

TUBBATAHA REEFS

Mesophotic Zone Exploration and Description

SCIENTIFIC REPORT

30/06/2024 - 13/07/2024

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1.INTRODUCTION

Mesophotic ecosystems (MEs) are defined as ecosystems that receive less than 1% of the sun's rays at their upper limit, which can range from -30 to -60 meters (m) of depth depending on the environmental conditions. Their lower limit is defined by the disappearance of primary producers, typically around -150 m (Cerrano, et al., 2019). They are generally divided by scientists into upper and lower zones with transition occurring around -60 meters (Baldwin, et al., 2018).

Tubbataha Reefs Natural Park (TRNP) is situated in the Sulu Sea (Philippines) approximately 120 nautical miles East of Puerto Princesa, capital of Palawan Island (see Figure 1). It covers a surface of 97,030 hectares (Alaba, et al., 2023) and comprises two atolls (North and South) and one reef (Jessie Beazley) (see Figure 2). It was entirely established as a no-take zone in 1988 and designated a World Heritage Site in June 2009. It is one of the world's iconic protected areas, recognized for its outstanding universal value, and is the largest no-take marine protected area in the Philippines. The park's management heavily relies on research and monitoring results to formulate science-based management actions and policies.

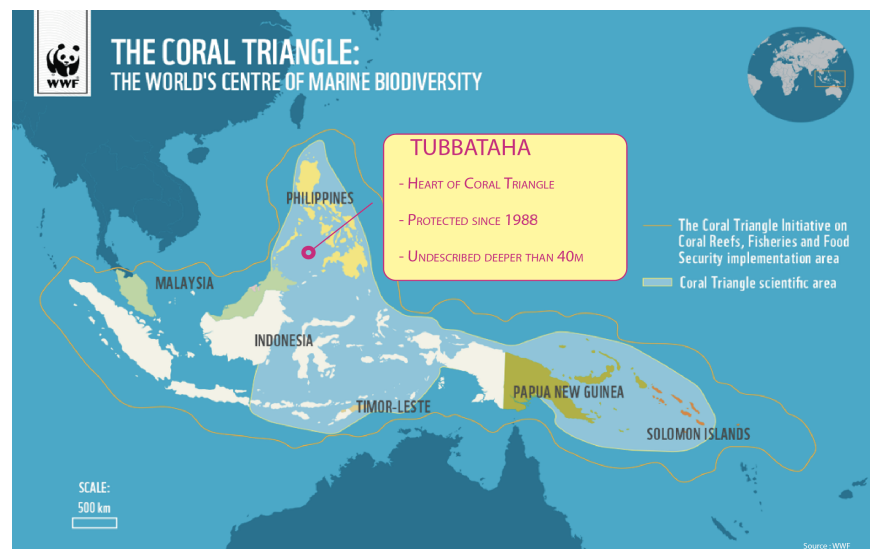


Figure 1: Tubbataha Reefs localization map, source: modified from wwf

Due to the remote location and the weather exposed environment (no islands or protected bay), access for recreational diving is only allowed for a short period of three months per year and permits must be granted. Under the control of park rangers (with permanent presence), all other human activities are forbidden. Those conditions allow TRNP to be preserved from most human impacts. Tubbataha's atolls and reefs appear to be surrounded by steep slope, walls and edges to a depth of -150 meters that should be hosting mesophotic communities (Munar, et al., 2024).

The Tubbataha Management Office (TMO) conducts annual coral reef monitoring at six sites since 1999 using underwater visual census (UVC) along band transects (Alaba, et al., 2021). This method has been wordily used for several decades to study biotic communities because it allows data collection from several targeted biotic communities on a common area. Based on the desired level of precision and the divers' training level, the data collection process may appear time consuming. In average, when using band transects, we estimate that each biotic community requires 20 to 30 minutes to collect visual data for a 25 m transect (Pavy, et al., 2023) (Reef Watch South Australia, 2008).

For safety reasons regarding the remoteness of TRNP and difficult access to a recompression chamber (> 5 hours) in case of emergency, surveys in the park are performed at depths of -5 m and -10 m. In 2023, surveys revealed an average of 24.7% hard coral cover and a fish population surpassing the country's yields (Alaba, et al., 2023).

Deeper communities have never been described or monitored. As a result, little is known about the habitat and biodiversity of the park's mesophotic area (-60 to -150 meters deep) (Alaba, et al., 2021).

Moreover, describing mesophotic communities, especially in one of the world's iconic marine parks, is crucial to improve their understanding and set appropriate management strategies (Loya, et al., 2016). This knowledge, as a baseline, could also benefit other regions, as mesophotic reefs may represent 60 to 80% of all reef habitats worldwide (Pinheiro & Hudson, 2020).

Due to environmental and physiological limitations, time is extremely limited at great depth (>100 m) and decompression stops are necessary when ascending to the surface. On average, 20 minutes at -120 m will generate 240 minutes of decompression stops. Consequently, conducting UVC band transects surveys in the mesophotic area seems unrealistic and will probably require several dives to complete the data collection for a single station.

To address this constraint and contribute to a better understanding of mesophotic ecosystems, the STEED methodology has been designed, developed and patented by Thomas Pavy in 2022 (ref: FR3137059). It aims to facilitate and speed up the data collection for biotic communities along band transect within the mesophotic zone down to -150 m. By so, the deployment of the STEED in TRNP could lead to data collection on a large set of stations in a few dives and along a complete depth gradient (-120 m to -10 m) on a single dive.

Led by Laurent Ballesta from Andromède Océanologie, Gombessa Expeditions are based on three core principles: unravelling scientific mysteries, overcoming diving challenges, and capturing unprecedented images. Laurent Ballesta employs a naturalistic and aesthetic perspective to depict the underwater world, from capturing the first images of the coelacanth at a depth of -120 m in Sodwana (South Africa) to illustrating the nighttime hunts of 700 sharks in Fakarava (French Polynesia).

In collaboration with TMO, the objectives of this study are:

- Scientifically describe mesophotic habitats and depth gradient within TRNP using STEED methodology. Description of habitats include several biotic communities such as ichthyofauna, gorgonian corals, mobile invertebrates and benthic communities.
- Illustrate mesophotic habitats and species using underwater photographs.
- Produce a short film (15 to 20minutes) to illustrate mesophotic habitats and species.

The expedition took place from June 29, 2024, to July 13, 2024. The team consisted of four divers (Laurent Ballesta, Florian Holon, Yanick Gentil and Thomas Pavy) and two surface supports (Laure Thierry de Ville d'Avray and Frederic Tardieu).

2. MATERIAL & METHODS

2.1. STEED SYSTEM DESCRIPTION

STEED stands for Synchronized Transect for Exploration and Ecosystem Description. The entire system consists of a submerged propeller coupled to a frame that supports three different imaging devices. In addition to having neutral buoyancy, it is balanced according to its intended use, making manipulation easier and diver security maintained. It can be used down to a maximum depth of -150 m. Imaging devices simultaneously gather data from several biotic communities (benthos, ichthyofauna, mobile invertebrates, and suspension feeders) along a band transect.

Imagery systems are composed of a stereo video system, a single video with a 45° inclination and a vertical camera set with intervalometer and calibrated by lasers.

In order to compensate for light and colors absorption at depth, STEED is equipped by two 6500 lumens video lights and two 150 watts strobe lights.

Devices references and settings are detailed in the table below.

Table 1: STEED's imagery devices characteristics and settings

Imagery system	Equipment	Settings
Stereo Video	Gopro Hero black 8 in T-Housing	Iso max 1600, Lens: Linear, No stabilization, resolution: 3,7K 50fps
45° single camera	Gopro Hero black 8 in T-Housing	Iso max 1600, Lens: Linear, No stabilization, resolution: 3,7K 50fps
Photo-quadrat	Sony ARII + 20mm lens in Seacam housing	Intervalometer to 1seconde, Iso: 800, F:13, S:200



Figure 2: STEED system during deployment in South Atoll, Tubbataha Reefs, Philippines

To guarantee consistency and efficiency, during all data collection (speed, distance to substrate, safety handling), the STEED system was deployed by a single operator (Thomas Pavy) during the entire expedition.

STEED system is designed to collect data along transect at constant speed with a SUEX XJS dive propulsion vehicle. During this study we set the speed at level 3.

Prior to data collection, all imagery devices must be switched on and synchronized by watch once recording has started.

Following synchronization, the operator can start collecting data along transects while holding the STEED parallel to the substrate and approximately 1 m above it. Data collection duration was defined to be 3 minutes per station i.e., 1 minute per transect. Depth must be constant for an entire station (3

transects) (see Figure 4). Direction of the transects were set to be away from other divers to reduce human disturbance, especially for ichthyofauna.

2.2. UNDERWATER PHOTOGRAPHS

Laurent Ballesta is a professional marine biologist and photographer. During his career, he has published 13 books dedicated to marine fauna and flora. He is co-director of the engineering company Andromède Océanologie and the leader of the Gombessa Expeditions created in 2013. He has won numerous prizes such as the Wildlife Photographer of the Year in 2024 awarded by the Natural History Museum of London for his spectacular and unprecedented illustrations of the Horseshoe crab in the Philippines. To illustrate mesophotic habitats and species encountered during our dives, Laurent Ballesta used Nikon cameras such as D6 and Z9 equipped with Seacam underwater housing and strobes.

2.3. SHORT FILM

Yanick Gentil is a professional cameraman (underwater and terrestrial) and technical diver. He has been a member of Gombessa expeditions since its origin in 2013 when the team conducted its scientific expedition on the Coelacanth in South Africa. Yanick Gentil operates his camera under extreme conditions including great depth (-150 m) or low temperatures (-40 °C). During our expedition in TRNP Yanick Gentil used a Sony A7SIII camera with Seacam underwater housing and Keldan video lights.

2.4. SAMPLING DESIGN

2.4.1. STUDY SITES

During the expedition we conducted 15 dives in total, including three shallow night-dives and 12 mesophotic-dives including 11 with data collection. Among the 12 mesophotic dives, four took place in North atoll, three in Jessie Beazley reef and five in South Atoll (see Figure 3 and Table 2).

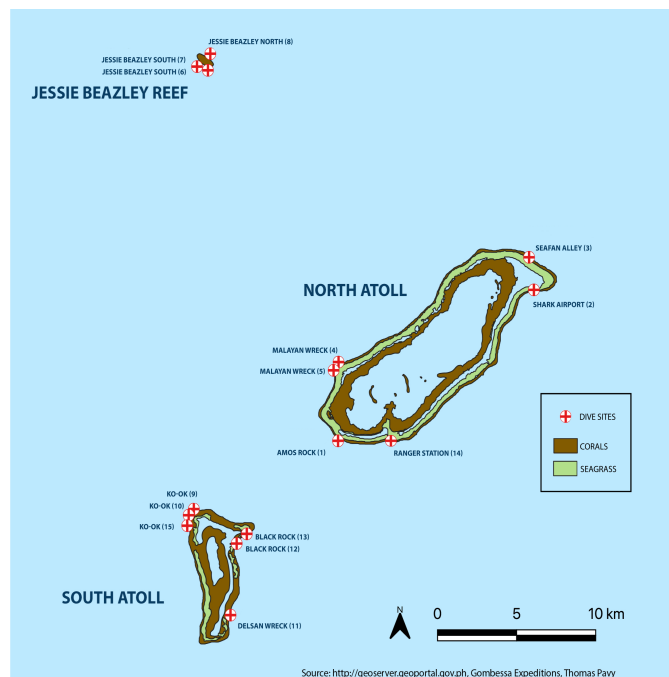


Figure 3: Dive sites map in Tubbataha Reefs Natural Park

The following table details technical information of all dives such as maximum depth reached, date and GPS coordinates.

Table 2 : Dive Log book including GPS coordinates (decimal degrees), dive duration (hour) and Max depth (meter) (dives with steed data collection in Bold font)

Dive	Date	Site	Latitude	Longitude	Duration (h:min:sec)	Max Depth (m)	Type
1	30/06/2024	Amos Rock	8.845417	119.8974	03:05:00	55	Day
2	01/07/2024	Shark Airport	8.92527	120.00795	04:00:00	83	Day
3	02/07/2024	Seafan Alley	8.94619	119.99668	04:57:00	96	Day
4	03/07/2024	Malayan wreck	8.8827	119.8888	04:43:00	35	Day
5	03/07/2024	Malayan wreck	8.8859	119.88995	01:04:00	25	Night
6	04/07/2024	Jessie Beazley South	9.04391	119.81601	05:40:00	117	Day
7	05/07/2024	Jessie Beazley South	9.04501	119.81323	03:52:00	74	Day
8	06/07/2024	Jessie Beazley North	9.04836	119.81562	03:51:00	125	Day
9	07/07/2024	Ko-Ok	8.80856	119.80663	04:27:00	85	Day
10	07/07/2024	Ko-Ok	8.80889	119.80730	01:30:00	30	Night
11	08/07/2024	Delsan wreck	8.748559	119.827794	03:41:00	105	Day
12	09/07/2024	Black Rock	8.79360	119.83366	04:19:00	95	Day
13	10/07/2024	Black Rock	8.795186	119.83572	03:27:00	113	Day
14	10/07/2024	Ranger Station	8.846234	119.919555	01:24:00	32	Night
15	11/07/2024	Ko-Ok	8.80563	119.80605	03:01:00	85	Day

2.4.2. DATA COLLECTION

Depending on the dive conditions such as current, visibility and ecosystems encountered, the STEED operator had to implement stations and transects at different depths at each sampled dive site (see Figure below). A site is composed of several stations implemented at different depths. A station is composed of three transects of 1 minute each (approximately 20 m) (see Table 4).

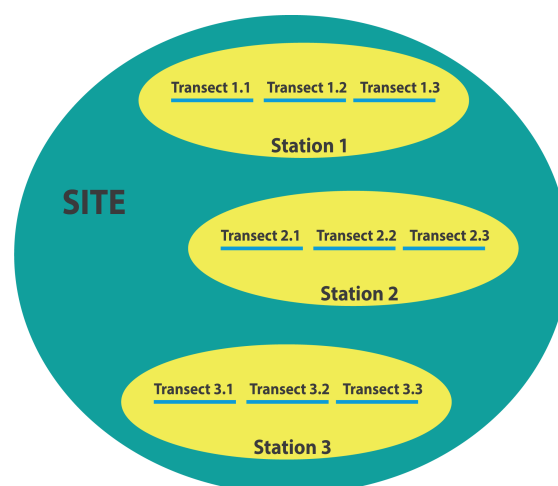


Figure 4: Schema of study sites with several stations composed of three transects each

2.4.3. VERTICAL GRADIENT AND HABITATS

During our 12 deep explorations (down to -127 m), we encountered eight different topographies along the depth gradient. This vertical zonation, based on slope and depth, was constant among all sites explored and sampled except for Deep Reefs (see Figure 5) that did not occur on every site. According to the literature (Munar, et al., 2024), this topography composed of walls and terraces follows the non-uniform sea level rise since LGM (Last Glacial Maximum).

For better clarity and consistency, the color gradient and denomination of habitats shown in Figure 5 will be used identically along the entire document.

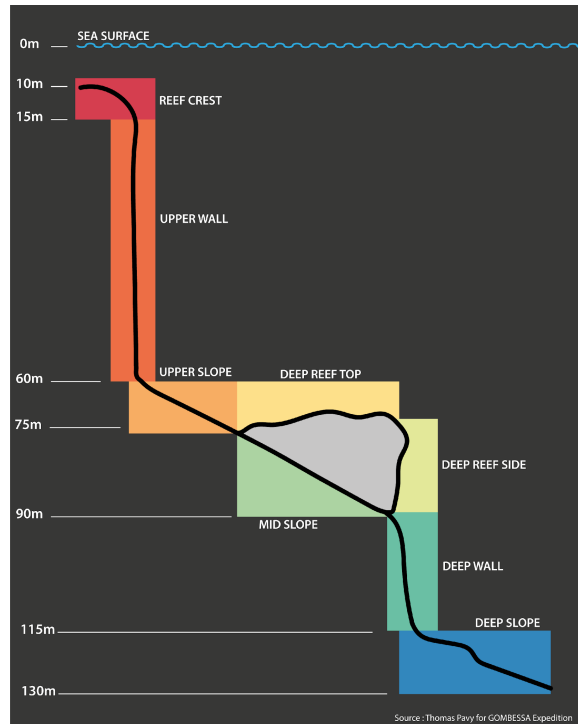


Figure 5: Vertical zonation of the different habitats observed along depth gradients in TRNP

Every time it was possible, we sampled three stations for each habitat. However, some habitats have been sampled only twice such as Deep Reef Top and Deep wall (see Table 3).

When more than three stations have been sampled per habitat, we decided to analyze only the three stations with the longest time of data collection and the best images quality. Thus, we have selected data to be processed from nine sites and excluded Amos Rock 40, Amos Rock 50 and JBA South 55 where habitats were redundant with other sites and data (see Table 3).

Table 3: Collected data (depth in m) per site and data selected for analysis (highlighted in color)

Habitats		Reef crest	Upper Wall	Upper Slope	Deep Reef Top	Deep Reef Side	Mid Slope	Deep Wall	Deep Slope
Depths Range		6-10m	10-60m	60-70m	70-80m	80-90m	70-90m	90-95m	95-120m
Sites	Amos Rock		40	50					
	Shark Airport				73		80		
	Seafan Alley		51	60	70	86			
	Malayan Wreck		40	60		80			
	JBA South	9	40-60				80		105
	JBA South			55					
	JBA North	9	40				80		120
	Ko-Ok		45	70					
	Deslan Wreck	7					90	105	
	Black Rock						90	105	115
	Ko-Ok			74					

2.5. DATA TREATMENT

2.5.1. STEREO CALIBRATION

2.5.1.1. Calibration setting

In order to set the stereo video calibration, we deployed a cube calibration on three dates: 03/07/24, 8/07/24 and 11/07/24. The cube was filmed at different angles and different distances with synchronized stereo cameras to make sure that all calibration points (see Figure 6) are visible on both cameras on the same video frame.

The calibration was set using the stereo video software VidSync (Neuswanger, et al., 2016).



Figure 6: Aluminum cube (50cm*50cm*50cm) and calibration points used for stereo video calibration

2.5.1.2. Calibration check

To verify calibration accuracy during each dive, we filmed a foldable plastic meter with centimeters graduations that we fold to form a rectangle (40 cm*60 cm) and positioned on the reef (Figure 7).

This rectangle was also used to verify laser calibration of the photo-quadrats camera set to have a 30 cm distance in between the two lasers.

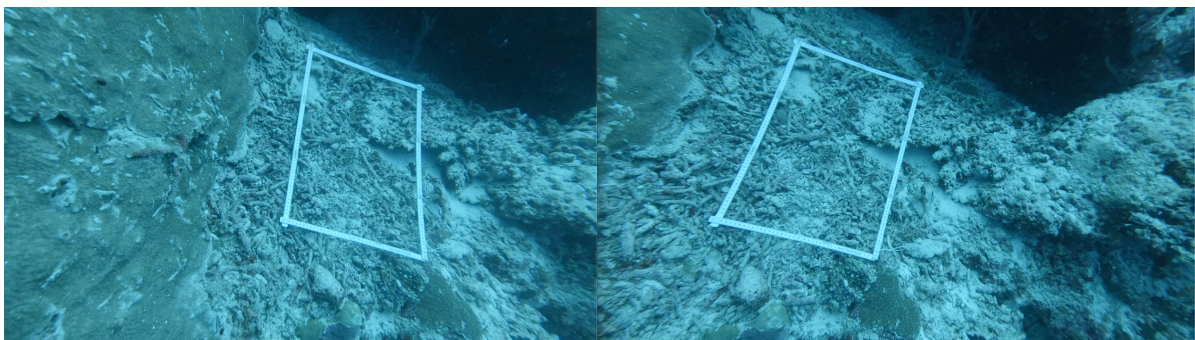


Figure 7: Foldable plastic meter deployed at each site to verify stereo video calibration settings

We took 10 measurements on the foldable plastique meter on each site. Measurements were taken at different random angles and distances. We then calculated the error for every measurement.

Figure 8 shows the average error in percentage for every site. The maximum mean error is $\pm 4,6$ % at Malayan Wreck and the minimum mean error is $\pm 2,2$ % at Jessie Beazley South.

The calibration check could not be conducted at Shark Airport and Sea Fan Alley as we did not deploy the foldable plastique meter (see Figure 8).

We consider the mean error scores acceptable (less than 5%), so we did not apply any correction coefficient to the measurements.

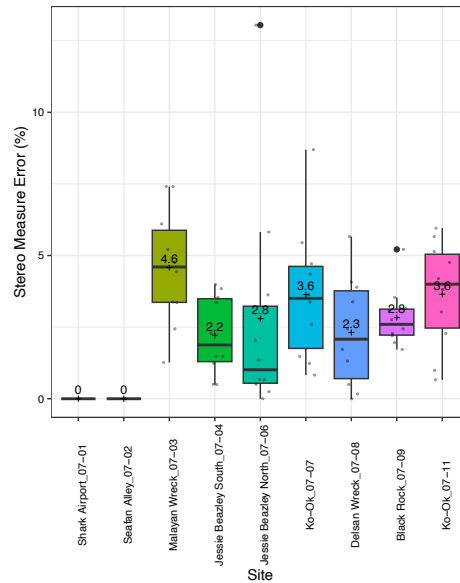


Figure 8: Mean stereo camera measurement error per sites in %

2.5.2. TRANSECTS UNIFORMIZATION

Using the stereo video software tool (Neuswanger, et al., 2016), we calculated the travel speed of STEED system at every station. We consider the speed to be constant for all transects of the same station. Using the duration of transects, we calculated the sampling distance in meters for every transect (see Table 4).

In order to uniformize data and sampling at all stations, we calculated and applied a standardization coefficient to abundances and biomass scores.

Coefficient is calculated as follows:

$$\text{Coeff} = 20 / \text{distance (in m) per transect}$$

After applying the coefficient, all transect results are given for a 20 m-long equivalent data (60 m per station).

Table 4: Study Site metadata including speed, duration and transect distance calculation.

Site	Date	Time	Depth	Habitats	Duration (s)	Speed (m/s)	Duration Transect (s)	m/Transect	m/Site
Shark Airport	01/07/2024	11:47	73	Deep Reef Top	185	0,342	61,7	21,1	63,3
Seafan Alley	02/07/2024	13:05	70	Deep Reef Top	145	0,297	48,3	14,4	43,1
Seafan Alley	02/07/2024	12:40	86	Deep Reef Side	123	0,38	41,0	15,6	46,7
Malayan Wreck	03/07/2024	11:56	40	Upper Wall	240	0,436	80,0	34,9	104,6
Malayan Wreck	03/07/2024	10:27	60	Upper Slope	164	0,364	54,7	19,9	59,7
Malayan Wreck	03/07/2024	10:56	80	Deep Reef Side	211	0,501	70,3	35,2	105,7
Jessie Beazley South	04/07/2024	14:55	9	Reef Crest	208	0,32	69,3	22,2	66,6
Jessie Beazley South	04/07/2024	12:58	60	Upper Wall	230	0,314	76,7	24,1	72,2
Jessie Beazley South	04/07/2024	12:32	105	Deep Slope	50	0,327	16,7	5,5	16,4
Jessie Beazley North	06/07/2024	13:16	9	Reef Crest	221	0,368	73,7	27,1	81,3
Jessie Beazley North	06/07/2024	12:01	40	Upper Wall	184	0,362	61,3	22,2	66,6
Jessie Beazley North	06/07/2024	11:29	80	Mid Slope	194	0,378	64,7	24,4	73,3
Jessie Beazley North	06/07/2024	11:17	120	Deep Slope	203	0,385	67,7	26,1	78,2
Ko-Ok	07/07/2024	10:50	70	Upper Slope	288	0,342	96,0	32,8	98,5
Delsan Wreck	08/07/2024	15:03	7	Reef Crest	183	0,26	61,0	15,9	47,6
Delsan Wreck	08/07/2024	13:00	90	Mid Slope	181	0,477	60,3	28,8	86,3
Delsan Wreck	08/07/2024	12:56	105	Deep Wall	136	0,463	45,3	21,0	63,0
Black Rock	09/07/2024	11:36	90	Mid Slope	107	0,395	35,7	14,1	42,3
Black Rock	09/07/2024	11:33	105	Deep Wall	105	0,402	35,0	14,1	42,2
Black Rock	09/07/2024	11:31	115	Deep Slope	106	0,402	35,3	14,2	42,6
Ko-Ok	11/07/2024	10:09	74	Upper Slope	181	0,379	60,3	22,9	68,6

2.5.3. TRANSECTS DATA PROCESSING

2.5.3.1. Photo-quadrats

We set the intervalometer of the photo-quadrat camera to 1 second. Giving so, we collected more than 100 images per station. Out of each station's images set, we randomly selected 20 pictures and visually verified that quality and sharpness was good enough for benthos organism's category identification.

Pictures were then cropped to 45 cm*45 cm (0.2025 m²) using rules of third and laser points calibration in a photography editing software (see Figure 9).

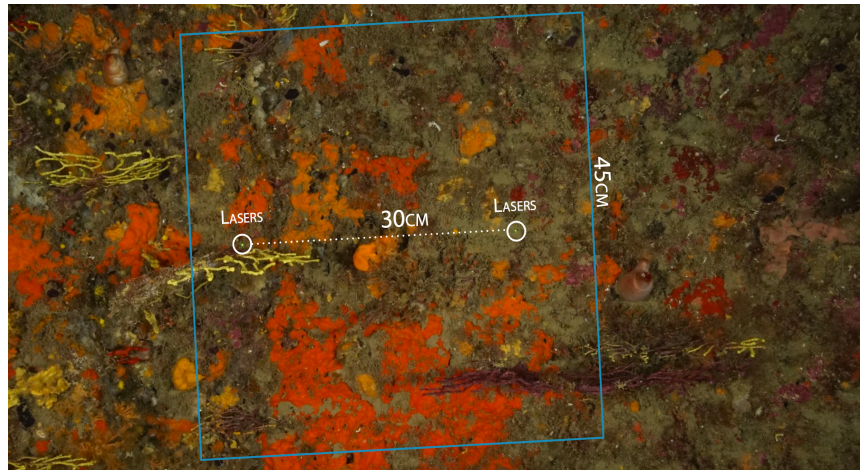


Figure 9: Example of photo-quadrats cropped using lasers calibration

After cropping images, we used the online resource CoralNet (Beijbom, et al., 2012) to generate 50 simple random points per photo-quadrat (Dethier, et al., 1993). All points were annotated within a set of 20 benthic organisms and categories listed in Figure 10. We chose those categories to be easily identified on photo-quadrats and yet differentiating major benthic organisms' groups.

	Hard Coral		Bryozoan		Rubbles		Macro Algae		Zoanthids
	Millepora		Sponge		Rock		Nephtheidae		Hydroid
	Soft Coral		Anemone		Sand		Tunicates		Gorgonian
	Dendrophyllia		Pennatula		Turf Algae		Anthipatharia		Crustose algae

Figure 10: Benthic organisms categories used for photo-quadrats annotations

2.5.3.2. Ichthyofauna

Ichthyofauna communities were studied through stereo video and the single camera with a 45° inclination. All videos were watched at a 0.33 speed rate. We identified and counted fishes to a species level as much as possible. On stereo video we counted abundances per species and measured fish's sizes for all individuals. In case of large schools, we measured one representative individual and considered all individuals to have the same size. Single camera with 45° inclination was analyzed for complementary species identification only (no abundances or sizes).

Due to difficulty of identifications on video, we excluded all fishes smaller than 5 cm i.e., Pomacentridae, Labridae and Anthiadidae.

We calculated the fish biomass (g/m²) with the following formula expressing the length and weight model (Kulbicki, et al., 1993):

$$W = a \cdot L^b$$

where W is the weight in g, L is the total length in cm measured with stereo videos, and a and b are length-weight relationship estimates from Fishbase (Froese & Pauly, 2000).

2.5.3.3. Invertebrates

To survey vagile invertebrates we screened the single camera with a 45° inclination at a 0.33 speed rate and counted all individuals with identification to species level.

2.5.3.4. Gorgonian corals

Gorgonian corals communities were described using several methods:

- Stereo video to measure the height of 30 random individuals per station. We also estimated the necrose percentage for each colony measured (from 0 to 100 %).
- We counted number of colonies and species present within 30 photo-quadrats (Andromède Océanologie, 2019) of 0.2025m² (45 cm*45 cm). As we are not qualified to name gorgonian corals species, we used visual differentiation between colonies to determine number of species per photo-quadrat.
- We also compiled photographs of all visually differentiated specimens for identification by Dr. Sonia J. Rowley (Assistant Researcher, Dept. Earth Sciences, University of Hawai'i at Mānoa) (Sánchez, et al., 2019) who identified specimens to a genus level.

2.5.4. UNDERWATER PHOTOGRAPHS

Laurent Ballesta illustrations were selected and edited using professional photographer software (Adobe Photoshop Lightroom).

2.5.5. SHORT FILM

In order to increase the diffusion potential of the short film, we decided to edit two versions. One version was edited in collaboration with Brut. media to be broadcasted on their YouTube channel and social medias. The second version was edited for the expeditions partners to communicate and raise awareness about TRNP mesophotic habitats and species. Both versions of the short film were edited using professional post-production software (Adobe Premiere Pro).

2.6. DATA ANALYSES

After being post-processed, data analyses have been performed using R-Studio (R Core Team, 2021). We separately analyzed all four biotic communities per station and per habitat to create plots using the R-studio packages ggplot2 (Wickham, 2016) (Loya, et al., 2016). Depending on biotic community, we looked at different biotic descriptors such as: species diversity, abundance, density, size or necroses.

3.RESULTS

3.1. SHORT FILM

A first short film (18minutes) has been broadcasted on the YouTube channel and the Instagram accounts of the media Brut. on the 25th of December 2024. The short film can be watched using the following link: <https://www.youtube.com/watch?v=ZGJs6kRO4xk>. The aim of this version was to introduce TRNP to a large audience and share the daily routine of the expedition.



Figure 11: Film poster on Brut.'s youtube channel

Another version of the short film was edited with English subtitle in order to be used to communicate and raise awareness about TRNP mesophotic habitats and species. This version won't be available online but will be transmitted to the expedition partners for their own use.

3.2. STEED EFFICIENCY

In total, we have collected data at 30 stations (2.6 stations per dive in average) between -120 m and -9 m, during our 11 mesophotic dives.

The efficiency of the system and its maneuverability allowed us to collect data for a station in 15 minutes (including camera setting and synchronization) instead of an estimated two hours for four biotic communities using conventional UVC methodology (Pavy, et al., 2023) (Reef Watch South Australia, 2008).

On the 06/07/24 in Jessie Beazley North (JBA North), we collected data at four stations (including four biotic communities each) with a single dive (-120, -80, -40 and -9 m) (see Table 5).

Table 5: Collected data per dive (depth in m) per site using the STEED methodology

	Habitats	Reef crest	Upper Wall	Upper Slope	Deep Reef Top	Deep Reef Side	Mid Slope	Deep Wall	Deep Slope
	Depths Range	6-10m	10-60m	60-70m	70-80m	80-90m	70-90m	90-95m	95-120m
Sites	Amos Rock		40	50					
	Shark Airport				73		80		
	Seafan Alley		51	60	70	86			
	Malayan Wreck		40	60		80			
	JBA South	9	40-60				80		105
	JBA South			55					
	JBA North	9	40				80		120
	Ko-Ok		45	70					
	Deslan Wreck	7					90	105	
	Black Rock						90	105	115
	Ko-Ok			74					

3.3. BENTHOS

In total, we analyzed 420 photo-quadrats (20 per station) for a total of 21 000 points annotated (50 per photo and thus 1000 (20*50) per station).

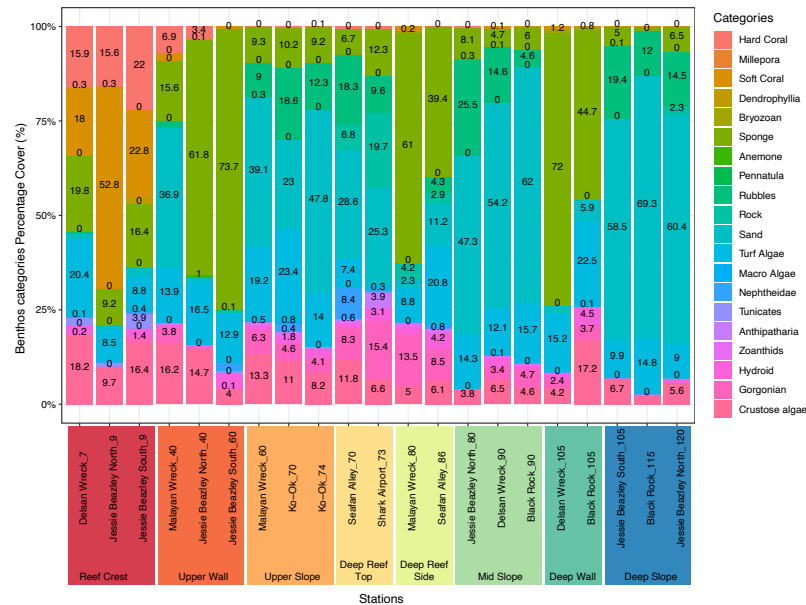


Figure 12: Benthic communities cover (in %) over all stations

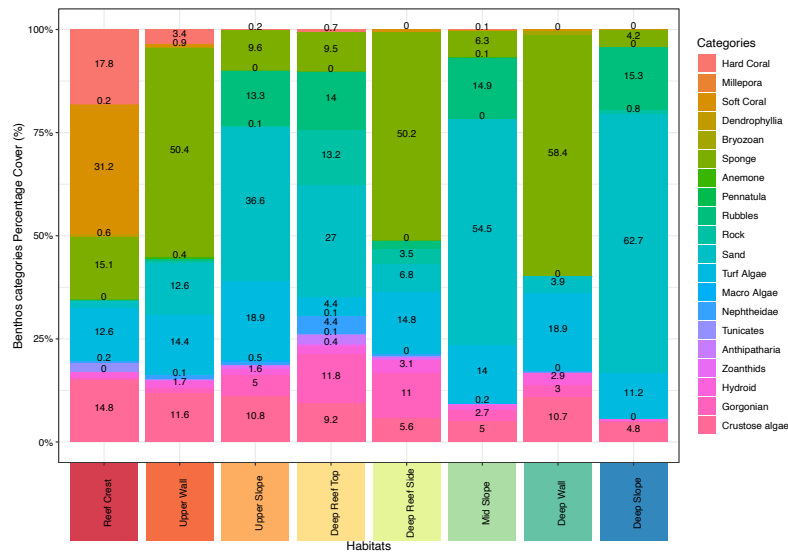


Figure 13: Mean benthic communities cover (in %) over all habitats

In the Reef Crest habitat, stations are dominated by Soft Corals 31.2 % (18 %, 52.8 % and 22.8 %) and Hard corals 17.8 % (15.9 %, 15.6 % and 22 %). Stations of the Upper Wall habitat are dominated by Sponges 50.4 % (61.8 % and 73.7 %) except the Malayan_Wreck_40 being dominated by Turf Algae 36.9 %. Within the Upper Slope habitat, the sand category is the most represented 36.6 % (39.1 %, 23 % and 47.8 %). The Deep Reef Top habitat is also dominated by sand 27 % (28.6 % and 25.3 %) but we observe a great representation of the Gorgonian category 11.8 % (8.3 % and 15.4 %). Sponges are the dominant category of the Deep Reef Side habitat 50.2 % (61 % and 39.4 %) and Deep Wall habitat 58.4 % (72 % and 44.7 %). Mid Slope habitat is dominated by sand 54.5 % (47.3 %, 54.2 %, 62 %) as well as Deep Slope habitat 62.7 % (58.5 %, 69.3 % and 60.4 %).



Figure 14: Benthic community dominated by sponges at Jessie Beazley South around 55 m (Upper Wall habitat)



Figure 15: Benthic community dominated by sand at Jessie Beazley South around 110 m (Deep Slope Habitat)

3.4. ICHTHYOFAUNA

During this study, we analyzed 63 videos out of 21 stations for a total of approximately 185 minutes. In total we identified 102 species of 58 genus and 25 families.

We observe the highest diversity of species on the Reef Crest Habitat with 56 species. The second most diverse habitat is the Upper Slope with 36 species observed. Species diversity decreases with depth to 8 species observed on Deep Slope habitat.

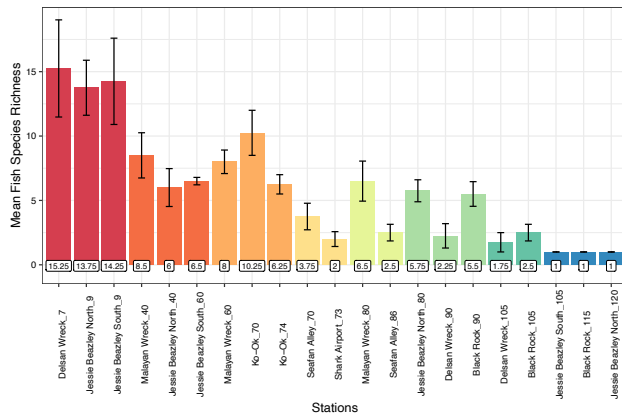


Figure 16: Mean fish species diversity observed per 20m transect

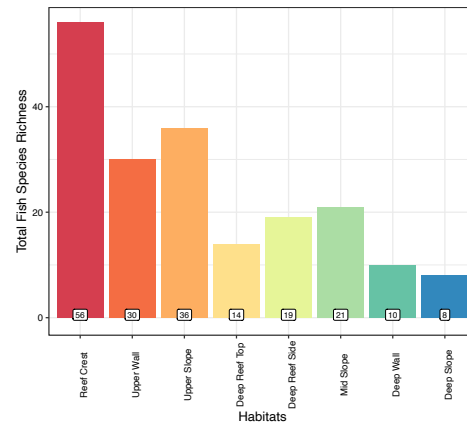


Figure 17: Total fish species diversity observed per habitat

According to Figure 18, ichthyofauna species change along the depth gradient. Indeed, few species such as *Naso hexacanthus* or *Zanclus cornatus* are widely vertically spread but many species are related to a specific habitat such as *Macolor niger* or *Melichthys vidua* on Reef Crest and *Aprion virescens* in Deep Slope.

We observe a group of species that spreads along intermediate habitats, to be considered as mesophotic (Upper Slope, Deep Reef Top, Deep Reef Side, Mid Slope and Deep Wall). This group includes *Paracaesio sordida*, *Genicanthus bellus*, *Cephalopholis polleni* or *Apolemichthys trimaculatus* (see Figure 18).

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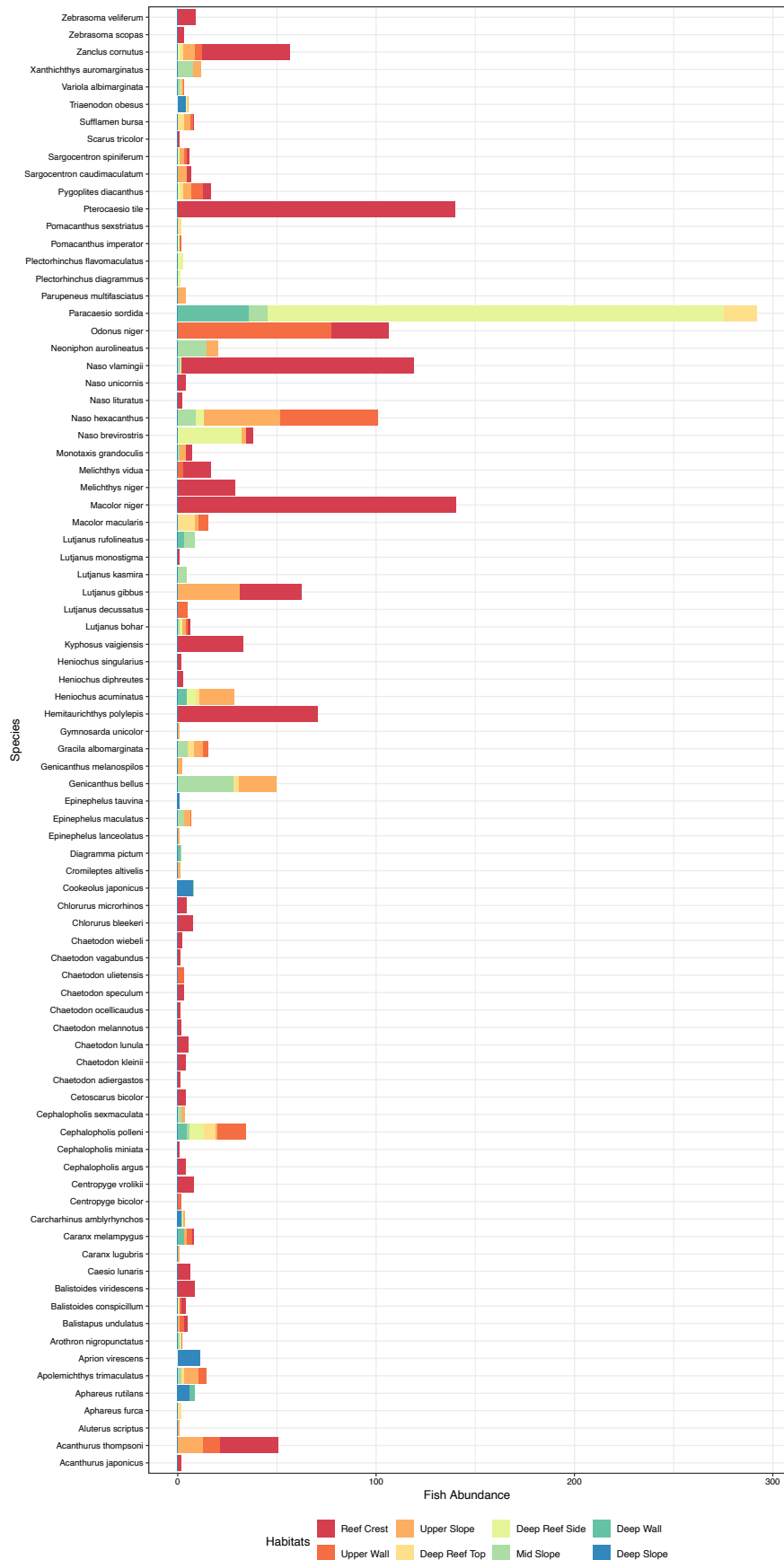


Figure 18: Total fish species abundance per habitats

Through the STEED's data analysis, we identify seven species never identified previously within TRNP: *Centropyge colini*, *Cephalopholis polleni*, *Cookeolus japonicus*, *Genicanthus bellus*, *Neoniphon aurolineatus*, *Pogonoperca punctatus* and *Xanthichthys caeruleolineatus*. All of their observations are made between -40 m and -115 m (see Figure 19). Since all observations are made deeper than -40 m, we consider them to be mesophotic species. The species with the largest depth gradient is *Genicanthus bellus* (-40 to -115 m). Some species are observed only once: *Centropyge colini*, *Pogonoperca punctatus* and *Xanthichthys caeruleolineatus*.

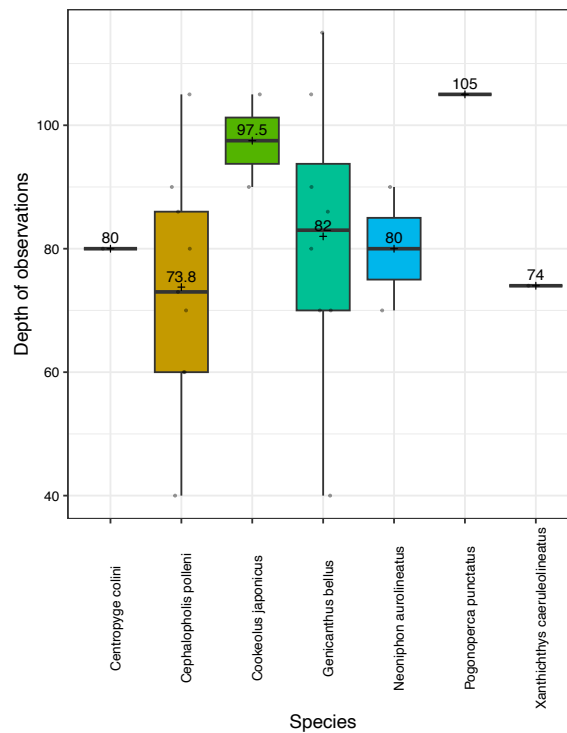


Figure 19: Species newly observed within TRNP during the expedition



Figure 20: *Xanthichthys caeruleolineatus* observed with stereo video at Ko-Ok site around 70m on 11/07/24



Figure 21 : Cookeolus japonicus observed with stereo video at Jessie Beazley South around 105m on 04/07/24



Figure 22: Neoniphon aurolineatus observed with stereo video at Black Rock around 90 m on 09/07/2024

Using Laurent Ballesta's photographs we also identify three additional species never identified previously within TRNP: *Hoplostiltilus marcosi*, *Hoplostiltilus randalli* and *Brotula multibarbata* (see Figure 23, Figure 24 and Figure 25).



Figure 23: *Hoplostiltilus marcosi* at Malayan Wreck around 80 m on 03/03/2024



Figure 24: *Brotula multibarbata* at Malayan Wreck around 60 m on 03/03/2024



Figure 25: *Hoplostiltilus randalli* at Ko-Ok around 85 m on 11/07/2024

The mean genus diversity per transect follows the same repartition through habitats and depths than mean species diversity. We observe a maximum mean of 14 genus per transect at Jessie Beazley North_9 and a minimum of one genus per transect in all stations of Deep Slope habitats (Jessie Beazley_105, BlackRock_115 and Jessie Beazley North_120). Maximum genus diversity per habitat is observed in Upper Slope with 33 genus, followed by Reef Crest with 32 genus. Minimum Genus diversity per habitat is reached at Deep slope with nine genus observed.

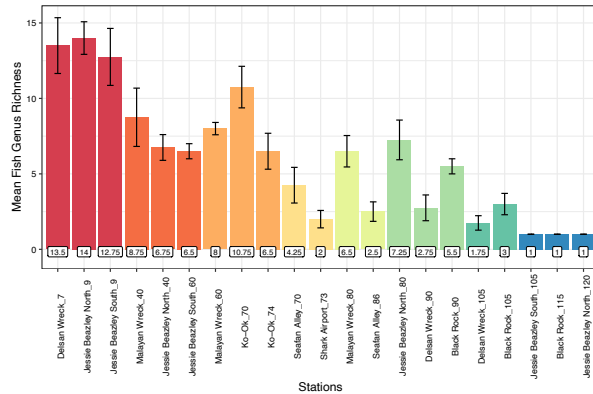


Figure 26: Mean fish genus diversity observed per 20m transect

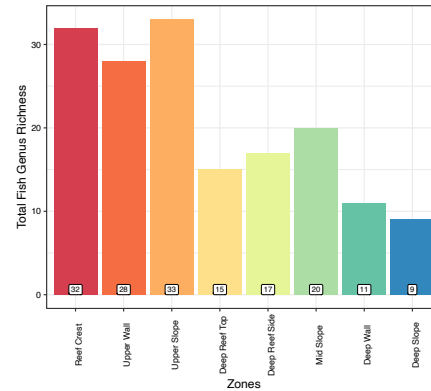


Figure 27: Total fish genus diversity observed per habitat

According to Figure 28, we observe a majority of genus with very large habitats gradients such as *Cephalopholis* (Reef Crest to Deep Wall), *Naso* (Reef Crest to Mid Slope), *Lutjanus* (Reef Crest to Deep Wall) or *Caranx* (Reef Crest to Deep Wall). On the other hand, some genus are habitat specific such as *Pterocaesio* (Reef Crest), *Zebrasoma* (Reef Crest), *Hemitaurichthys* (Reef Crest), *Decapterus* (Upper Slope), *Cookeolus* (Deep Slope) or *Aprion* (Deep Slope).

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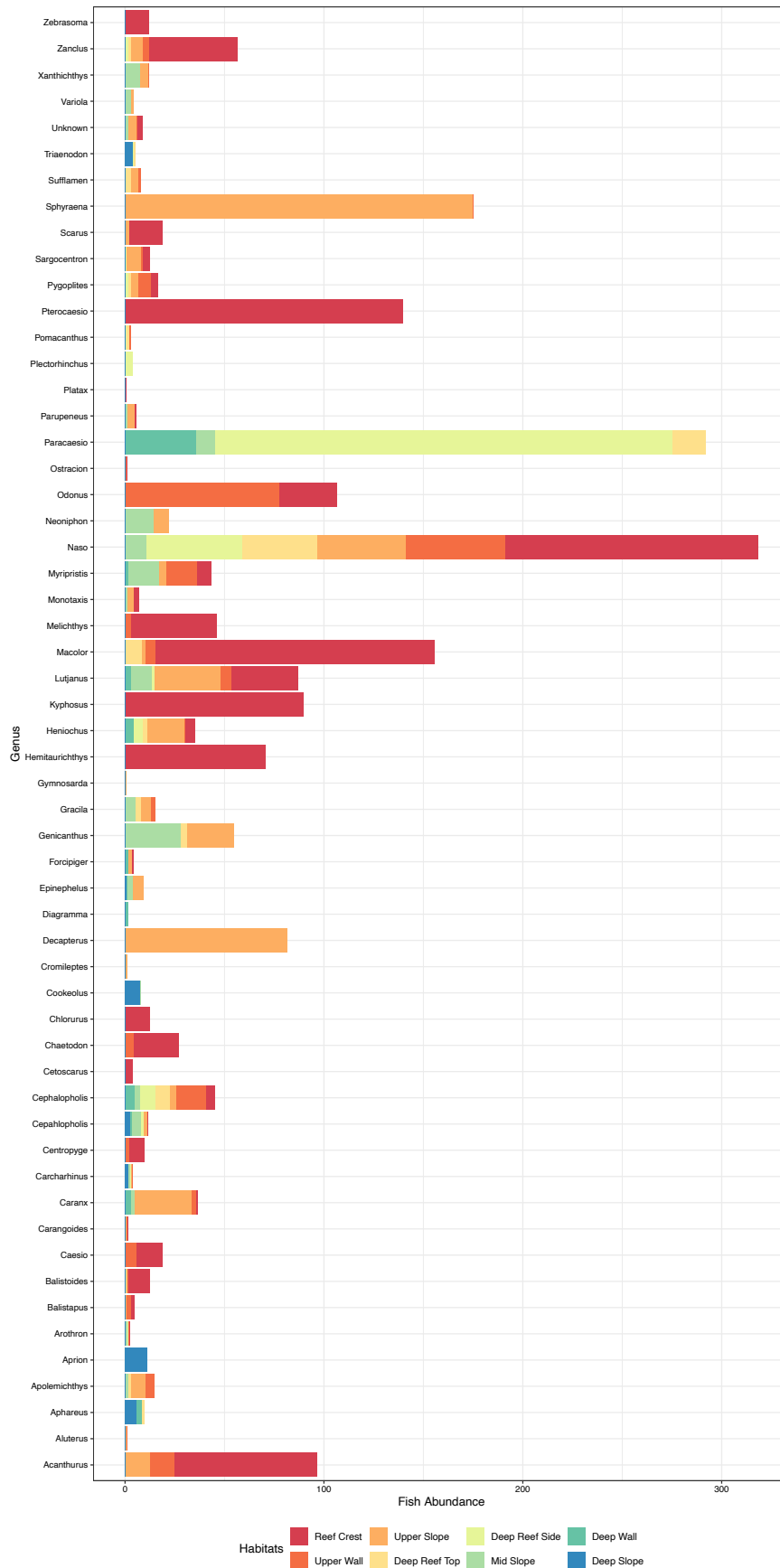


Figure 28: Total fish genus abundance per habitats

The highest fish abundance is reached at Jessie Beazley South_9 with a mean of 181.7 individuals per transect. Reef Crest habitat shows the highest total abundance with 926.6 individuals. The lowest total fish abundance occurs in Deep Slope habitat with 32.1 individuals, Mid Slope habitat has the second highest abundance with 500.7 individuals.

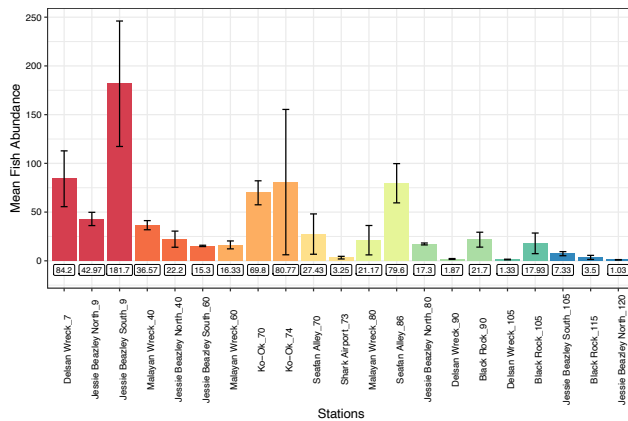


Figure 29: Mean fish abundance per 20m transect

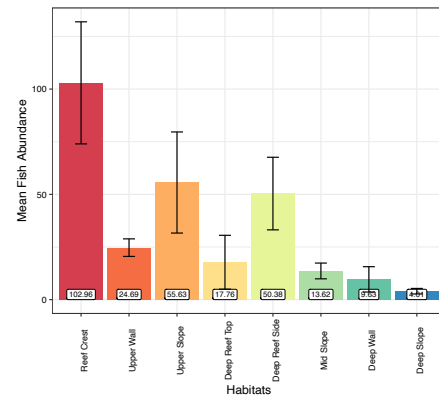


Figure 30: Total fish abundance per habitat



Figure 31: School of *Naso caeruleacauda* and *Naso hexacanthus* at Malayan Wreck around 60 m

The highest mean fish biomass per habitat is reached at Reef Crest with 58.8 g/m². The habitat with the lowest mean fish biomass is Deep Wall with 3.2 g/m². The station with the highest biomass in g/m² is Jessie Beazley South_9 with 126.5 g/m² (Reef Crest) followed by Ko-Ok_70 with 70.3 g/m² (Upper Slope) and Malayan Wreck_80 with 59.9 g/m² (Deep Reef Side).

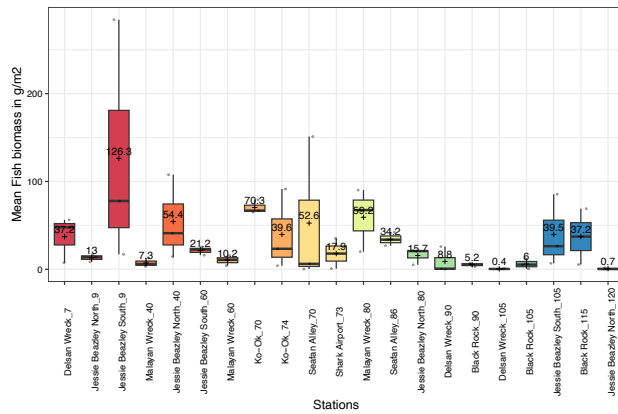


Figure 32: Mean fish biomass in g/m² per station

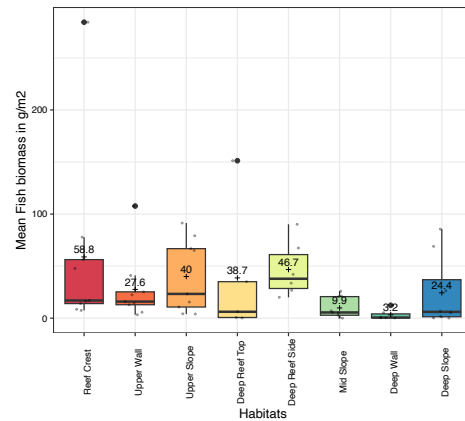


Figure 33: Mean fish biomass in g/m² per habitat

During our mesophotic dives, we also observed and illustrates outstanding species such as *Rhincodon typus* (Figure 34), *Epinephelus lanceolatus* (Figure 35) or *Galeocerdo cuvier* (Figure 36).



Figure 34: *Rhincodon typus* cruising above divers at Jessie Beazley South around 85 m on 04/07/2024



Figure 35: *Epinephelus lanceolatus* at Jessie Beazley South around 50 m on 05/07/2024



Figure 36: Galeocerdo cuvier at Shark Airport around 95 m on 01/07/2024

On the 06/06/2024 at Jessie Beazley South, we came across a nesting ground of *Abudefduf vaigiensis* around 10 m. The phenomenon covered approximately 50m².



Figure 37: Abudefduf vaigiensis cleaning eggs at Jessie Beazley North on the 06/07/2024 around 10 m.

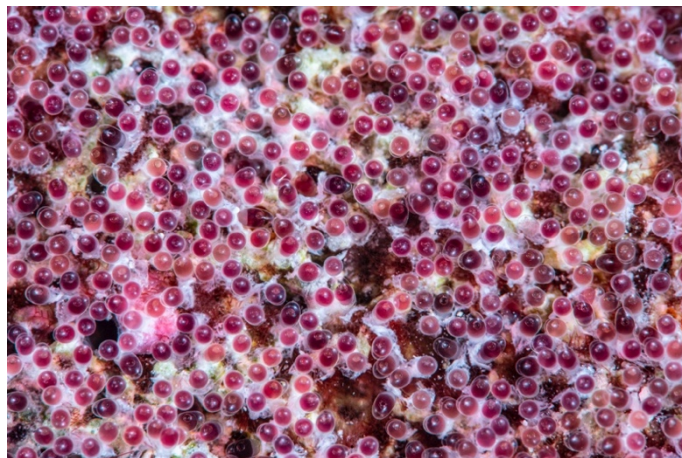


Figure 38: Close up on Abudefduf vaigiensis's eggs at Jessie Beazley North on the 06/07/2024 around 10 m.

3.5. MOBILE INVERTEBRATES

We identify only three species of mobile invertebrates after examining 21 videos for a total of approximately 63 minutes. All observations are members of the subphylum Asterozoa. Occurrence and abundance are weak with two occurrences maximum per species and a maximum of 2.8 individuals (*Fromia* sp at BlackRock_90).

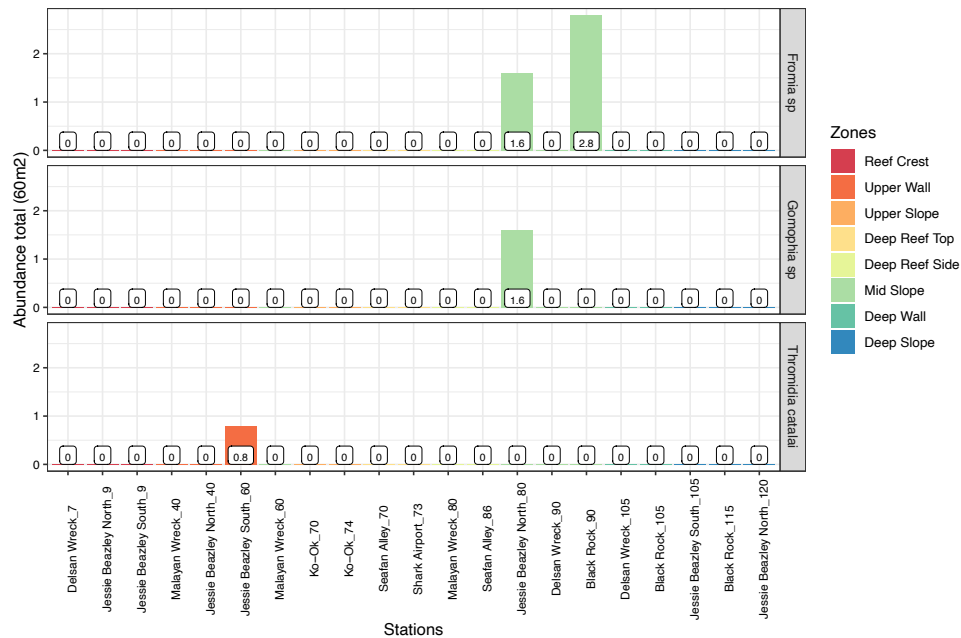


Figure 39: Vagile invertebrates' identification and abundances over all stations



Figure 40: *Fromia* sp observed with STEED at Black Rock around 90 m on 09/07/24

The *Thromidia catalai* is observed in the Upper Wall habitat. *Gomophia* sp. and *Fromia* sp. are found in the Mid Slope habitat.



Figure 41: Gomophia sp observed with STEED at Jessie Beazley South around 80m on 06/07/24



Figure 42: Thromidia catalai observed with STEED at Jessie Beazley South around 60m on 06/06/24

However, Laurent Ballesta encountered and illustrated one specimen of two other species of mobile invertebrates, *Thelenota rubralineata* and *Panulirus versicolor* (see Figure 43 and Figure 44).



Figure 43 : Panulirus versicolor



Figure 44: Thelenota rubralineata

3.5.1. OVULIDAE

Using a macro lens on his Nikon camera, Laurent Ballesta found and photographed 11 ovulidae species (see Figure 45 to Figure 56) of ten genus. Ovulidae were found in gorgonian corals, soft corals and sponges.



Figure 45: *Pellasimnia* sp



Figure 46: *Dentiovula dorsuosa*

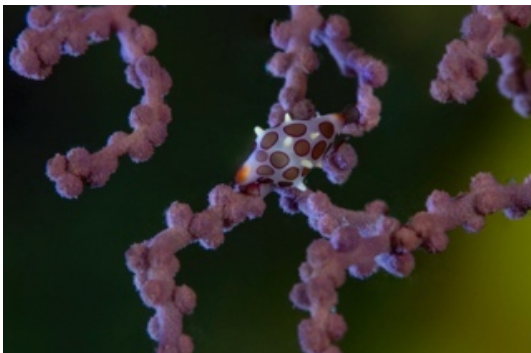


Figure 47: *Primovula rosewateri*



Figure 48: *Primovula roseomaculata*



Figure 49: *Cuspidovula bellica*



Figure 50: *Naviculavolva deflexa*



Figure 51: *Aclyvolva coarctata*

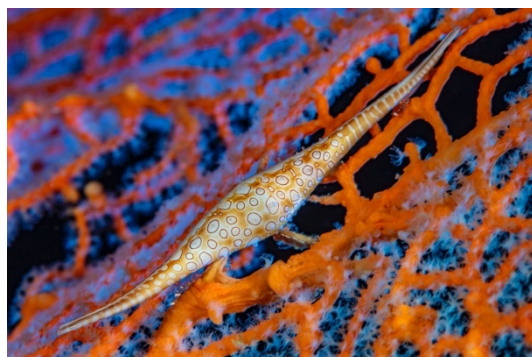


Figure 52: *Calcarovula longirostrata*

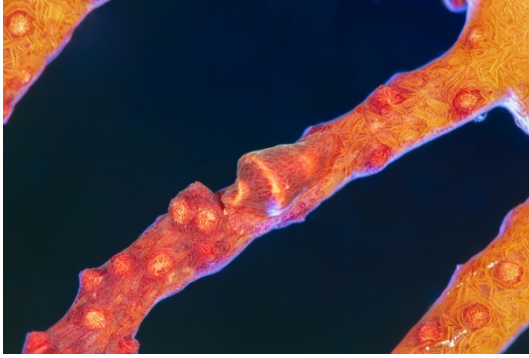


Figure 53: *Dentionvula mariae*



Figure 54: *Phenacovolva rosea*



Figure 55: *Habuprionovolva aenigma*



Figure 56: *Aclyvolvula coarctata*

3.6. GORGONIAN CORALS

The density of gorgonian corals varies with depth and station. With 11.6 colonies/m² (Deep Reef Side), Malayan Wreck_80 presents the highest mean colony density. Jessie Beazley North_9 is empty of gorgonian corals community with 0 colonies/m² (Reef Crest).

With 7.1 species/m², SharkAirport_73 (Deep Reef Side) harbors the highest mean diversity of gorgonian corals.

Generally, gorgonian corals are the most abundant and the most diverse in Mid Slope, Deep Reef Top and Deep Reef Side habitats.

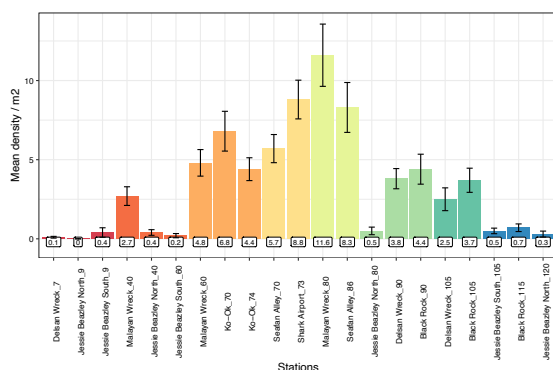


Figure 57: Mean colony density of gorgonian corals per stations

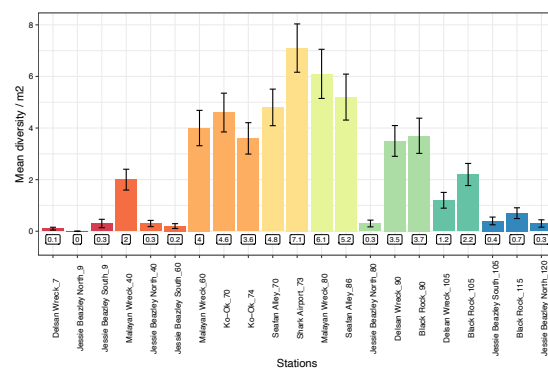


Figure 58: Mean colony species diversity of gorgonian corals per stations

Regarding the height of gorgonian corals colonies, the tallest colonies are measured in Mid Slope habitat with a maximum size of 216 cm and an average of 58.2 cm. Deep Reef Top shows colonies up

to 196 cm and average of 62.7 cm. Reef Crest habitat reveals the smallest average height with 24.2 cm. Deep Reef Side and Deep Wall also shows small height with 30.3 cm and 26.6 cm in average.



Figure 59: Gorgonian corals diversity and density at Shark Airport around 80 m on 01/07/2024



Figure 60: Gorgonian corals diversity and density at Shark Airport around 80 m on 01/07/2024

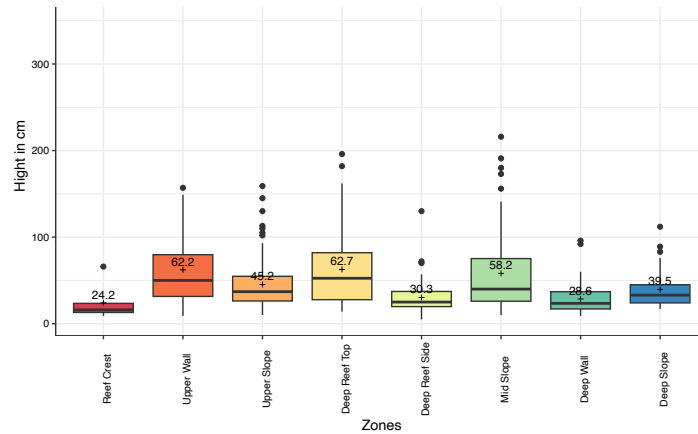


Figure 61: Mean colony height (cm) of gorgonian corals per station

Jessie Beazley North and Jessie Beazley South are the locations where necrosis on gorgonian coral colonies is the most frequently seen. In those locations, necrosis occurs between -40 and -120 m and affects almost 100 % of the colonies to a near 100 % rate. Black Rock_115 presents a mean necrosis affection per colony of 18.2 %. Other locations are less necrosed with rates between 0 and 10 %.

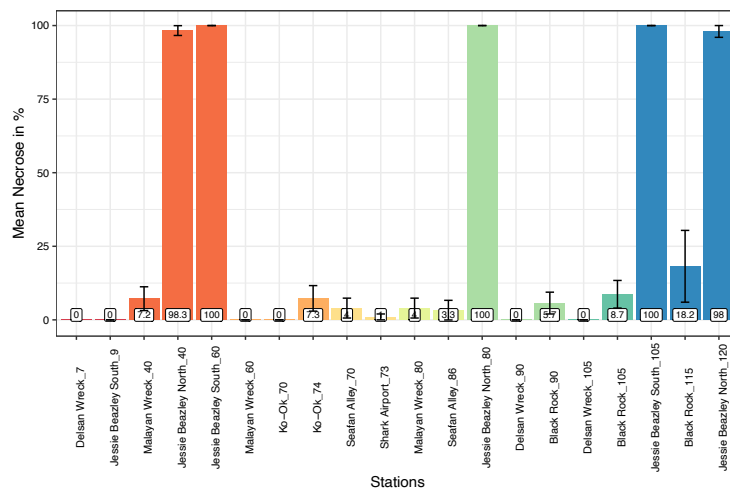
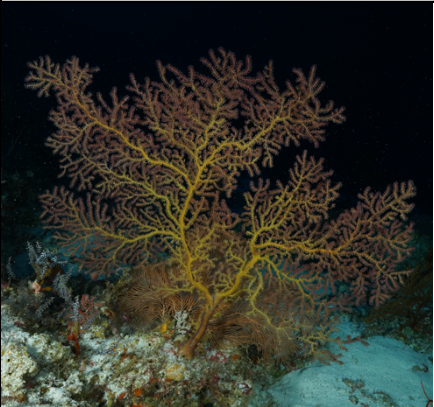
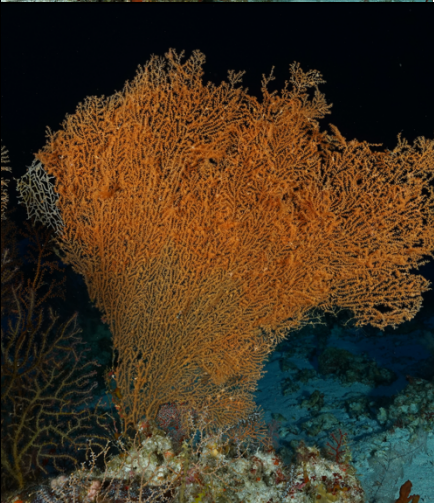
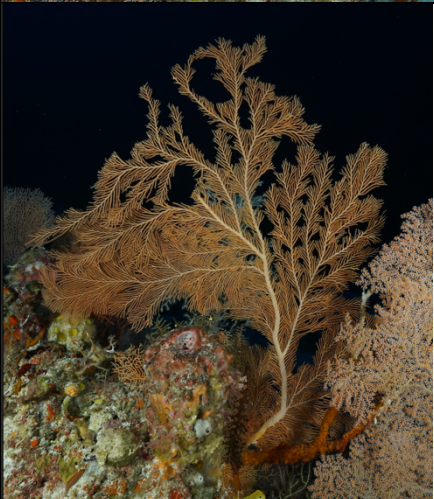
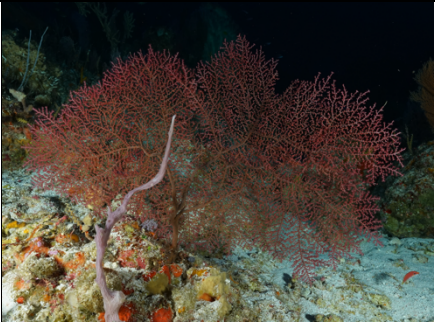
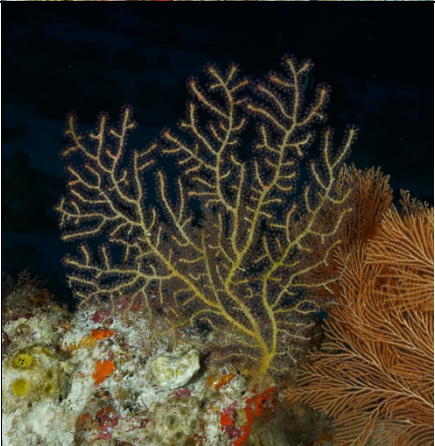






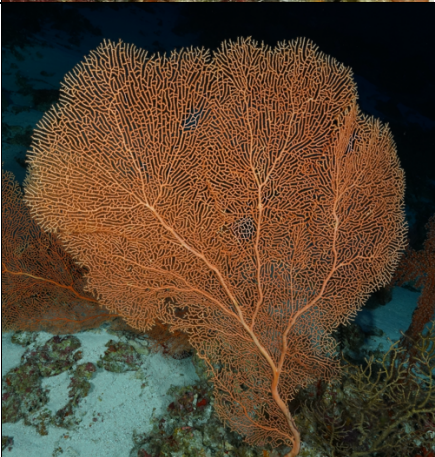
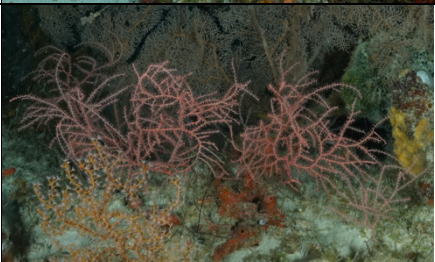
Figure 62: Mean necrose (in %) per colony of gorgonian corals per stations

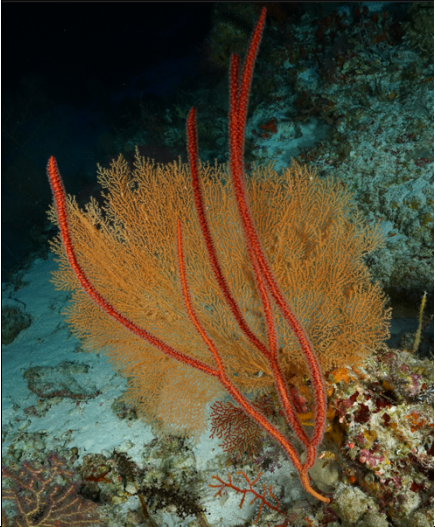

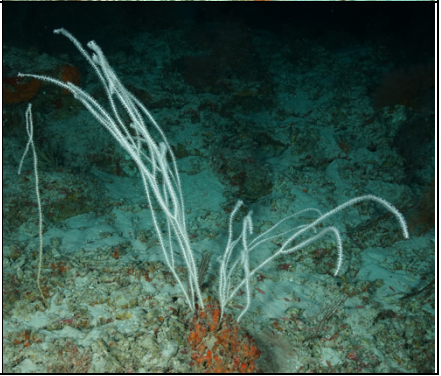
The following table illustrates the genus identification using photographs done by Dr. Sonia J. Rowley (Sánchez, et al., 2019). It reveals 17 genus (see Table 6).




Table 6: Gorgonian coral identification results by Dr. Sonia J. Wroley

Id	Order	Family	Genus	Photo
2a	Malacalcyonacea	Paramuriceidae	<i>Echinogorgia</i>	
3	Malacalcyonacea	Paramuriceidae	<i>Acanthogorgia</i>	
5	Scleralcyonacea	Primnoidae	<i>Callogorgia</i>	

6	Malacalcyonacea	Anthogorgiidae	<i>Muricella</i>	
7	Malacalcyonacea	Paramuriceidae	<i>Bebryce</i>	
9	Malacalcyonacea	Anthogorgiidae	<i>Anthogorgia</i>	
10	Scleralcyonacea	Ellisellidae	<i>Nicella</i>	

12	Malacalcyonacea	Paramuriceidae	<i>Paracis</i>	
14	Malacalcyonacea	Siphonogorgiidae	<i>Siphonogorgia</i>	
17	Malacalcyonacea	Subergorgiidae	<i>Annella</i>	
18	Scleralcyonacea	Ellisellidae	<i>Heliania</i>	

19	Scleralcyonacea	Ellisellidae	<i>Ellisella</i>	
20	Scleralcyonacea	Ellisellidae	<i>Dichotella</i>	
22	Scleralcyonacea	Ellisellidae	<i>Viminella</i>	

31	Scleralcyonacea	Ellisellidae	<i>Verrucella</i>	
34	Malacalcyonacea	Melithaeidae	<i>Melithaea</i>	
37	Malacalcyonacea	Astrogorgiidae	<i>Astrogorgia</i>	

4.DISCUSSION

4.1. AN INNOVATIVE AND EFFICIENT METHODOLOGY

We have deployed our technical diving experiences and safety procedures to operate 11 mesophotic dives to a maximum depth of -127 m cumulating 52 hours underwater per diver, thus 210 hours in total (4 divers). During those explorations, we deployed the innovative STEED methodology to collect data on four biotic communities among 30 stations (between -120 m and -9 m). At Jessie Beazley North, on the 06/07/24, we even managed to collect data at four stations (-120, -80, -40 and -9 m, including four biotic communities each) on a single dive (3h51min including decompression stops), considerably fastening mesophotic habitats exploration and description. Such an efficient methodology is essential for the study of remnant and pristine sites like TRNP where the diving window is short because the topography does not offer environments protected from strong weather at sea.

Robust ecological assessments are essential to understand the biodiversity and functions of mesophotic habitats as they remain vulnerable to anthropogenic pressures and environmental changes (Pinheiro & Hudson, 2020). However, collecting scientific data in mesophotic environments presents significant challenges due to logistical, technological, and environmental limitations. Methods such as photo-quadrats and video transects require specialized equipment, such as high-resolution cameras and artificial lighting, along with highly trained personnel to operate in challenging underwater conditions (Pyle, 2019). At depths greater than -40 m, technical diving or remotely operated vehicles (ROVs) are often necessary, increasing operational costs and complexity (Munar, et al., 2024). Short bottom times due to decompression limits, strong currents, and poor visibility can further reduce the quality and quantity of data collected, particularly in habitats with steep walls or sandy substrates where standard protocols are difficult to implement (Pizarro, et al., 2017). Realizing such data collection in one time using STEED allows to save time, reduce costs (compare to ROV or AUV deployment) (Pyle, 2000) and increase safety by reducing the number of technical dives.



Figure 63: Deployment of STEED methodology in Deep Slope habitat

4.2. STRUCTURE AND COMPOSITION OF BENTHIC COMMUNITIES

We described and illustrated TRNP biotic communities and habitats from the photic zone (-10 m) to the mesophotic zone (-120 m) for the first time.

The analysis of 420 photo-quadrats revealed significant differences in the composition of benthic communities depending on depth. Those differences create a strong gradient along the bathymetric profile with eight habitats in a short distance (less than 150 meters estimated).

Out of those eight habitats, we can identify four major benthic community groups:

- The Crest comprising Reef Crest habitat (-10 to -15 m), dominated by soft corals 31.2 % and hard corals 17.8 % for a total of 49% covered by cnidarians, indicating rich habitats that benefit from strong light exposure and currents (Zamani & Madduppa, 2011).

- The Vertical Walls that comprise Upper Wall (-15 to -60 m), Deep Reef Side (-75 to -90 m) and Deep Wall (-90 to -115 m). Walls are dominated by sponges with 50.4 %, 50.2 % and 58.4 % (and up to 73.7 % at Jessie Beazley South_60). This could be explained by the verticality of those habitats, limiting access to sun's ray for benthic organisms such as symbiosis cnidarians (Hard corals) and primary producers (algae) (Pyle, 2019). Sponges play a key role in nutrient cycling due to their filtration capacity (Bell, 2008). In addition to the results from the STEED methodology we observed numerous massive specimens of barrel sponges (*Xestospongia* sp) with size estimated to be up to 2 m. Those organisms are growing slowly (McGrath, et al., 2018), suggesting a long-term stability of these habitats with low disturbance and sedimentation.



Figure 64: Divers next to a large specimen of *Xestospongia* sp on Upper Wall habitat

- The Slopes including Upper Slope (-60 to -75 m), Mid Slope (-75 to -90 m) and Deep Slope (-115 to -130 m) are dominated by sand with a maximum coverage of 62.7 % in Deep Slope. Rubbles are also represented with 13.3 %, 14.9 % and 15.3 %. They demonstrate a low hard substrate cover, a characteristic of environments subjected to higher sedimentation (Bak, et al., 2005), probably due to their low inclination (estimated less than 45°). Yet crustose algae represent up to 10.8 % in Upper Slope and primary producers (Turf Algae) decrease with depth from 9.6 % in Upper Slope to 4.2 % in Deep Slope.

- Deep Reefs composed by the Deep Reef Top habitat are also dominated by abiotic categories with 27 % of sand, 13.2 % of rock and 13.3 % of rubbles due to their gentle slope inclination. Primary producers are still well represented with 9.5 % of turf algae and 9.2 % of crustose algae. This habitat

particularly suits gorgonians corals as they cover 11.8 % due to their environment characterized by low light and currents that facilitate suspension feeding (Bongiorni, et al., 2010).



Figure 65: Benthic communities composed of Gorgonian corals, sponges and zoanthids in the deep reef top habitat

4.3. ICHYTOFAUNA COMMUNITIES CHANGE WITH DEPTH

The Reef Crest displays the highest species diversity (56 species) and abundance (926.6 individuals), which can be explained by the structural complexity of these coral habitats that offer various niches for fish communities. Stations such as Jessie Beazley South_9 (181.7 individuals/transect) showed exceptional fish abundances, likely reflecting optimal environmental conditions and connectivity with other resource-rich habitats such as Cagayancillo (Deocadez, et al., 2008) (Holbrook, et al., 2000).



Figure 66: School of *Lutajnus rivulatus* and *Monotaxis grandoculis* over Reef Crest Habitat in Jessie Beazley South around 8 m

As diversity decreases with depth, it reaches a minimum in Deep Slope habitats with eight species, a trend well-documented in mesophotic and deep environments due to reduced primary productivity and structural complexity (Loya, et al., 2016).

Our results demonstrate a significant change in diversity and abundance of fish across habitats and depths. In accordance with literature, (Pyle, 2019) we observe a change in fish community around -60 m with a group of species that spreads along intermediate habitats (-60 to -115 m) considered as mesophotic (Upper Slope, Deep Reef Top, Deep Reef Side, Mid Slope and Deep Wall). This group

includes *Paracaesio sordida*, *Genicanthus bellus*, *Cephalopholis polleni* or *Apolemichthys trimaculatus*. The Upper Slope habitat (-60 to -75 m) is the second most diverse and abundant habitat with 36 species and 500.7 individuals, revealing the importance of the fish community in the upper mesophotic zone.

Results also seems to indicate a change of fish community around -115 m with a group of species only observed in lower mesophotic habitats. Those observations comprise *Aprion virescens* (Deep Slope), *Aphareus rutilans* (Deep Slope and Deep Wall) or *Cookeolus japonicus* (Deep Slope and Deep Wall), *Epinephelus tauvina* (Deep Slope).

Despite a low species diversity and abundance, Deep Slope habitat shows a relatively important biomass with an average of 24.4 g per m² due to the observations of large specimens (>1 m) from Carcharhinidae family (*Carcharhinus amblyrhynchos* and *Triaenodon obesus*). We also observed and illustrated specimens of large Carcharhinidae between 80 and 95 m such as *Rhincodon typus* and *Galeocerdo cuvier*.

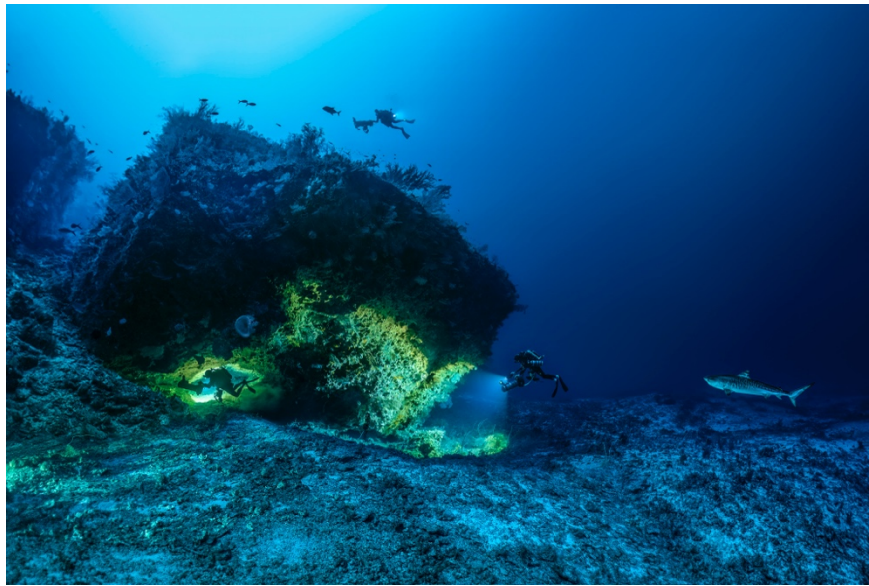


Figure 67: *Galeocerdo cuvier* and Deep Reef at Shark Airport around 95 m on 01/07/2024

The identification of 10 fish species never identified previously within TRNP between - 40 m and - 115 m (*Centropyge colini*, *Cephalopholis polleni*, *Cookeolus japonicus*, *Genicanthus bellus*, *Neoniphon aurolineatus*, *Pogonoperca punctatus*, *Xanthichthys caeruleolineatus*, *Hoplolatilus marcusi*, *Hoplolatilus randalli* and *Brotula multibarbata*) underlines the differences in fish community between the photic (over 700 fish species previously identified in TRNP (Alaba, et al., 2023)) and mesophotic zone. It also reveals the necessity to improve mesophotic habitat knowledge (Copus & Pyle, 2019).



Figure 68: Genicanthus bellus Male in Upper Slope habitat



Figure 69: Cephalopholis polleni in Upper wall habitat



Figure 70: Centropyge colini in Upper wall habitat

4.4. MOBILE INVERTEBRATES OCCURENCES

The low occurrence of mobile invertebrates (*Thromidia catalai*, *Gomphoria sp.*, and *Fromia sp.*) observed in this study could be either attributed to the sampling method less suited for these organisms, leading to an under-detection, or to the relative absence of invertebrates. Furthermore, their presence in Upper Wall and Mid Slope habitats aligns with heterogeneous benthic environments, where these species find refuge and food (Pratchett, et al., 2008). Despite the observation and illustration by Laurent Ballesta of one specimen of *Thelenota rubralineata* and one specimen of *Panulirus versicolor*, the STEED operator did not observe (visually) any mobile invertebrates during data collection, which tend to confirm the results from the STEED methodology.

The photographic collection of Ovulidae found by Laurent Ballesta allowed us to identify 11 species with a great variety of morphologies and colors. They are considered as parasite of their host as they behave as carnivorous grazers (Nocella, et al., 2024). This diversity represents 10% of the 120 species known in Philippines and 5 % of the 269 known worldwide (Zvonareva, et al., 2020).

4.5. GORGONIAN DEEP REEFS

According to our results, TRNP shelters 17 genus of gorgonian corals. Nonetheless, diversity and density show variability among habitats and depths with a maximum density reached at Malayan Wreck_80 (11.6 colonies/m²) and a maximum diversity of 7.1 specie/m² at Shark Airport_73. Tallest specimens have been measured using stereo videos within mesophotic habitats (216 cm in Mid Slope and 196 cm in Deep Reef Top).

Deep Reef Top and Deep Reef Side host the most diverse and dense gorgonians corals population (see Figure 71).

Even if those two habitats harbor close scores of diversities and density, their mean colony height differ. Indeed, Deep Reef Top present tall specimens with a mean height of 62.7 cm for only 30.3 cm for Deep Reef Side. We assume this difference to be in relation with the inclination of substrate (horizontal on Deep Reef Top and Vertical on Deep Reef Side) and the recruitment of different species with different morphological characteristics.

These preferences for depth and topography reflect the ecological preferences of gorgonians, which prefer mesophotic habitats with low light and moderate currents that facilitate planktonic feeding (Bongiorni, et al., 2010).



Figure 71: STEED deployment in Deep Reef Top habitat with gorgonian corals

Gorgonian corals population of the North atoll and South atoll do not suffer from necrosis. Indeed, six stations show null necrosis rates and a maximal necrosis rate of 8.7 % observed in Black Rock_105. This low global necrosis rate indicates low disturbance and environment stability as gorgonian corals are slow-growing organisms easily affected by physical and environmental stressors (Cupido, et al., 2009).

However, Jessie Beazley South & North are concerned by a near-systematic occurrence of necrosis affecting all colonies to a 100% rate, between -40 and -120 m (Figure 72). This suggests an acute environmental stress event in the past. It is not possible to estimate the date of the event from our observations.



Figure 72: Gorgonian corals affected by 100% necrosis in Jessie Beazley South, 120m

Gorgonians surfaces affected by necrosis are mostly colonized by parasite anemone *Nemanthus annamensis* (see Figure 73).



Figure 73: Gorgonian coral skeleton entirely colonized by *Nemanthus annamensis*

Given that fishing and diving activities never occur in TNRP, this necrosis may be due to multiple environmental factors, such as pathogenic infections, rising temperatures, or excessive sedimentation or even cold upwellings (Quintanilla, et al., 2019). According to Sonia J. Rowley, the last hypothesis is thought to concern TRNP, as cold upwellings could bring gorgonians to their coldest threshold.

4.6. HABITATS DIVERSITY ALONG DEPTH GRADIENT

Following our visual observations, band transects results have provided us the necessary information to describe eight distinct habitats stratified along a depth gradient from -10 to -120 m (see Figure 74 and Figure 75). As we did not observe Deep Reef on every site, we believe that they could be originated from landslide at the Reef Crest. Indeed, we witness cracks and large irregularity in the Reef Crest when we observed Deep Reef at depth suggesting that they could be the results of past gravity related geomorphological processes.

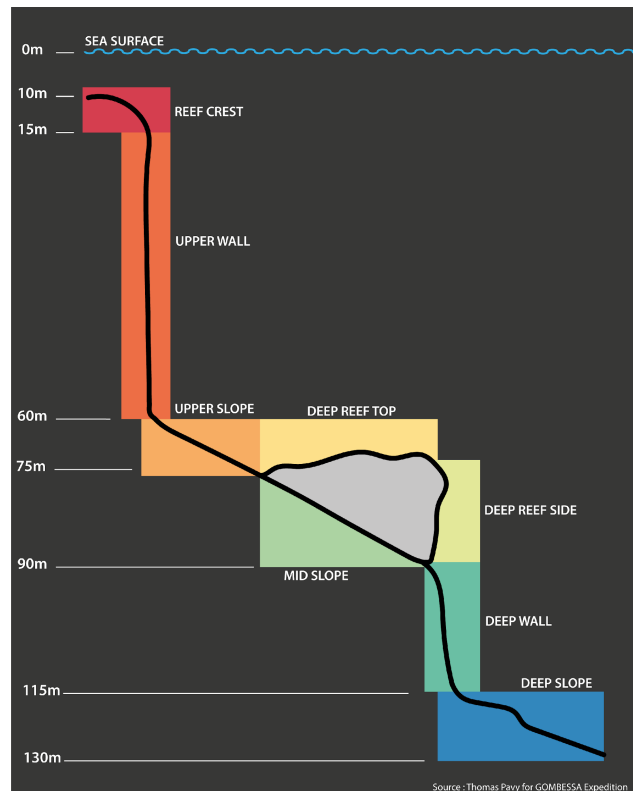


Figure 74: Vertical zonation of the different habitats observed along depth gradients in TRNP

Habitats descriptions could be synthetized as follows (illustrated in appendix 6.4 and 6.5):

- Reef Crest: Shallow reef dominated by hard and soft corals with high diversity and abundance of ichthyofauna. Gorgonian corals are small and scattered.
- Upper Wall: Dominated by sponges with few large gorgonian corals, mostly *Melithaea sp.*
- Upper Slope: Dominated by sand and some rocks with a dense and diverse gorgonian corals community. Abundance and diversity of ichthyofauna is important.
- Deep Reef Top: Dominated by rocks and rubbles with large specimens of gorgonian corals.
- Deep Reef Side: Dominated by sponges with small and diverse gorgonian corals with abundance in ichthyofauna.
- Mid Slope: Dominated by sand and some rocks with a dense and diverse gorgonian corals community. Abundance and diversity of ichthyofauna is important.
- Deep Wall: Dominated by sponges with low density and diversity of gorgonian corals. Abundance and diversity of ichthyofauna is limited.
- Deep Slope: Dominated by sand, rubbles and rocks with almost no gorgonian corals. Abundance and diversity of ichthyofauna is limited.

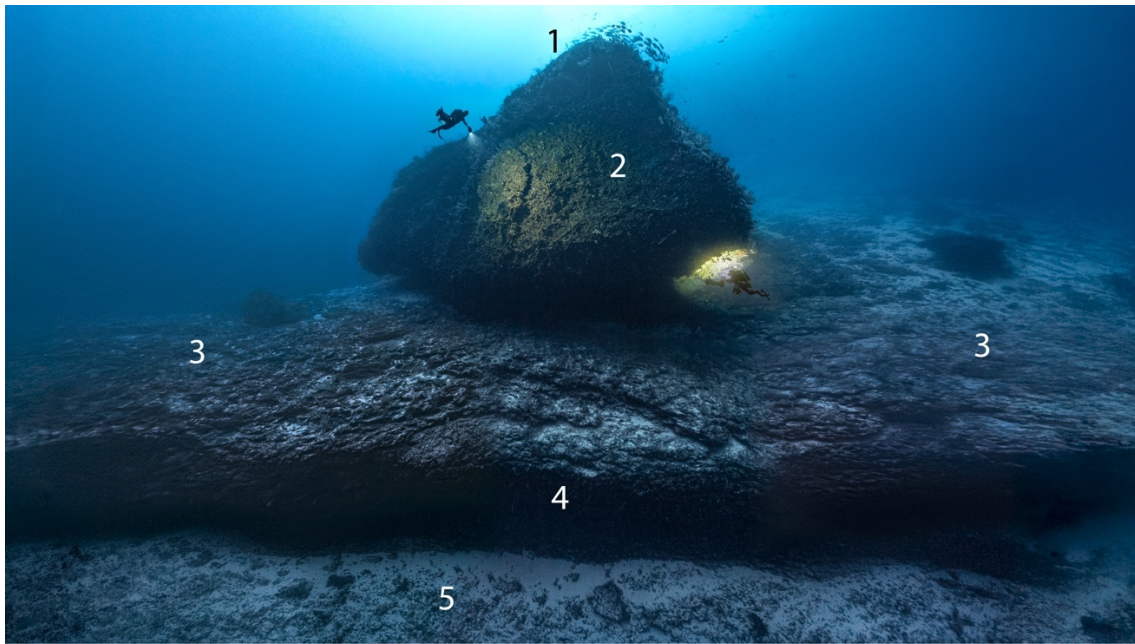


Figure 75: Divers next to a Deep Reef with Mid Slope habitat on side and Deep wall at bottom (1: Deep Reef Top, 2: Deep Reef Side, 3: Mid Slope, 4: Deep Wall, 5: Deep Slope)

Using this habitats description synthesis, we can correlate our understanding about the biotic communities' stratification (Ichthyofauna, Benthos, Gorgonian corals and mobile invertebrates) along the depth gradient in TRNP to emphasize key features.

Habitats with vertical inclination ($\approx 90^\circ$) such as walls are dominated by sponges and tend to be occupied by a less diverse and abundant ichthyofauna community compared to other habitats with limited inclination ($<45^\circ$). Indeed, habitats with inclination inferior to 45° and appropriate environmental conditions such as light and current are dominated by ecosystem engineers (Hastings, et al., 2007) and harbor diverse and abundant ichthyofauna communities. This finding is pertinent to a certain depth as diversity and abundance of all four biotic communities seem to drastically decrease deeper than -115 m, with a habitat dominated by sand 62.7 % and rubbles 15.3 %.

Given that, we identified two core zones along the vertical gradient:

- Photic core zone (-10 to -15 m), comprising the Reef Crest and exposed to important light, variable currents and low sedimentation. These conditions offer an appropriate environment to soft corals and hard corals to dominate (Schutter, et al., 2012) and host a diverse and abundant ichthyofauna community.

- Mesophotic core zone (-60 to -90 m), composed of Deep Reef Top and Deep Reef Side, Upper Slope and Mid Slope. This zone is exposed to low light, moderate currents and consistent sedimentation which correspond to adequate conditions for gorgonian corals to develop (Sánchez, et al., 2021) and engineer a habitat supporting life for a diverse and abundant ichthyofauna community.

In addition, it is important to mention, as explained in paragraph 4.3 and the literature (Lesser, et al., 2019), that we observe a change in fish community around -60 m with a group of species that spreads along intermediate habitats (-60 to -115 m) suggesting that Shallow core zone and Deep core zone host different ichthyofauna communities.



Figure 76: Deep reef habitat with ichthyofauna communities, black corals and gorgonian corals

5. CONCLUSION

Our expedition aimed to scientifically describe and illustrates mesophotic habitats (-60 to -150 m), species and depth gradient within Tubbataha Reefs Natural Park (Philippines), a world's iconic protected areas declared in 1988. To face the challenges related to technical diving and data collection at depth, we deployed an innovative methodology called STEED. The method is time and cost effective when aiming at doing a first biodiversity assessment in unexplored zones. During our dives, we collected data on four biotic communities (ichthyofauna, gorgonian corals, mobile invertebrates and benthos) among 30 stations (between -120 m and -9 m). The skills and expertise of Laurent Ballesta and Yanick Gentil allowed us to produced aesthetic and qualitative medias (underwater photographs and short film) used to communicate and raise awareness about TRNP mesophotic habitats and species.



Figure 77: Deployment of the STEED methodology with gorgonian corals communities in Deep Reef Top habitat

Our results concerning four biotic communities allow to describe eight distinct habitats in the Natural Park mesophotic zones, only recently surveyed on a geomorphological perspective using ROVs (Munar, et al., 2024). Habitats are stratified along a depth gradient from -10 to -120 m and listed as follow: Reef Crest (-10 to -15 m), Upper Wall (-15 to -60 m), Upper Slope (-60 to -75 m), Deep Reef Top (-60 to -75 m), Deep Reef Side (-75 to -90 m), Mid Slope (-75 to -90 m), Deep Wall (-90 to -115 m), Deep Slope (-115 to -130 m).

Overall, there is a clear biodiversity gradient from the surface to the mesophotic zone but a homogeneity between sites on the two atolls (North, South) and the reef (Jessie Beazley).

Habitats with vertical inclination ($\approx 90^\circ$) such as walls are dominated by sponges and tend to be occupied by a less diverse and abundant ichthyofauna community. Indeed, habitats with inclination inferior to 45° and appropriate environmental conditions such as light and current are dominated by ecosystem engineers (Hastings, et al., 2007) and harbor diverse and abundant ichthyofauna communities.

We identified two core zones along the vertical gradient:

- Photic core zone (-10 to -15 m), exposed to important light, variable currents and low sedimentation, offering appropriate conditions soft corals and hard corals to dominate (Schutter, et al., 2012) and host a diverse and abundant ichthyofauna community.
- Mesophotic core zone (-60 to -90 m), exposed to low light, moderate currents and consistent sedimentation which correspond to adequate conditions for gorgonian corals to develop (Sánchez, et

al., 2021). In this zone, further study on specific topics such as ichthyofauna or gorgonian corals including samplings could lead to deeper findings and understandings.

Therefore, the importance of mesophotic habitats in TRNP (Upper Wall, Deep Reef Side, Deep Wall, Upper Slope) and particularly the “Mesophotic core zone” should not be underestimated. Those depths (-60 to -150m), almost unexplored in the Sulu Sea, harbor unique biodiversity, including rare fish and gorgonian species (such as for example: *Centropyge colini*, *Pogonoperca punctatus*, *Xanthichthys caeruleolineatus* or *Genicanthus bellus*).

We encountered large specimens of sensitive and slow growing organisms such as sponges and gorgonian corals, indicating stability in the environmental conditions and low disturbance (Cupido, et al., 2009). However, we also described the occurrence of a mass mortality event on gorgonian corals in the past. Such phenomenon reminds us of the necessity of describing mesophotic communities to improve their understanding and set appropriate management strategies (Loya, et al., 2016) (Rocha, et al., 2018).

Moreover, Laurent Ballesta’s and Yanick Gentil’s skills and expertise allowed us to produce aesthetic and qualitative medias (underwater photographs and short film) used to communicate and raise awareness about TRNP mesophotic habitats and species.

This study, through innovative methodology and technical diving abilities, contributes to a better knowledge of TRNP’s mesophotic ecosystems typology and depth stratification. Collected data and results could also be used as references for future surveys in TRNP or in the coral triangle area.

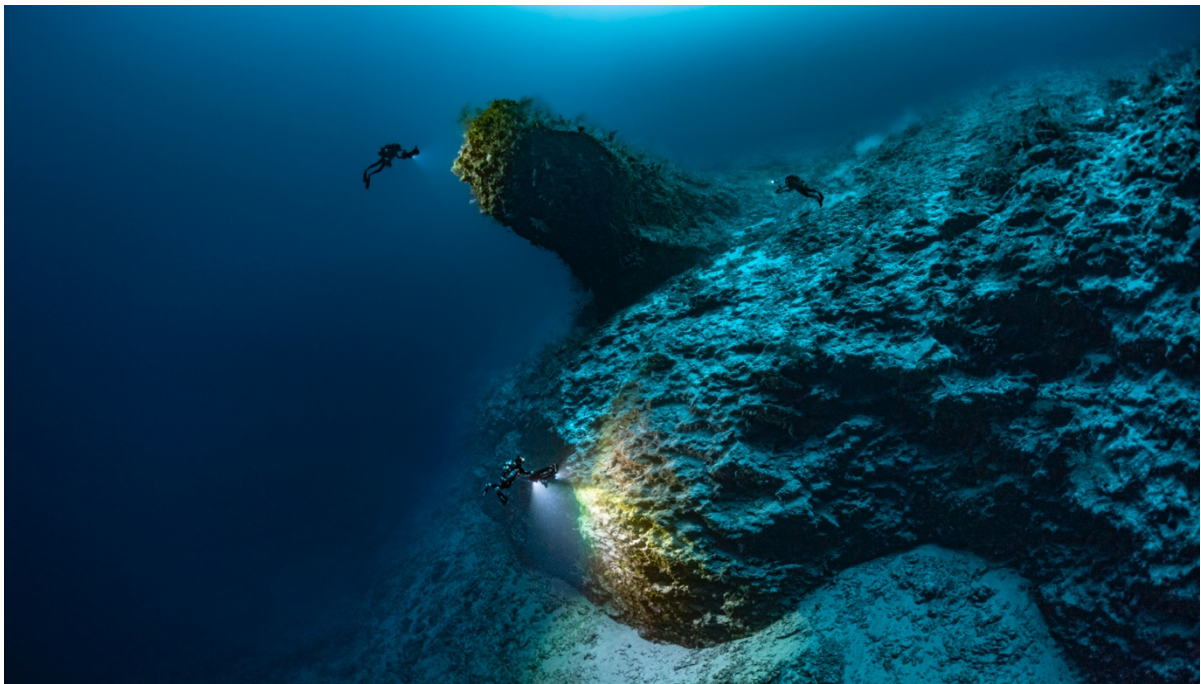


Figure 78: Example of Deep Reef over Deep wall habitat

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APPENDIX

6.1. ICHTHYOFAUNA SPECIES OBSERVED :

Species	Reef Crest	Upper Wall	Upper Slope	Deep Reef Top	Deep Reef Side	Mid Slope	Deep Wall	Deep Slope
<i>Abudefduf vaigiensis</i>	1	0	0	0	0	0	0	0
<i>Acanthurus japonicus</i>	1	0	0	0	0	0	0	0
<i>Acanthurus pyroferus</i>	1	0	0	0	0	0	0	0
<i>Acanthurus thompsoni</i>	1	1	1	0	0	0	0	0
<i>Aluterus scriptus</i>	0	0	1	0	0	0	0	0
<i>Aphareus furca</i>	0	0	0	1	0	0	0	0
<i>Aphareus rutilans</i>	0	0	0	0	0	0	1	1
<i>Apolemichthys trimaculatus</i>	0	1	1	1	0	1	0	0
<i>Aprion virescens</i>	0	0	0	0	0	0	0	1
<i>Arothron nigropunctatus</i>	0	1	0	0	1	1	0	0
<i>Balistapus undulatus</i>	1	1	1	0	0	0	0	0
<i>Balistoides conspicillum</i>	1	1	0	1	0	0	0	0
<i>Balistoides viridescens</i>	1	0	0	0	0	0	0	0
<i>Brotula multibarbata</i>	0	1	0	0	0	0	0	0
<i>Caesio lunaris</i>	1	0	0	0	0	0	0	0
<i>Caranx lugubris</i>	0	0	1	0	0	0	0	0
<i>Caranx melampygus</i>	1	1	1	0	0	0	1	0
<i>Carcharhinus amblyrhynchos</i>	0	0	1	0	1	1	0	1
<i>Centropyge bicolor</i>	0	1	0	0	0	0	0	0
<i>Centropyge colini</i>	0	0	0	0	1	0	0	0
<i>Centropyge vrolikii</i>	1	0	0	0	0	0	0	0
<i>Cephalopholis argus</i>	1	0	0	0	0	0	0	0
<i>Cephalopholis miniata</i>	1	1	0	0	0	0	0	0
<i>Cephalopholis polleni</i>	0	1	1	1	1	1	1	0
<i>Cephalopholis sexmaculata</i>	1	0	1	0	0	1	0	0
<i>Cephalopholis urodeta</i>	1	0	0	0	0	0	0	0
<i>Cetoscarus bicolor</i>	1	0	0	0	0	0	0	0
<i>Chaetodon adiergastos</i>	1	0	0	0	0	0	0	0

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Species	Reef Crest	Upper Wall	Upper Slope	Deep Reef Top	Deep Reef Side	Mid Slope	Deep Wall	Deep Slope
<i>Chaetodon baronessa</i>	1	0	0	0	0	0	0	0
<i>Chaetodon kleinii</i>	1	0	0	0	0	0	0	0
<i>Chaetodon lunula</i>	1	0	0	0	0	0	0	0
<i>Chaetodon melannottus</i>	1	0	0	0	0	0	0	0
<i>Chaetodon ocellicaudus</i>	1	0	0	0	0	0	0	0
<i>Chaetodon speculum</i>	1	0	0	0	0	0	0	0
<i>Chaetodon triangulum</i>	1	0	0	0	0	0	0	0
<i>Chaetodon ulietensis</i>	0	1	0	0	0	0	0	0
<i>Chaetodon vagabundus</i>	1	0	0	0	0	0	0	0
<i>Chaetodon wiebeli</i>	1	0	0	0	0	0	0	0
<i>Chlorurus bleekeri</i>	1	0	0	0	0	0	0	0
<i>Chlorurus microrhinos</i>	1	0	0	0	0	0	0	0
<i>Cookeolus japonicus</i>	0	0	0	0	0	1	0	1
<i>Cromileptes altivelis</i>	0	0	1	0	0	0	0	0
<i>Diagramma pictum</i>	0	0	0	0	0	0	1	0
<i>Epinephelus lanceolatus</i>	0	0	1	0	0	0	0	0
<i>Epinephelus maculatus</i>	0	0	1	0	0	1	0	0
<i>Epinephelus tauvina</i>	0	0	0	0	0	0	0	1
<i>Forcipiger flavissimus</i>	0	0	1	0	0	0	0	0
<i>Galeocerdo cuvier</i>	0	0	0	0	0	1	0	0
<i>Genicanthus bellus</i>	0	1	1	1	1	1	1	1
<i>Genicanthus melanospilos</i>	0	0	1	0	0	0	0	0
<i>Gracila albomarginata</i>	0	1	1	1	0	1	0	0
<i>Gymnosarda unicolor</i>	0	0	1	0	0	0	0	0
<i>Gymnothorax flavimarginatus</i>	0	0	0	0	1	0	0	0
<i>Hemitaenichthys polylepis</i>	1	0	0	0	0	0	0	0
<i>Heniochus acuminatus</i>	0	1	1	1	1	0	1	0
<i>Heniochus diphreutes</i>	1	0	0	0	0	0	0	0
<i>Heniochus singularis</i>	1	0	0	0	0	0	0	0
<i>Hoplolatilus marcosi</i>	0	0	0	0	0	1	0	0
<i>Hoplolatilus randalli</i>	0	0	0	0	0	1	0	0

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Species	Reef Crest	Upper Wall	Upper Slope	Deep Reef Top	Deep Reef Side	Mid Slope	Deep Wall	Deep Slope
<i>Kyphosus vaigiensis</i>	1	0	0	0	0	0	0	0
<i>Lutjanus bohar</i>	1	1	1	0	1	1	0	0
<i>Lutjanus decussatus</i>	0	1	0	0	0	0	0	0
<i>Lutjanus gibbus</i>	1	0	1	0	0	0	0	0
<i>Lutjanus kasmira</i>	0	0	0	0	0	1	0	0
<i>Lutjanus monostigma</i>	1	0	0	0	0	0	0	0
<i>Lutjanus rufolineatus</i>	0	0	0	0	0	1	1	0
<i>Macolor macularis</i>	0	1	1	1	0	0	0	0
<i>Macolor niger</i>	1	0	0	0	0	0	0	0
<i>Melichthys niger</i>	1	0	0	0	0	0	0	0
<i>Melichthys vidua</i>	1	1	0	0	0	0	0	0
<i>Monotaxis grandoculis</i>	1	0	1	0	0	1	0	0
<i>Naso brevirostris</i>	1	0	1	0	1	0	0	0
<i>Naso hexacanthus</i>	0	1	1	0	1	1	0	0
<i>Naso lituratus</i>	1	0	0	0	0	0	0	0
<i>Naso unicornis</i>	1	0	0	0	0	0	0	0
<i>Naso vlamingii</i>	1	0	0	0	0	1	0	0
<i>Neoniphon aurolineatus</i>	0	0	1	0	0	1	0	0
<i>Odonus niger</i>	1	1	0	0	0	0	0	0
<i>Paracaesio sordida</i>	0	0	0	1	1	1	1	0
<i>Parupeneus multifasciatus</i>	0	0	1	0	0	0	0	0
<i>Plectorhinchus diagrammus</i>	0	0	0	0	1	0	0	0
<i>Plectorhinchus flavomaculatus</i>	0	0	0	0	1	0	0	0
<i>Pogonoperca punctatus</i>	0	0	0	0	0	0	0	1
<i>Pomacanthus imperator</i>	0	1	0	0	1	0	0	0
<i>Pomacanthus sexstriatus</i>	0	0	0	1	0	0	0	0
<i>Pterocaesio tile</i>	1	0	0	0	0	0	0	0
<i>Pygoplites diacanthus</i>	1	1	1	1	1	0	0	0
<i>Rhincodon typus</i>	0	0	0	0	0	1	0	0
<i>Sargocentron caudimaculatum</i>	1	1	1	0	0	0	0	0
<i>Sargocentron spiniferum</i>	1	1	1	0	1	0	0	0

Species	Reef Crest	Upper Wall	Upper Slope	Deep Reef Top	Deep Reef Side	Mid Slope	Deep Wall	Deep Slope
<i>Scarus tricolor</i>	1	0	0	0	0	0	0	0
<i>Sufflamen bursa</i>	0	1	1	1	0	0	0	0
<i>Triaenodon obesus</i>	0	0	0	1	1	0	0	1
<i>Variola albimarginata</i>	0	0	1	0	0	1	0	0
<i>Xanthichthys auromarginatus</i>	0	1	1	0	0	1	0	0
<i>Xanthichthys caeruleolineatus</i>	0	0	1	0	0	0	0	0
<i>Zanclus cornutus</i>	1	1	1	1	1	0	0	0
<i>Zebrasoma scopas</i>	1	0	0	0	0	0	0	0
<i>Zebrasoma veliferum</i>	1	0	0	0	0	0	0	0

6.2. MOBILE INVERTEBRATES SPECIES OBSERVED :

6.2.1. ASTEROIDEA:

- *Gomophia sp*
- *Thromidia catalai*
- *Fromia sp*

6.2.2. OVULIDAE:

- *Pellasmia sp*
- *Dentiovula dorsuosa*
- *Primovula rosewateri*
- *Primovula roseomaculata*
- *Cuspidovula bellica*
- *Naviculavolva deflexa*
- *Calcarovula longirostrata*
- *Dentiovula mariae*
- *Phenacovolva rosea*
- *Habuprionovolva aenigma*
- *Aclyvolva coarctata*

6.2.3. STICHOPODIDAE:

- *Thelenota rubralineata*





6.2.4. PALINURIDAE:





- *Panulirus versicolor*

6.3. GORGONIANS CORALS GENUS OBSERVED :





- *Echinogorgia*
- *Acanthogorgia*
- *Callogorgia*
- *Muricella*
- *Bebryce*
- *Anthogorgia*
- *Nicella*
- *Paracis*
- *Astrogorgia*
- *Siphonogorgia*
- *Annella*
- *Heliania*
- *Ellisella*
- *Dichotella*
- *Viminella*
- *Verrucella*
- *Melithaea*





6.4. HABITATS ILLUSTRATIONS

Habitats	illustrations
Reef Crest at Jessie Beazley South around 10 m	
Upper Wall at Black Rock around 40 m	
Upper Slope at Malayan Wreck around 65 m	
Deep Reef Top at Shark Airport around 70 m	

<p>Deep Reef Side at Delsan Wreck around 85 m</p>	
<p>Mid Slope at Delsan Wreck around 90 m</p>	
<p>Deep Wall at Delsan Wreck around 95 m</p>	
<p>Deep Slope at Black Rock around 110 m</p>	

6.5. DEEP REEF HABITAT ILLUSTRATIONS

Habitats	illustrations
Deep Reef at Shark Airport around 95 m	
Deep Reef at Shark Airport around 95 m	
Deep Reef at Shark Airport around 95 m	
Deep Reef and Deep Wall at Black Rock around 100 m	

<p>Deep Reef at Ko-Ok around 85 m</p>	
<p>Deep Reef at Ko-Ok around 85 m</p>	
<p>Deep Reef Top at Shark Airport around 80 m</p>	
<p>Deep Reef at Black Rock around 80 m</p>	



TUBBATAHA REEFS MESOPHOTIC ZONE EXPLORATION AND DESCRIPTION

30/06/2024 - 13/07/2024

PARTNERS :



SUEX



AQUALUNG

