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Frederic Sinniger*, Ritzelle L. Albelda, Rian Prasetia, Héloïse Rouzé, Erlangga D. Sitorus, and Saki Harii

1 Sesoko Station, Tropical Biosphere Research Center, University of the Ryukyus, Sesoko 3422, Motobu, Okinawa 905-0227, Japan
2 Faculty of Science, University of the Ryukyus, Nishihara, Okinawa 903-0213, Japan

* Corresponding author: F. Sinniger E-mail: fredsinniger@hotmail.com

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Abstract Coral reef ecosystems extend beyond the standard SCUBA diving depth. These ecosystems found between approximately 30 and over 150 m are referred to as mesophotic coral ecosystems (MCEs). Mesophotic coral communities have already been reported from Okinawa over 50 years ago. However, since then little additional knowledge has been obtained on the distribution and diversity of mesophotic corals in the region. Here, we provide an overview of the coral communities observed at selected sites in the region around Sesoko Island. Using photo-quadrats, we surveyed coral communities and specifically the contribution of the dominant coral genera to the total coral cover between different sites at depths ranging from 30 to 80 m. We found that deep coral communities around Sesoko Island hold a high potential biodiversity and need to be taken into account into coastal management plans.

Keywords MCE, Photo-quadrats, Coral cover, Depth

Introduction

While both local populations and scientists have known shallow coral reef communities for centuries, coral ecosystems below 30 m depth are still largely unknown. These ecosystems, referred to as mesophotic coral ecosystems (MCEs), are found between 30–40 m depth and down to about 170 m depth depending on the locations (Hinderstein et al. 2010; Rouzé et al. 2021). In the late 1960’s in Okinawa, Dr. Yamazato, who was the director of Sesoko Station for a long time, reported for the first time on coral communities down to 100 m depth in various places in the Ryukyu Islands. The closest site from Sesoko Island was across Nago Bay on the west coast of Okinawa Island (Yamazato et al. 1967). This report is among the earliest reports on MCEs in the world, shortly after the study of Wells in the Marshall Islands (Wells 1954). Dr. Yamazato was the first to publish mesophotic coral observations in situ, using a small submersible and the findings relative to mesophotic corals were summarised in the proceedings of the first International Coral Reef Symposium (ICRS) (Yamazato 1972). Since then, MCEs have received increasing attention particularly in the last decade for both their presumed potential of acting as a refuge for shallow coral species in a warming ocean (Bongaerts and Smith 2019), and for the increasingly diverse and unique communities that are found at these depths (Lesser et al. 2019; Stefanoudis et al. 2019). However, while the scientific attention on MCEs has increased recently, most studies have focused on a few specific locations and there is still little understanding of the extent and distribution of MCEs in most of the coral reef regions (Bongaerts et al. 2019).

Moreover, little is known on the depth range and zonation of MCEs in most regions of the world. While upper MCEs around 40 m depth can still be accessed by standard SCUBA diving (with strong limitations), investigating deeper parts of the MCEs necessitates either technical diving or remote systems such as remotely operated vehicles (ROVs) or autonomous underwater vehicles (AUVs). All these techniques require significant funding and skills
(Armstrong et al. 2019; Pyle 2019). In this context, the use of simpler systems such as time-lapse photo-quadrat systems or drop camera can already provide precious quantitative information (Sinniger et al. 2019).

Sesoko Island is located in the Northern part of Okinawa Island, just south of the Motobu Peninsula. Due to the presence of Sesoko Station, a marine station of the University of the Ryukyus, shallow reefs surrounding the island have benefited from numerous studies in the last 50 years. Some mesophotic research has been conducted around Sesoko Island in Okinawa, but most of the research in the area was conducted on a single site at 40 m depth (Sinniger et al. 2013; Prasetia et al. 2016; Prasetia et al. 2017). The area surrounding the island is rich in different environments, from steep slopes to nearly flat sunken reefs and several “Sone”, a term used to describe deep pinnacles rising from the sea bottom up to several tens of meters but not reaching the surface. Here, we use time-lapse photo-quadrats to provide an overview of the coral communities and their depth range in a variety of habitats around Sesoko Island.

**Material and methods**

A total of 15 sites in 8 locations at depths below 30 m around Sesoko Island were surveyed in this study (Table 1, Fig. 1). Coral communities were investigated through photo-quadrats. The photo-quadrat system used in this research was described in Sinniger et al. (2019) and was equipped either with GoPro cameras (from Hero3 Black to Hero7 Black) or Canon G15 cameras set with a time lapse mode using the Canon Hack Development Kit (Montabone 2010). Photo-quadrats (0.5×0.5 m) were either deployed by divers or remotely from the boat when depths were not accessible to SCUBA diving. Two quadr-
Systematic quadrat systems were deployed in parallel and 4 consecutive quadrats per system were pooled as one replicate to cover a total of 1 m², with 4 replicates analysed at each site. The exception was off Minna-Sone (72–73 m depth) with only 2 replicates (total of 8 photo-quadrats) exploitable for analyses. At the deepest locations, random photo-quadrats were obtained in an attempt to identify the deepest limit of coral distribution. Some additional observations were made using a ROV (BlueROV2, Blue Robotics, USA) along the wall east of Sesoko to estimate the maximum depth of corals at this site as vertical surfaces are not suitable for photo-quadrats (Fig. 1).

Quadrat data were analysed with the software photоП quad (Trygonis and Sini 2012), with 100 points overlaid in a randomly stratified way across each quadrat. This high number of points was chosen to minimize the amount of coral colonies missed, while keeping acceptable the time required analysing quadrats. Under each point the benthos was characterised into one of the following 4 categories: Algae (including both fleshy and coralline algae), Non-scleractinian Anthozoa, Scleractinia, and Others. Scleractinian corals were identified to the lowest taxonomic level allowed by the image resolution. In some cases, the identification was assisted by morphological vouchers available from the same sites and depth ranges. However, when a reliable genus level identification could not be ascertained, corals were classified as “undet”. In addition, Porites and Montipora were pooled, as in several instances of encrusting or foliose specimens, image resolution did not allow to confidently make the distinction between these two genera. For example, Porites lichen (Dana, 1846) can easily be confused with Montipora on the photo-quadrats. For the analyses, even though some characteristic species could be identified to the species level, all identifications were limited to the genus level. For the coral community composition, only the five dominant genera in terms of overall cover were distinguished, and all the other genera were pooled into “Others”. Benthic cover was calculated by dividing the number of points for a category by 100 (total number of overlaid points).

All statistical analyses were performed using R soft-
ware (R Development Core Team 2020) with the vegan package (Oksanen et al. 2019). Non-metric multidimensional scaling (NMDS) based on Bray-Curtis (BC) dissimilarities was performed to visualize coral community differences across depth ranges. Permutational multivariate analysis of variance (PERMANOVA) was used to determine the significance of the variance between depth ranges. Similarity of percentage (SIMPER) determined the contribution of each category and taxa to the dissimilarities between depth ranges.

**Results and discussion**

Coral cover varied between 2.8±1.4 (mean±SE) and 48.6±1.0 % between the sites studied (Figs. 2, 3). While the lowest coral cover was observed at one of the deepest sites, Sesoko-Sone at 71–72 m depth, even within the shallowest depth range (zone 1), coral cover varied between 4.9±0.9 % at Minna-Sone (30–40 m depth) and 48.6±0.9 % at Shigeo Reef MA3 (38–39 m depth). The quadrats taken off Minna-Sone at 72–73 m depth still showed 19.4±11.4 % coral cover, more than the cover in half of the sites at shallower depth zones. However, the deepest zone appeared significantly different from the intermediate zone with algae responsible for most of the dissimilarity between these depth ranges (Tables S1, S2). While algae were not the focus of this study, the prevalence of algae at all depths shows the necessity to investigate the contribution of algae in mesophotic ecology in future studies.

The depth range of sites studied here allows comparison with each of the three depth zones described by Yamazato (1972): zone 1 extends between 30 and 50 m depth where corals are abundant; zone 2 extends between 50 and 70 m depth with lower coral cover, and zone 3 extends between 70 and 100 m with sparse corals. However, none of the shallowest sites (corresponding to zone 1) of our study showed such high cover as that described by Yamazato et al. (1967). Our findings also do not clearly reflect the decrease in abundance with depth described in Yamazato (1972), although the limitation in number of sites and quadrats in our study must be taken into consideration.

![Fig. 2](https://example.com/fig2.jpg) **Fig. 2** Photoquadrats examples. A) Zone 1, Shigeo Reef Loggers site, 40 m depth; B) Zone 2, Awa JS7 site, 56 m depth; C) Zone 3, off Minna-Sone, 72 m depth; D) Zone 3, dense corallimorpharian community at 71 m on Sesoko-Sone.
Interestingly, the “non-scleractinian” anthozoan cover is higher in zone 3 sites (Fig. 3). While it indeed corresponds to the expected increase in gorgonians and black corals with depth (that can be difficult to estimate using photo-quadrat data), Sesoko-Sone was characterized by an abundance of corallimorpharians at the site surveyed with up to 800 individuals/m² (Fig. 2D) at about 70 m depth.

The maximum depth of corals observed in additional random quadrats was between 80 and 82 m depths in the three Sone deep sites (Sesoko-Sone, off Minna-Sone and Onna-Sone). This depth also corresponds to the transition from hard substrata to sand. Interestingly, this 80 m depth limit may not only be due to a change of suitable substratum. Limited ROV observations along the vertical wall off Motobu Peninsula and southeast of Sesoko Island did not reveal scleractinian corals deeper than 80 m despite the wall extending down to over 90 m depth. This depth limit could be influenced by oceanographic factors (e.g. internal waves, upwelling) or latitudinal limitations (e.g. solar insolation) (Muir et al. 2015; Kahng et al. 2019). However, more widespread and detailed observations in the 80–100 m depth zone are needed in order to establish with confidence the maximum extent of zooxanthellate scleractinians in this region.

The combination of high diversity/low abundance and low numbers of quadrats limited this study to the dominant coral genera. As for the coral cover, the different sites showed high heterogeneity in terms of dominant coral genera (Fig. 4), even between sites located within hundreds of meters of each other, such as the five sites in Shigeo Reef. Nonetheless, the data suggest that both Acropora and Porites/Montipora (this category being predominantly Porites) dominate mainly in the shallowest zone down to 50 m depth (upper mesophotic). At sites below 50 m depth, Acropora is only present in quadrats deployed off Minna-Sone at 73 m depth. In the 1967 survey, Acropora was also mainly observed at sites in the zone 1 (30–50 m depth) (Yamazato 1972). Dominance of Leptoseris, a depth preferential coral (Pochon et al. 2015), increases below 50 m depth (Fig. 4). Known depth generalists, such as Pachyseris and Seriatopora appeared to be influenced more by site specificities than depth patterns. These trends are well visualized in the NMDS plot (Fig. 5), on which Acropora and Leptoseris drive the replicates in nearly opposite directions and have a clear influence on the distinction between the shallowest and the deepest zone (Table S3, S4).

![Fig. 3 Dominant cover categories at each site. The depth distinctions correspond to the three zones of Yamazato (1972). Asterisks indicate two sites were the categories other than scleractinian corals were pooled as “Others”. The “Algae” category includes both coralline and fleshy algae.](image-url)
Fig. 4  Community composition of the scleractinians at each site focusing on the 5 main genera encountered in this study. % Coral cover refers to the contribution of the main genera to the total coral cover.

Fig. 5  NMDS plot of BC dissimilarities calculated based on the cover values of coral genera. Each point represents one replicate. Colors represent the depth zones, and the letters in each point indicate the site. AFS9: Awa-FS9, AJS7: Awa-JS7, AJS9: Awa-JS9, KS: Kita-no-Sone, MMS: Minami-no-Sone, MS: Minna-Sone, OI: Off Iejima, OM: Off Minna-Sone, OS: Onna-Sone, SL: Shigeo-Loggers, SMA3: Shigeo-MA3, SMA4: Shigeo-MA4, SMA5: Shigeo-MA5, SS: Sesoko-Sone, ST: Shigeo-TGP.
The results presented here provide an overview of the mesophotic communities around Sesoko Island, but the high diversity of rarely occurring corals suggests that more quadrats are needed to reliably estimate the whole scleractinian diversity at these sites. Even with 100 points analysed in each 0.5×0.5 m quadrats, many corals were missed in the quadrats. The heterogeneity of the communities observed precludes characterization of a “typical” mesophotic community in this area. Variability of mesophotic communities has also been observed over a 500 km stretch of the Great Barrier Reef (Bridge et al. 2011). However, the richness in communities over a small spatial scale observed in this study makes this area particularly valuable for conservation and further mesophotic studies. In this context, it is essential to improve our knowledge of these ecosystems and the factors threatening them. For example, there is little baseline information on how mesophotic corals will react to global environmental changes, or how they can tolerate or recover from anthropogenic disturbances such as the intensive use of the Awa area off Motobu Peninsula as parking site for construction barges.

Overall, we conclude that MCEs around Sesoko Island hold a great potential coral biodiversity, while at the same time, they are potentially highly threatened by the simple ignorance of their existence.

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Compliance
Coral colonies were sampled under permits issued by Okinawa prefectural government, Japan (No. 27–28, 28–21 and 29–17).

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**Electronic supplementary material**

ESM Tables. S1-S4 can be downloaded from the J-STAGE website: https://doi.org/10.3755/galaxea.G2021_S11N

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