. Mar. Geol. 417, 106009 https://doi.org/10.1016/j.margeo.2019.106009.

Hughes, J.A., Bett, B.J., 2007. Angola Block 18WAD and Block 31 pre-operational environmental survey, October 2005: analysis of seabed images taken using WASP (Wide-Angle Seabed Photography) National Oceanography Centre Research and Consultancy Report No 29. National Oceanography Centre, Southampton, 40pp.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., et al., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr. Biol. 17, 360–365. https://doi.org/10.1016/j.cub.2006.12.049.

Huvenne, V.A., Robert, K., Marsh, L., Iacono, C.L., Le Bas, T., Wynn, R.B., 2018. Rovs and Auvs. In: Micallef, A., Krastel, S., Savini, A. (Eds.), Submarine Geomorphology. Springer, Cham, pp. 93–108.

James, L.C., Marzloff, M.P., Barrett, N., Friedman, A., Johnson, C.R., 2017. Changes in deep reef benthic community composition across a latitudinal and environmental gradient in temperate Eastern Australia. Mar. Ecol. Prog. Ser. 565, 35–52. https://doi.org/10.3354/meps11989.

Jankowski, M.W., Gardiner, N.R., Jones, G.P., 2015. Depth and reef profile: effects on the distribution and abundance of coral reef fishes. Environ. Biol. Fish. 98, 1373–1386. https://doi.org/10.1007/s10641-014-0365-1.

Kaehler, S., Ribbink, A., Scott, L., 2008. ACEP final report 2007/8: nearshore and offsore studies in the western Indian ocean. In: Final Scientific Cruise Report, African Coelacanth Ecosystem Programme Grahamstown, South Africa, p. 290.

Kahng, S.E., García-Sais, J.R., Spalding, H.L., Brokovich, E., Wagner, D., Weil, E., Hinderstein, L., Toonen, R.J., 2010. Community ecology of mesophotic coral reef ecosystems. Coral Reefs 29, 255–275. https://doi.org/10.1007/s00338-010-0593-6.

Kahng, S.E., Akkaynak, D., Shlesinger, T., Hochberg, E.J., Wiedenmann, J., Tamir, R., Tchernov, D., 2019. Light, temperature, photosynthesis, heterotrophy, and the lower depth limits of mesophotic coral ecosystems. In: Loya, Y., Puglise, K.A., Bridge, T.C. L. (Eds.), Mesophotic Coral Ecosystems. Springer, Cham, pp. 801–828.

Kirk, J.T.O., 2011. Light and Photosynthesis in Aquatic Ecosystems. Cambridge University Press, New York.

Klaus, R., 2014. Coral Reef Atlas and Outlook -South Western Indian Ocean Islands (Report to the Indian Ocean Commission. ISLANDS Project).

Laverick, J.H., Piango, S., Andradi-Brown, D.A., Exton, D.A., Bongaerts, P., Bridge, T.C., Lesser, M.P., Pyle, R.L., Slattery, M., Wagner, D., Rogers, A.D., 2018. To what extent do mesophotic coral ecosystems and shallow reefs share species of conservation interest? A systematic review. Environ. Evid. 7 (15) https://doi.org/10.1186/s13750-018-0127-1.

Le Bas, T., 2016. RSOBIA—a new OBIA toolbar and toolbox in ArcMap 10.x for segmentation and classification. Photogramm. Eng. Rem. Sens. 70, 1081–1091. https://doi.org/10.3990/2.448.

Levin, N., Beger, M., Maina, J., McClanahan, T., Kark, S., 2018. Evaluating the potential for transboundary management of marine biodiversity in the Western Indian Ocean. Australas. J. Environ. Manag. 25, 62–85. https://doi.org/10.1080/14486563.2017.1417167.

Lieske, E., Myers, R., 2002. Coral Reef Fishes: Indo-Pacific and Caribbean. Princeton University Press, Princeton.

Ling, S.D., Mahon, I., Marzloff, M.P., Pizarro, O., Johnson, C.R., Williams, S.B., 2016. Stereo-imaging AUV detects trends in sea urchin abundance on deep overgrazed reefs. Limnol Oceanogr. Methods 14, 293–304. https://doi.org/10.1002/lom3.10089.

Littler, M.M., Littler, D.S., 2011. Algae. In: Hopley, D. (Ed.), Encyclopedia of Modern Coral Reefs. Encyclopedia of Earth Sciences Series. Springer, Dordrecht.

McLachlan, A., Defeo, O., 2017. Surf-zone Zooplankton and Nekton. The Ecology of Sandy Shores. Academic Press, London.

Medeiros, P.R., Grempel, R.G., Souza, A.T., Ilarri, M.I., Rosa, R.S., 2010. Non-random reef use by fishes at two dominant zones in a tropical, algal dominated coastal reef. Environ. Biol. Fish. 87, 237–246. https://doi.org/10.1007/s10641-010-9593-1.

Muhando, C.A., 2009. Coral reef monitoring in Tanzania: an analysis of the last 20 years. West. Indian Ocean J. Mar. Sci. 8, 203–214. https://doi.org/10.4314/wiojms.v8i2.56981.

Obura, D., 2012. The diversity and biogeography of Western Indian Ocean reef-building corals. PloS One 7, e45013. https://doi.org/10.1371/journal.pone.0045013.

Obura, D., Gudka, M., Rabi, F.A., Gian, S.B., Bijoux, J., Freed, S., Maharavo, J., Mwaura, J., Porter, S., Sola, E. Wickel, J., 2017. reportCoral Reef Status Report for the Western Indian Ocean (2017). Global Coral Reef Monitoring Network (GCRMN)/ International Coral Reef Initiative (ICRI): Indian Ocean Commission. 144pp.

Osuka, K.E., Stewart, B., McClean, C., Roche, R., Turner, J., Samoilys, M., 2020. Protection Outcomes for Fish Trophic Groups across a Range of Management Regimes. Manuscript submitted for publication.

Pinheiro, H.T., Goodbody-Gringley, G., Jessup, M.E., Shepherd, B., Chequer, A.D., Rocha, L.A., 2016. Upper and lower mesophotic coral reef fish communities evaluated by underwater visual censuses in two Caribbean locations. Coral Reefs 35, 139–151. https://doi.org/10.1007/s00338-015-1381-0.

Platts, P.J., McClean, C.J., Lovett, J.C., Marchant, R., 2008. Predicting tree distributions in an East African biodiversity hotspot: model selection, data bias and envelope uncertainty. Ecol. Model. 218, 121–134. https://doi.org/10.1016/j.ecolmodel.2008.06.028.

Pörtner, H.O., 2010. Oxygen-and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. J. Exp. Biol. 213, 881–893. https://doi.org/10.1242/jeb.037523.

Pyle, R.L., 2019. Advanced technical diving. In: Loya, Y., Puglise, K.A., Bridge, T.C.L. (Eds.), Mesophotic Coral Ecosystems. Springer, Cham, pp. 959–972.

Pyle, R.L., Copus, J.M., 2019. Mesophotic coral ecosystems: introduction and overview. In: Loya, Y., Puglise, K.A., Bridge, T.C.L. (Eds.), Mesophotic Coral Ecosystems. Springer, Cham, pp. 3–27.

Ruiz, G.M., Freestone, A.L., Fofonoff, P.W., Simkanin, C., 2009. Habitat distribution and heterogeneity in marine invasion dynamics: the importance of hard substrate and artificial structure. In: Wahl, M. (Ed.), Marine Hard Bottom Communities. Springer-Verlag, Berlin, pp. 321–332.

Samoilys, M.A., Maina, G.W., Osuka, K., 2011. Artisanal Fishing Gears of the Kenyan Coast. CORDIO/USAID, Mombasa.

Samoilys, M.A., Halford, A., Osuka, K., 2019. Disentangling drivers of the abundance of coral reef fishes in the Western Indian Ocean. Ecol. Evol. 9, 4149–4167. https://doi.org/10.1002/ece3.5044.

Schmahl, G.P., Hickerson, E.L., Precht, W.F., 2008. Biology and ecology of coral reefs and coral communities in the flower garden banks region, northwestern Gulf of Mexico. In: Riegl, B.M., Dodge, R.E. (Eds.), Coral Reefs of the USA. Springer, Dordrecht, pp. 221–261.

Sekadende, B., Scott, L., Anderson, J., Aswani, S., Francis, J., Jacobs, Z., Jebri, F., et al., 2020. The small pelagic fishery of the Pemba Channel, Tanzania: what we know and what we need to know for management under climate change. Ocean Coast Manag. 197, 105322. https://doi.org/10.1016/j.ocecoaman.2020.105322.

Sherman, C., Nemeth, M., Ruíz, H., Bejarano, I., Appeldoorn, R., Pagán, F., Schärer, M., Weil, E., 2010. Geomorphology and benthic cover of mesophotic coral ecosystems of the upper insular slope of southwest Puerto Rico. Coral Reefs 29, 347–360. https://doi.org/10.1007/s00338-010-0607-4.

Sherman, C.E., Locker, S.D., Webster, J.M., Weinstein, D.K., 2019. Geology and geomorphology. In: Loya, Y., Puglise, K.A., Bridge, T.C.L. (Eds.), Mesophotic Coral Ecosystems. Springer, Cham, pp. 849–878.

Sigler, M.F., Rooper, C.N., Hoff, G.R., Stone, R.P., McConnaughey, R.A., Wilderbuer, T. K., 2015. Faunal features of submarine canyons on the eastern Bering Sea slope. Mar. Ecol. Prog. Ser. 526, 21–40. https://doi.org/10.3354/meps11201.

Simon-Lledó, E., Bett, B.J., Huvenne, V.A., Schoening, T., Benoist, N.M., Jeffreys, R.M., Durden, J.M., Jones, D.O., 2019. Megafaunal variation in the abyssal landscape of the clarion clipperton zone. Prog. Oceanogr. 170, 119–133. https://doi.org/10.1016/j.pocean.2018.11.003.

Souter, D., Obura, D., Lindeˊn, O., 2000. Coral Reef Degradation in the Indian Ocean. Status Report 2000. CORDIO. SAREC Marine Science Program. Sweden, Stockholm.

Spalding, H.L., Amado-Filho, G.M., Bahia, R.G., Ballantine, D.L., Fredericq, S., Leichter, J.J., Nelson, W.A., Slattery, M., Tsuda, R.T., 2019. Macroalgae. In: Loya, Y.,

Puglise, K.A., Bridge, T.C.L. (Eds.), Mesophotic Coral Ecosystems. Springer, Cham, pp. 507–536.

Stefanoudis, P.V., Smith, S.R., Schneider, C.W., Wagner, D., Goodbody-Gringley, G., Xavier, J., Rivers, M., Woodall, L., Rogers, A., 2018. Deep Reef Benthos of Bermuda: Field Identification Guide. Nekton, Oxford.

Stefanoudis, P.V., Rivers, M., Smith, S.R., Schneider, C.W., Wagner, D., Ford, H., Rogers, A.D., Woodall, L.C., 2019. Low connectivity between shallow, mesophotic and rariphotic zone benthos. Roy. Soc. Open Sci. 6, 190958 https://doi.org/10.1098/rsos.190958.

Sterne, T.K., Retchless, D., Allee, R., Highfield, W., 2019. Predictive modelling of mesophotic habitats in the north-western Gulf of Mexico. Aquat. Conserv. 30, 846–859. https://doi.org/10.1002/aqc.3281.

Stewart, B.D., Jones, G.P., 2001. Associations between the abundance of piscivorous fishes and their prey on coral reefs: implications for prey-fish mortality. Mar. Biol. 138, 383–397.

Sumida, P.Y.G., Yoshinagaa, M.Y., Madureira, L.A.S.P., Hovland, M., 2004. Seabed pockmarks associated with deepwater corals off SE Brazilian continental slope, Santos Basin. Mar. Geol. 207, 159–167. https://doi.org/10.1016/j.margeo.2004.03.006.

Turner, J.A., Andradi-Brown, D.A., Gori, A., Bongaerts, P., Burdett, H.L., Ferrier-Pagès, C., Voolstra, C.R., Weinstein, D.K., Bridge, T.C., Costantini, F., Gress, E., 2019. Key questions for research and conservation of mesophotic coral ecosystems and temperate mesophotic ecosystems. In: Loya, Y., Puglise, K.A., Bridge, T.C.L. (Eds.), Mesophotic Coral Ecosystems. Springer, Cham, pp. 989–1003.

Tyler, E.H., Speight, M.R., Henderson, P., Manica, A., 2009. Evidence for a depth refuge effect in artisanal coral reef fisheries. Biol. Conserv. 142, 652–667. https://doi.org/10.1016/j.biocon.2008.11.017.

Verfuss, U.K., Aniceto, A.S., Harris, D.V., Gillespie, D., Fielding, S., Jiménez, G., Johnston, P., Sinclair, R.R., Sivertsen, A., Solbø, S.A., Storvold, R., 2019. A review of unmanned vehicles for the detection and monitoring of marine fauna. Mar. Pollut. Bull. 140, 17–29. https://doi.org/10.1016/j.marpolbul.2019.01.009.

Wedding, L.M., Friedlander, A.M., 2008. Determining the influence of seascape structure on coral reef fishes in Hawaii using a geospatial approach. Mar. Geodes. 31, 246–266. https://doi.org/10.1080/01490410802466504.

Wilson, M.F.J., O'Connell, B., Brown, C., Guinan, J.C., Grehan, A.J., 2007. Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. Mar. Geodes. 30, 3–35. https://doi.org/10.1080/01490410701295962.

Wölfl, A.C., Snaith, H., Amirebrahimi, S., Devey, C.W., Dorschel, B., Ferrini, V., Huvenne, V.A., Jakobsson, M., Jencks, J., Johnston, G., Lamarche, G., 2019. Seafloor mapping – the challenge of a truly global ocean bathymetry. Front. Mar. Sci. 6 (283) https://doi.org/10.3389/fmars.2019.00283.

Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semi-parametric generalized linear models. J. Roy. Stat. Soc. B 73, 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x.

Woods, S., 2012. GAMs with GCV/AIC/REML Smoothness Estimation and GAMMs by PQL. R Package Version 1.7–9. Available at: http://cran.rproject.org/web/packages/mgcv/index.html.

Wynn, R.B., Huvenne, V.A.I., Le Bas, T.P., Murton, B.J., Connelly, D.P., Bett, B.J., Ruhl, H.A., Morris, K.J., Peakall, J., Parsons, D.R., Sumner, E.J., Darby, S.E., Dorrell, R.M., Hunt, J.E., 2014. Autonomous Underwater Vehicles (AUVs): their past, present and future contributions to the advancement of marine geoscience. Mar. Geol. 352, 451–468. https://doi.org/10.1016/j.margeo.2014.03.012.

Zelada Leon, A., Huvenne, V.A., Benoist, N., Ferguson, M., Bett, B.J., Wynn, R.B., 2020. Assessing the repeatability of automated seafloor classification algorithms, with application in Marine Protected Area Monitoring. Rem. Sens. 12, 1572. https://doi.org/10.3390/rs12101572.