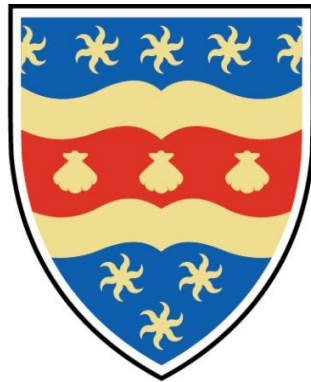


Seagrass-reef ecosystem connectivity of fish and
invertebrate communities in Zamboanguita, Philippines



**UNIVERSITY OF
PLYMOUTH**



Naomi Westlake

BSc. Marine Biology 2020/21

Project Advisor: Dr Stacey DeAmicis

Seagrass-reef ecosystem connectivity of fish and invertebrate communities in Zamboanguita, Philippines

Westlake, Naomi

School of Science and Engineering, University of Plymouth, Devon, PL4 8AA

naomi.westlake@students.plymouth.ac.uk

ABSTRACT

Seagrass meadows are important coastal marine ecosystems that are frequently found in close proximity to coral reefs, and temporarily play host to a wide range of reef species for many reasons. Seagrass populations are declining globally, and these losses pose a great risk to areas such as South-East Asia where the livelihoods of people are heavily dependent on seagrass-reef systems. Hence, seagrass ecosystem management within these regions is extremely important. The aim of this study was to gain a greater understanding of seagrass-reef ecosystem connectivity within the Indo-Pacific, and to use findings to inform future marine reserve planning in the region. Visual census belt surveys (n = 140) were conducted within the Seagrass, Interface and Reef zones of three Marine Protected Areas (MPAs) in Zamboanguita, Philippines, with fish and invertebrate communities compared across zones. Species diversity trends varied across sites, as did fish abundance, fish biomass, and fish community composition trends. For Malatipay and Lutoban South MPAs, fish assemblages did not differ across zones, and Seagrass and Reef zones shared approximately 20 % of species, indicating high ecosystem connectivity. Presumed habitat uses by fish at these sites include foraging and nursery grounds, as well as potential breeding by a pair of longface emperors. In contrast, Dalakit MPA fish assemblages were significantly different in each zone. Ecosystem connectivity was lower at this site, with Seagrass and Reef zones only sharing 8 % of species. These differences are likely due to dissimilarity in site configuration of Dalakit MPA compared with the other two sites, namely the lack of an Interface zone and small reef area. Though invertebrate community composition varied across sites, connectivity trends were similar for all three MPAs: invertebrate assemblages differed across zones, with differences likely driven by ecological niche requirements. Though ecosystem connectivity for invertebrates was low on an 'individual' level, Seagrass and Reef zones still shared 17 % to 30 % of species, and thus connectivity likely still occurs as gene flow across zones. Based on these findings, I recommend that seagrass meadows be incorporated into additional MPAs within Negros Oriental, Philippines; by protecting commercial fish species during important seagrass-reef migrations, distinct invertebrate communities within the seagrass and genetic connectivity, this will allow for both greater food security, and greater conservation of overall diversity and ecosystem health within the region.

KEY WORDS: Connectivity, Seagrass Ecology, Reef Ecology, Marine Protected Area, Fisheries, Indo-Pacific

1. INTRODUCTION

Ecological connectivity is broadly defined as the flow of organisms and ecological processes across landscapes (Taylor et al. 1993), and can exist across both terrestrial and aquatic realms. Within the marine environment, water movements facilitate the passive exchange of nutrients, chemical pollutants, pathogens and sediments amongst components of the seascape (Grober-Dunsmore et al. 2009). Furthermore, organismal connectivity occurs through the movement of propagules, juveniles or adults across habitat patches (Dibacco et al. 2006); depending on the species and its life history stage, this movement may occur as dispersal, active migration or standard daily movements, and can range from local to global scales. For instance, Shanks (2009) found that marine propagules can disperse from anywhere between 0.5 m and 500 km, whereas one female humpback whale has been known to migrate over 9800 km between breeding grounds (Stevick et al. 2011). Organismal connectivity can exist both between multiple ecosystems of the same type, such as hydrothermal vents (Vrijenhoek 2010), and across ecosystems of different types, such as seagrass beds and coral reefs (Verweij et al. 2008) (hereafter referred to as 'ecosystem connectivity'). Due to our broad understanding of marine ecosystem connectivity, approaches towards monitoring this phenomenon are varied, and continue to evolve. Methods include (but are not limited to) molecular analysis of muscle and bone tissues (Verweij et al. 2008), genetic analysis to identify gene flow (Toonen et al. 2011, Vrijenhoek 2010), satellite tagging of larger marine organisms (eg, sharks; Duffy et al. 2012, manta rays; Armstrong et al. 2020), and observational surveys of distribution and abundance (Henriques & Almada 1998).

Seagrass beds are becoming increasingly recognised for their connections to coral reef ecosystems. As the only truly marine angiosperms, seagrasses form vast underwater meadows, and are known to occur in all coastal regions of the world except Antarctica (Hemminga & Duarte 2009, p.6). Alongside their innate biodiversity value, seagrasses provide a wide range of valuable ecosystem services on both local and global scales. Ecosystem services include high primary productivity (around $1012 \text{ g DW m}^{-2} \text{ yr}^{-1}$; Duarte & Chiscano 1999), improved water quality (Hemminga & Duarte 2009, p. 250), coastal protection (Terrados & Borum 2004), nutrient cycling (Hemminga & Duarte 2009, p. 251-253) and carbon sequestration (around $0.08 \text{ Pg C yr}^{-1}$; Duarte & Cebrián 1996). Furthermore, seagrass meadows provide a complex habitat for a diverse range of biota, found both on and amongst their leaves, including diatoms (Sullivan 1979), cyanobacteria (Hamisi et al. 2004), epiphytic algae (Bologna and Heck 1999), and epifauna (Orth et al. 1984, Virnstein et al. 1984, Doropoulos et al. 2009). Though seagrass meadows alone are important marine habitats, they are often found in near coral reefs in the tropics and, through ecosystem connectivity, frequently become part of a more complex system within coastal zones (Short et al. 2011). In fact, where a seagrass meadow directly neighbours a coral reef, it can be argued that an 'ecotone' arises, rather than a simple boundary: the concept of an ecotone assumes an ecologically distinct area with properties that do not exist in either of the adjacent ecosystems, and a community that is commonly characteristic of, and sometimes restricted to, the ecotone (Odum 1953). Hence, it is now well-known that in addition to supporting many resident species, seagrasses near to coral reefs often temporarily play host to a wide range of reef species for many different reasons. Many species forage for prey in seagrass meadows. While this is predominantly applicable to fish species, other taxa such as tiger sharks (Heithaus et al. 2002) and adults of the endangered green sea turtle (Arthur et al. 2008) are known to frequent seagrasses to hunt. It is also common for many fish species to show diel migrations, with different species foraging over seagrass beds at different times (Weinstein & Heck 1979, Robblee &

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Zieman 1984, Hitt et al. 2011). In addition, reef species frequently use seagrass meadows as a nursery ground, exhibiting ontogenetic habitat shifts (Brewer et al. 1995, Gillanders et al. 2003, Unsworth et al. 2008, Honda et al. 2013, Unsworth et al. 2014). By providing refuge to commercial species during their vulnerable juvenile life stages, seagrass meadows support global fisheries and local food security (Unsworth et al. 2014, 2019). Seagrass beds are also often used by reef species as a spawning site: species such as the ring cowrie (*Monetaria annulus*), the blue-ribbon wrasse (*Stethojulis trilineata*) and the common cuttlefish (*Sepia officinalis*) are known to deposit their eggs on seagrass blades (Bloor et al. 2013, Jiang et al. 2020), though this is not particularly widespread among reef species. It is important to note that services and functions vary across the 72 recognised species of seagrass (Short et al. 2011), and with meadow composition. For instance, meadows that offer greater structural complexity tend to support communities of high species abundance and diversity (DeAmicis & Foggo 2015). Highly complex meadows have also been found to support organisms of many sizes, whereas meadows of moderate complexity supported a higher abundance of smaller organisms and fewer larger organisms (Jinks et al. 2019). Many of the seagrass functions that are linked to reef species either directly or indirectly benefit local human populations, but are perhaps not as widely recognised or understood as their large-scale ecosystem services.

Though seagrasses are an extremely valuable marine ecosystem, their importance is frequently overlooked, and increasingly under threat. Seagrasses are disappearing worldwide: 65 % have already been lost across the globe (Lotze et al. 2006), and seagrasses continue to decline at a rate of approximately 7 % per year (Waycott et al. 2009). While seagrass losses are occasionally the result of natural disturbances such as earthquakes (Marsden et al. 2016), cyclones (Poiner et al. 1989), flooding (Preen et al. 1995), disease (Short et al. 1986) and herbivore activity (Zimmerman et al. 1996), declines are usually caused by human activities. Perhaps the most common anthropogenic cause of seagrass mortality is eutrophication, which has been documented in a wealth of studies from across the globe (see Burkholder et al. 2007 for review): as nutrient input increases, shading by phytoplankton and epiphyte growth increase, both of which result in a reduction in the amount of light reaching seagrasses (Ralph et al. 2007). Changes in land use, such as deforestation, also lead to high soil erosion rates and an increase in sediment transport by rivers; this increase in silt export subsequently causes deterioration of the underwater light climate for seagrasses, and can often result in the burial of seagrass plants (Hemminga & Duarte 2000, p.266). Though siltation effects on seagrass are particularly acute in South-East Asia (Fortes 1988, Terrados et al. 1998, Tanaka et al. 2014), they have been documented elsewhere across the globe (Talbot et al. 1990, Manzanera et al. 1998, Krupp et al. 2009). Other anthropogenic threats to seagrasses include coastal engineering (De Jonge & De Jong 1992, Holon et al. 2015) and mechanical damage from boating or fishing activities (Walker et al. 1989, Erftemeijer & Lewis 2006), though these tend to result in fairly regional declines. In addition to these known causes of decline, it has also been suggested that invasive species may pose a threat to seagrass survival; DeAmicis (2012) found that levels of defensive polyphenolic compounds were lower in *Zostera marina* plants growing in close conjunction with the invasive macroalga *Sargassum muticum*, potentially increasing vulnerability. Regardless of the cause, seagrass losses consequently mean the loss of ecosystem services that they provide, and their connectivity to coral reef ecosystems. Hence, seagrass losses pose a great risk to areas where the livelihoods of many people heavily depend on the ecosystem services and functions provided by coral reefs, and by default, seagrasses.

This is the case in South-East Asia, where millions of people are employed directly in marine capture fisheries, and millions more earn their living by building boats, distributing fish, or supplying goods

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

and services needed by fishers (Bailey & Pomeroy 1996). Unfortunately, seagrass populations are under increasing threat in South-East Asia, as human population growth increases the density of already heavily populated coastal areas (Small & Nicholls 2003, Gerland et al. 2014). As this is predicted to continue, food demand will inherently increase, placing higher anthropogenic pressure on seagrass populations within the region. Prospective climate change in South-East Asia is also expected to have negative consequences for seagrasses. Precipitation levels are predicted to increase within the region which, through run-off, is expected to increase eutrophication (Sinha et al. 2017), a well-known cause of seagrass mortality. Additionally, the frequency and intensity of natural disasters in South-East Asia is increasing (Asian Development Bank 2013), and as many of these future disturbances will undoubtedly cause damage to coastal regions, this also poses a threat to seagrasses. Combined with prospective human population growth, the increased need for hard coastal protection against natural disasters in South-East Asia will likely increase coastal artificialisation within the region (Firth et al. 2013), yet again to the detriment to seagrass populations. With this combination of particularly vulnerable seagrass populations and the amplified threat that seagrass losses pose to livelihoods in South-East Asia, seagrass ecosystem management within the region is extremely important.

Although many studies have attempted to address connectivity that exists between seagrass and reef ecosystems, results are largely region-specific (Ogden & Zieman 1977, Parrish 1989, Birkeland & Amesbury 1987, Van der Velde et al. 1992, Gillanders et al. 2003, Unsworth et al. 2008), which restricts global applicability, and highlights the need to consider ecosystem connectivity on a site-by-site basis. Furthermore, with the increasing threat that climate change and human population growth pose to seagrass populations within South-East Asia, and thus to their associated connectivity, there is a growing need to understand how connectivity may be altered or lost in this region, and to protect it where possible. Consequently, the aim of this study was to gain a greater understanding of seagrass-reef ecosystem connectivity within the Indo-Pacific, and to use my findings to inform future marine reserve planning in the region. In order to achieve this, volunteers from Marine Conservation Philippines conducted underwater belt surveys within Seagrass, Interface (where applicable) and Reef zones for three MPA sites situated off the coast of Zamboanguita, Philippines. With each MPA considered as a distinct ecological unit, fish and invertebrate communities were compared across zones, and any trends in ecosystem connectivity were identified and discussed. Based on previous findings that species diversity is commonly highest at the ecotone between juxtaposed habitats due to a 'mixing of biotas' (Denys & Tschardt 2002, Magura 2002, Kark 2013), it was hypothesised that fish and invertebrate species diversity would be highest in the Interface zone, however, for one site (Dalakit MPA) where an Interface zone does not exist, species diversity was predicted to be highest in the Reef zone. Furthermore, fish abundance and fish biomass were predicted to be highest in the Reef zones across all MPA sites. Based on the abundant literature on seagrass-associated fishes (discussed above) and due to their high mobility, it was hypothesised that within each MPA, fish ecosystem connectivity would be high, and therefore fish communities would not differ across zone. In contrast, due to their limited mobility and variable niche requirements, invertebrate communities within each MPA were predicted to have lower ecosystem connectivity than fish communities, and were therefore predicted to differ across zone. Finally, it was hypothesised that neighbouring zones would share higher percentages of species than nonadjacent zones (i.e. Seagrass and Reef), and this trend was predicted to be stronger for fish communities, again based on their high mobility.

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

2. METHODS & MATERIALS

2.1 Study Sites

Dive surveys were conducted within three Marine Protected Areas (MPAs) off the south-east coast of Negros Oriental, Philippines: Malatapay MPA, Lutoban South MPA and Dalakit MPA (see Appendix A for the coordinates of each MPA; Figure 1). All three MPAs are locally managed by the Zamboanguita municipal government unit, and are regularly monitored by the non-profit non-governmental organisation Marine Conservation Philippines (MCP). Each MPA consists of both coral reef and seagrass zones, but these differ in area and depth. Ten species of seagrass are known to occur across the three MPAs (Appendix B), though these vary in abundance depending on the site.

Waters within the region have a tidal range of approximately 1.80 m (Tide Forecast 2021), and temperatures range from 25 °C to 32 °C throughout the year. All surveys were conducted between 1st December 2019 and 29th February 2020; this aligns with the North-East monsoon (or 'Amihan') season in the Philippines, which is characterised by cooler atmospheric and water temperatures, and little to no rainfall in the Western and Central Visayas (including Negros Oriental).

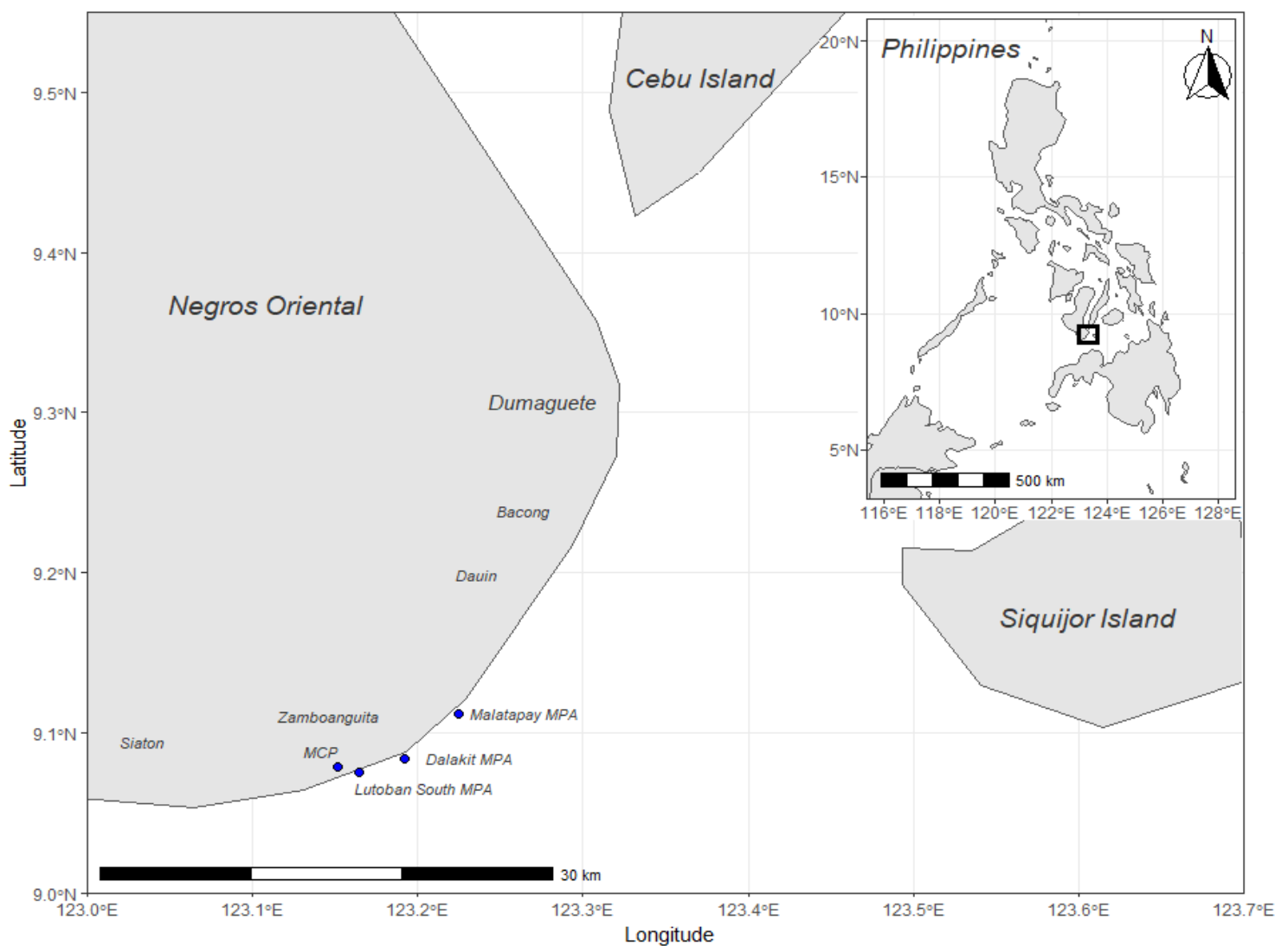


Figure 1: Location of Marine Conservation Philippines, and the approximate locations of the three MPA sites off the south-east coast of Negros Oriental, Philippines.

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

2.1.1 Malatapay MPA

‘Maluay’ Malatapay MPA has been demarcated since 2018, but is not yet an accredited MPA. It covers 8 ha, and consists of a dense coral reef with a very large plateau at 5 m depth. This plateau contains wide patches of seagrass beds, with *Cymodocea rotundata*, *Syringodium isoetifolium*, and *Thalassia hemprichii* occurring in highest abundance, and reef areas primarily composed of hard corals, algae, and sponges. The reef then forms a steep slope from 9 m to 16 m depth, which consists mainly of hard corals, sponges and rubble. Within Malatapay MPA, the seagrass zone is found closer to the shoreline than the reef zone, and the two zones neighbour one another, allowing for the existence of an ‘interface’ zone between them.

Though the site is protected from strong currents, it experiences high pressure from coastal activities, which include a large weekly cattle market and intense daily boat traffic (primarily tourism trips to Apo Island), both of which result in anchoring and pollution, including frequent oil leaks. In addition, there is a river mouth north of the market area that brings sediment and nutrient loads into the surrounding areas, which subsequently travel south with the currents towards the MPA. Further direct damage from boating has been minimised by the recent establishment and demarcation of Malatapay MPA, as it has forced boat traffic to relocate parking to the sandy area south of the MPA.

2.1.2 Lutoban South MPA

Lutoban ‘Gac-Ang’ MPA was established in 2000, and covers 24 ha. Similar to Malatapay MPA, it also consists of a dense coral reef with a very large plateau at 5 m depth. Once again, this plateau is occupied by wide patches of seagrass, though *Enhalus acoroides*, *Halophila spp.*, *Syringodium isoetifolium* and *Thalassia hemprichii* occur in the highest abundances at this site, and the plateau also contains reef areas that are primarily composed of hard corals, algae, and sponges. Much like that of Malatapay MPA, the reef at Lutoban South also forms a steep slope from 9 m to 16 m depth, though it consists mainly of hard corals, soft corals and sponges at this site. The arrangement of Lutoban South MPA is very similar to that of Malatapay MPA, with the seagrass zone being closer to the shoreline than the reef, and with the existence of an ‘interface’ zone where the seagrass and reef meet.

Like Malatapay MPA, Lutoban South MPA is protected from strong currents, but a river mouth north of the site affects its sanctuary. Lutoban South MPA is situated next to a small village but is less accessible than Malatapay MPA due to its expansive intertidal sand bank and seagrass bed. Therefore, the site experiences different coastal pressures, such as reduced boating and increased invertebrate gleaning by locals, and incomplete demarcation means there is still frequent fishing inside the MPA and constant fishing in the buffer zone. Also, due to lack of communication with the local government, the MPA has also not been fully accepted by the nearest community.

2.1.3 Dalakit MPA

‘Poblacion’ Dalakit MPA was established in 2014, and like Malatapay MPA, it covers 8 ha. It consists of a shallow coral reef, sand and large seagrass beds; while the reef is similar in density and composition (hard corals, algae and sponges) to that of the other two MPA sites, it is comparatively small, and only occurs between 2 m and 4 m depth. Dalakit MPA also contains an extensive seagrass

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

zone, which is much larger than that of the other two sites, though its species composition has not been properly surveyed: as the ten seagrass species found across the other two MPAs are known to occur within most of the local sites, their occurrence within Dalakit MPA can be speculated, but the true species composition remains unknown. The arrangement of Dalakit MPA differs considerably to the other MPAs, as the reef zone occurs closer to the shoreline than the seagrass zone. Unlike the other two sites, the reef and seagrass zones are separated by a distinct area consisting of sandy and rocky substrate, and thereby do not directly neighbour one another; as such, there is no 'interface' zone within this site.

In a sandy area outside of Dalakit MPA, there is an artificial reef composed of tyres that supports an array of marine life. Like the other two sites, the MPA is situated close to a river mouth, but in this case, the mouth occurs south of the site which perhaps reduces the effects of sedimentation and eutrophication. Demarcation of Dalakit MPA is usually complete, and generally experiences lower pressure from tourism and boating than the other sites due to the small size of the reef.

2.2 Survey Methodology

A total of 140 underwater surveys were conducted across the three MPA sites (Malatipay $n = 65$; Lutoban South $n = 51$; Dalakit $n = 24$) between 1st December 2019 and 29th February 2020. Dive pairs conducted 5 m wide x 30 m long belt surveys (150 m^2) across Seagrass, Seagrass-Reef Interface (where present; hereafter referred to as 'Interface') and Reef zones at each MPA. Underwater compasses were used to ensure that every transect line was parallel to the shoreline when reeling out, and each diver used an underwater slate and pencil to record survey data. Seagrass surveys were conducted in areas with only seagrass substrate (i.e. no reef) at least 15 m from the closest reef, and were within a depth range of 0 m to 7 m. Interface surveys were conducted in areas where the seagrass and reef substrates met, consisting of roughly 50 % of each substrate, and were also within a depth range of 0 m to 7 m. Reef surveys contained less than 10 m of sand substrate over a 30 m long point-intercept transect, and were conducted using a random stratified sampling strategy, which recognised three distinct depth ranges: Shallow (3 m to 7 m), Medium (9 m to 13 m), and Deep (15 m to 19 m). All surveys were conducted during the day except for three night surveys within Dalakit MPA, which were purely exploratory and not intended for use as a separate survey treatment; thus, these night surveys were considered as 'Dalakit Invertebrate Seagrass' surveys for the purpose of data analyses.

Divers were trained in fish and invertebrate species identification according to MCP's Reef Monitoring Species Lists; these included 95 fish species (Appendix C), some of which have multiple identifiable life phases, and 91+ invertebrate species (subject to any additional sea cucumber species; Appendix D). For each transect, divers tallied both species abundance and the size category of each organism (total length 0-5 cm; 5-10 cm; 10-20 cm; 20-30 cm; 10 cm increments up to 100 cm; 100 cm+), which was used to estimate biomass and maturity stage. Prior to conducting any surveys for data collection purposes, divers were tested for ≥ 90 % accuracy in overall survey quality (i.e. species ID, abundance and sizing) compared with a fully-trained MCP staff member in order to minimise diver bias. After each survey dive, data recorded on underwater slates were collated and photographed, and subsequently entered into a Microsoft Excel spreadsheet. Abundance data were later used to calculate the overall species diversity of each zone within each MPA site (by means of Simpson's Diversity Index), as well as Jaccard's Similarity Index between zones. Size category data

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

were subsequently used to calculate fish biomass across zones, using either known species biomass coefficients or approximate family biomass coefficients for the Philippines (or the nearest region). For family level biomass, the coefficient for the most common fish species in the family was chosen, and all biomass calculations used standard length of fish to allow room for error in diver size estimations (i.e. total length of fish).

2.2.1 Fish Survey Technique

All 95 target fish were identified to species, genus or family level, and are monitored by MCP for either their commercial importance or their ability to act as a reef health indicator, or both (Appendix B). Prior to starting fish surveys, divers waited 15 minutes after reeling out the 30 m transect line to allow for the return of any fish that may have been displaced by diver presence. With one diver on each side of the transect line, divers remained in the centre of their 2.5 m wide survey area, and swam in a straight line (parallel to the transect line) whilst carrying out the survey (Figure 2). Divers monitored the entire 3D area of the belt survey within 10 minutes; whilst most of this time was spent monitoring the areas ahead of and below them, both divers looked above and behind them every 3 m (approximately 1 minute intervals). Divers maintained visual contact with their buddy at all times to communicate any fish movement across the transect line (thereby minimising duplicate counts), and to ensure the rate of movement along the transect line was similar for both divers.

Based on available people power and time restrictions, a minimum of four fish surveys were conducted within each depth category in the Reef zone (Shallow; Medium; Deep), representing the fish community over an area of 600 m² (four x 150 m²). These surveys were then compiled together to represent the entire Reef zone. This methodology was extended to both the Interface and Seagrass zones, with a minimum of four fish surveys being conducted in each as both zones were limited to shallow depths.

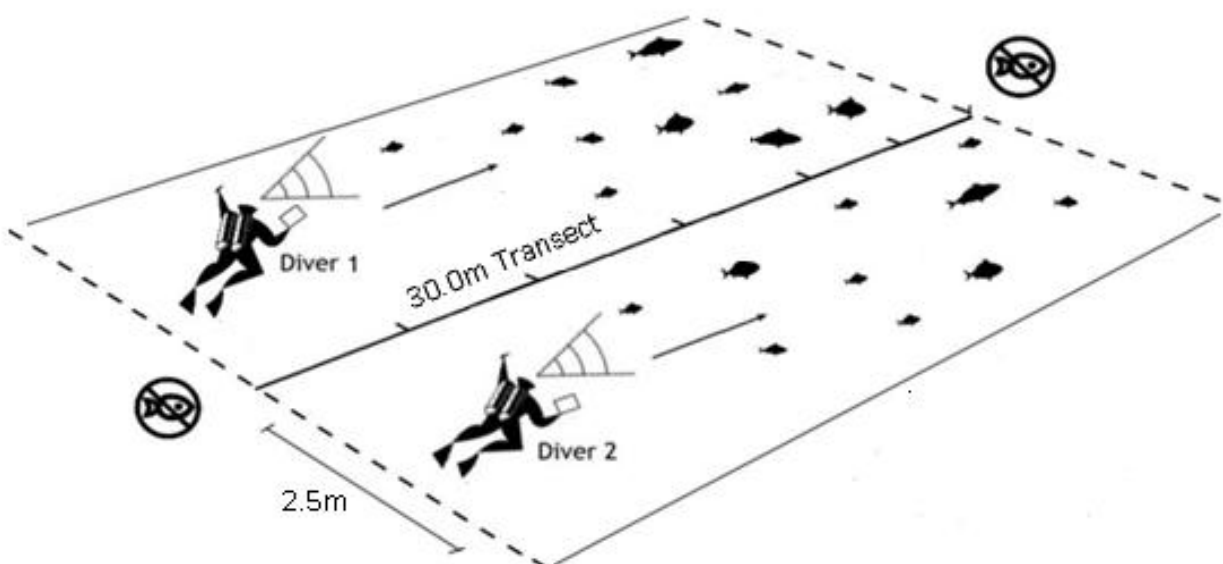


Figure 2: Fish belt survey technique conducted across three zones, three depth ranges and three MPA sites. Image adapted from Reef Check's 2016 'Tropical Monitoring Instruction' image.

2.2.1 Invertebrate Survey Technique

Most of the 91 target invertebrates were identified to species, genus or family level, though a select few were identified to a higher classification level (eg, Order, Class). Invertebrate species are monitored by MCP for a wide variety of reasons, including but not limited to: commercial importance (either as food or within the shell trade), ability to act as a reef health indicator, local consumption and high touristic value (Appendix C). For invertebrate surveys, divers started perpendicular (270° or 90°) to the transect line, with one diver on each side. Both divers swam away from the transect line until they reached the 2.5 m width boundary, monitoring approximately 1m of benthos on either side of them. Upon reaching the boundary, divers rotated 90° so that they were situated parallel to the transect line (0°), swam approximately 2 m forward, and then rotated another 90° to swim towards the transect line (90° or 270°). Divers repeated this swimming pattern, travelling along the transect area in an extended 'S' shape (Figure 3). Divers monitored the entire area of the belt survey within 20 minutes; whilst much of this time was spent monitoring the area below them, both divers occasionally looked above them to account for any pelagic invertebrates (eg, squid). Divers made frequent visual contact with their buddy to communicate any invertebrates situated directly underneath the transect line and perhaps moving across it (thereby minimising duplicate counts), and to ensure the rate of movement along the transect line was similar for both divers.

Based on available people power and time restrictions, a minimum of six invertebrate surveys were conducted within each depth category in the Reef zone (Shallow; Medium; Deep), representing the invertebrate community over an area of 900 m² (six x 150 m²): additional survey effort is required for invertebrate monitoring due to their visual crypticity. These surveys were then compiled together to represent the entire Reef zone. This methodology was extended to both the Interface and Seagrass zones, with a minimum of six invertebrate surveys being conducted in each as both zones were limited to shallow depths.

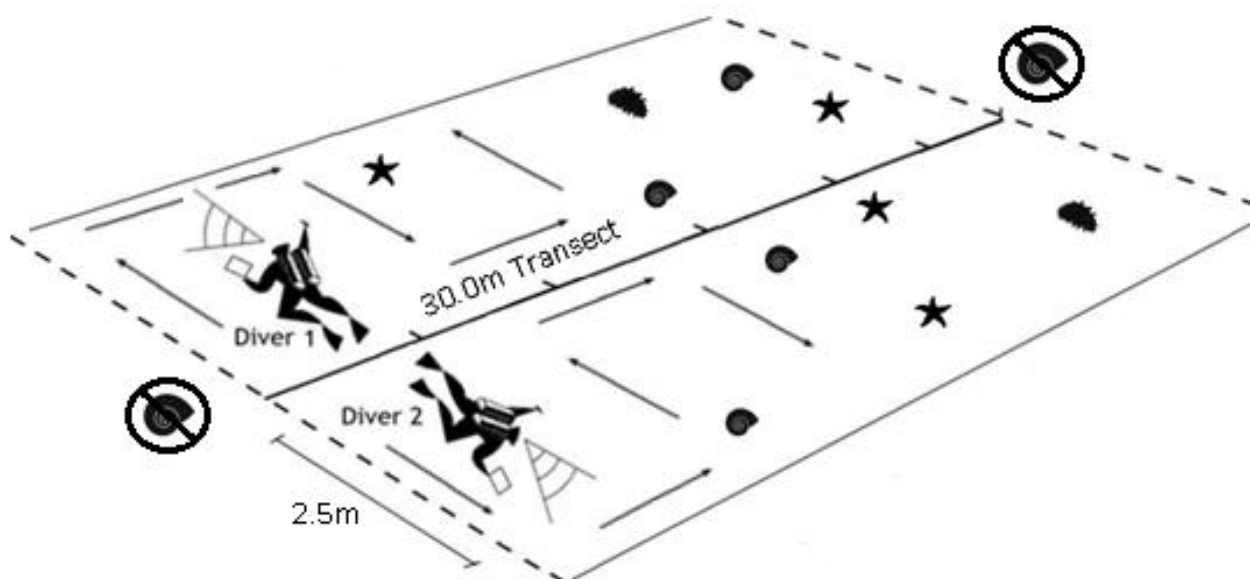


Figure 3: Invertebrate belt survey technique conducted across three zones, three depth ranges and three MPA sites. Image adapted from Reef Check's 2016 'Tropical Monitoring Instruction' image.

2.4 Statistical Analyses

2.4.1 Fish Communities

All statistical analyses were performed using R software, version 3.6.2 (R Core Team 2019). For Malatapay MPA and Lutoban South MPA, data were tested for homogeneity using Levene's test, and transformed using square-root where appropriate (only Malatapay Fish Abundance data). Separate one-way Analysis of Variance (ANOVA) tests were used to assess the effect of zone on Simpson's species diversity, total fish abundance and total fish biomass. Where results were significant, post-hoc tests were carried out using Tukey's Honest Significant Difference (Tukey's HSD) analyses. For Dalakit MPA, data were tested for homogeneity and normality using Levene's and Shapiro-Wilk's tests respectively. Where data were not normally distributed (only Dalakit Simpson's species diversity data), both square-root and log transformed data failed to meet the normality assumption; thus, subsequent analysis to test the effect of zone on Simpson's species diversity was non-parametric (Wilcoxon Rank Sum test). For data that met homogeneity and normality assumptions, two unpaired t-tests were used to test the effect of zone on total fish abundance and total fish biomass.

To explore community differences between the three zones, a multivariate approach was taken. Community dissimilarity was calculated as the Bray-Curtis distance of square root-transformed abundance data (using the "vegan" package). A permutations test indicated heterogeneity of data for Malatapay MPA and Lutoban South MPA, and visual assessments of the data in two non-metric multi-dimensional scaling (nMDS) plots (using "ggplot2" package) confirmed that the centres of distribution did not differ for the three zones; thus, no permutational multivariate analysis of variance (PERMANOVA) or Tukey's HSD tests were carried out for these MPA sites. For Dalakit MPA, a permutations test indicated that data were homogeneous, and therefore a PERMANOVA was carried out on the data to investigate zonal community differences. SIMPER analysis was subsequently carried out for each MPA site to investigate which species (if any) were responsible for driving community differences.

2.4.2 Invertebrate Communities

Data for Malatapay MPA and Lutoban South MPA were tested for homogeneity using Levene's test. For Malatapay MPA, Simpson's species diversity data were heterogeneous, and both square-root and log transformed data failed to meet the homogeneity assumption; thus, subsequent analysis to test the effect of zone on Simpson's species diversity was non-parametric (Welch's ANOVA). Whilst investigating the effect of zone on Simpson's species diversity in Lutoban South MPA, a species abundance anomaly (bell's urchin = 343) was removed from a survey in the Seagrass zone for data analysis purposes. Simpson's species diversity data for Lutoban South MPA were homogeneous, and therefore a one-way ANOVA was used; as the result was significant, post-hoc tests were carried out using Tukey's HSD. For Dalakit MPA, data were tested for homogeneity and normality using Levene's and Shapiro-Wilk's tests respectively. As the data met both assumptions, an unpaired t-test was used to test the effect of zone on Simpson's species diversity.

A multivariate approach was taken to explore community differences between the three zones; community dissimilarity was calculated as the Bray-Curtis distance of square root-transformed

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

abundance data (using the "vegan" package). A permutations test indicated homogeneity of data for Malatapay MPA and Dalakit MPA, and therefore PERMANOVAs were carried out on the data for each MPA to investigate zonal community differences. For Lutoban South MPA, a permutations test indicated heterogeneity, but a visual assessment of the data in an nMDS plot confirmed that the centres of distribution differ for the two sites. This allowed for a PERMANOVA to be carried out on the heterogeneous data, and post-hoc tests were subsequently carried out using Tukey's HSD. Finally, SIMPER analysis was conducted for each MPA site to explore which species (if any) were responsible for driving community differences.

3. RESULTS

3.1 Fish Communities

3.1.1 Malatapay MPA

Simpson's fish species diversity was lowest in the Seagrass (one-way ANOVA, $F_{2,30} = 11.83$, $p < 0.001$; Figure 4). Total fish abundance was higher in the Interface and Reef zones than in the Seagrass zone (one-way ANOVA, $F_{2,30} = 17.92$, $p < 0.001$; Figure 5a), and zone had no effect on total fish biomass (one-way ANOVA, $F_{2,30} = 1.236$, $p > 0.05$; Figure 5b). The Seagrass fish community had a considerably higher percentage of Top Predators (12.7 %) than the other two zones, and was otherwise dominated by Reef Fish (59.2 %; Figure 6a). The Interface community had a relatively even composition, with a slightly higher percentage of Herbivores (34.7 %; Figure 6b), whereas the Reef community was largely composed of Planktivores and Reef Fish (44.4 % and 34.5 % respectively; Figure 6c). Dispersals differed between groups, and though zonal fish communities were not significantly different from one another, the Interface and Reef communities were more similar to one another than they were to the Seagrass community (Figure 7). Of all target fish species, 52.63 % were identified across the 33 fish surveys conducted in Malatapay MPA, and while adjacent zones had higher percentages of shared fish species, the nonadjacent Seagrass and Reef zones still shared 19.57 % of species (Jaccard's Similarity Index; Figure 8). SIMPER analysis revealed that 17 species were responsible for driving the main community differences between the Seagrass and Interface zones (92 % variability overall; Table 1a), 15 species for the Seagrass and Reef zones (94 % variability overall; Table 1b), and only two species for the Interface and Reef zones (53 % variability overall; Table 1c).

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

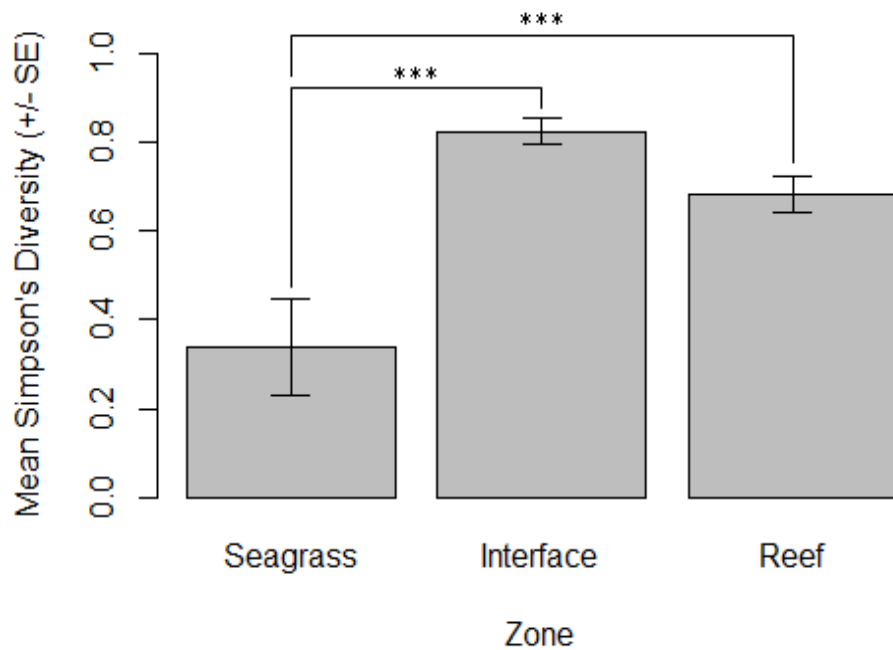


Figure 4: The effect of zone on Simpson's species diversity index across 33 fish surveys (SG n = 6, INT n = 7, RF n = 20) conducted within Malatapay MPA, Philippines. Connecting bars represent results of post-hoc analyses (Tukey's HSD), whereby asterisks indicate level of significance (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$).

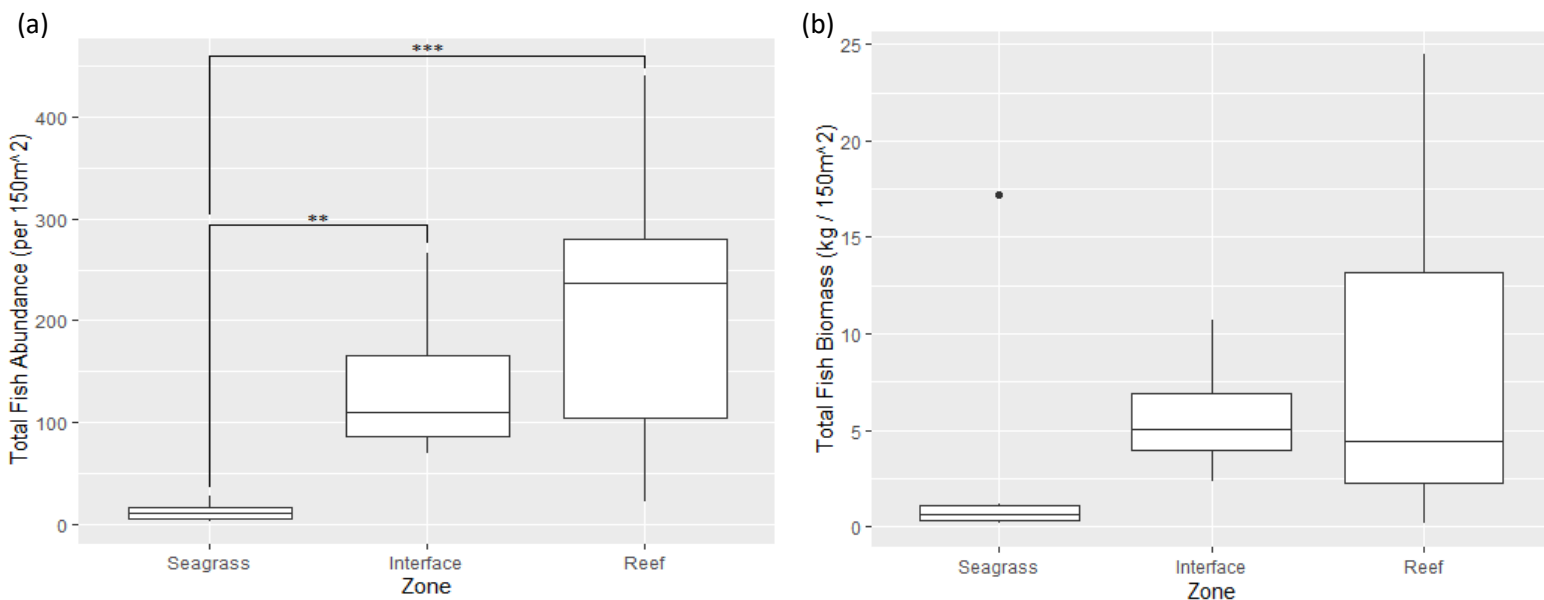


Figure 5: The effect of zone on total fish abundance (a) and total fish biomass (b) across 33 fish surveys (SG n = 6, INT n = 7, RF n = 20) conducted within Malatapay MPA, Philippines. Connecting bars represent results of post-hoc analyses (Tukey's HSD), whereby asterisks indicate level of significance (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$).

Malatapay MPA

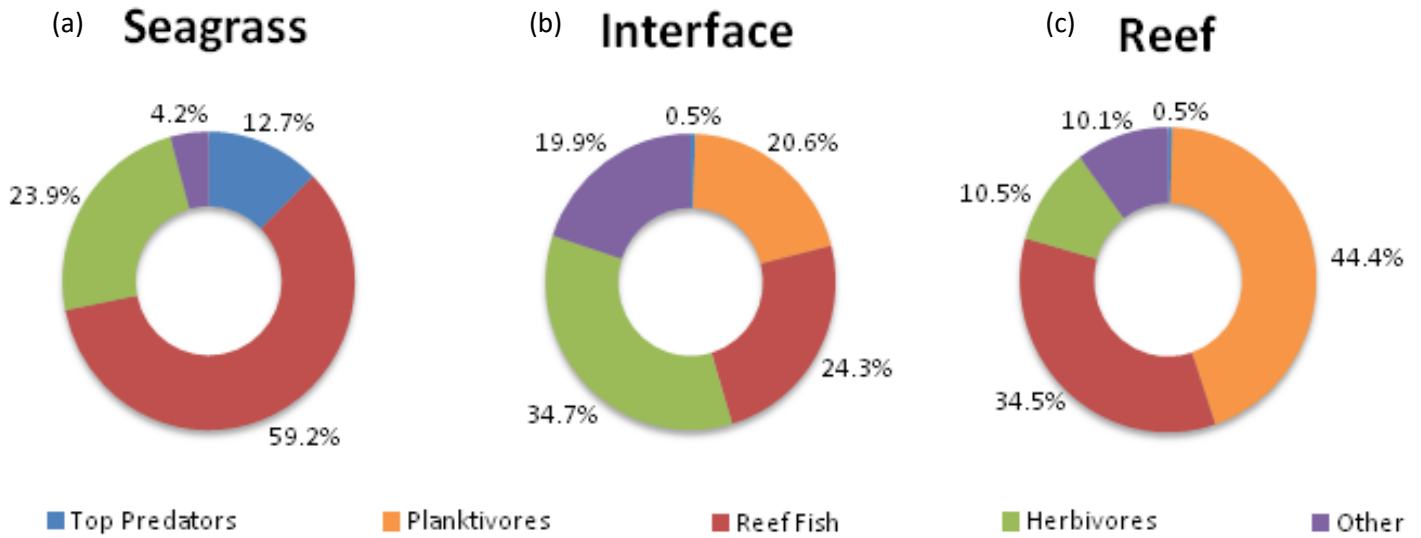


Figure 6: Composition of fish communities in Seagrass (a), Interface (b) and Reef (c) zones within Malatapay MPA, Philippines. Fish species were categorised by primary function, and each chart is composed of all surveys combined from within the given zone (SG n = 6, INT n = 7, RF n = 20). Percentages indicate group contribution to the overall fish abundance within the zone (SG n = 71, INT n = 948, RF n = 4536).

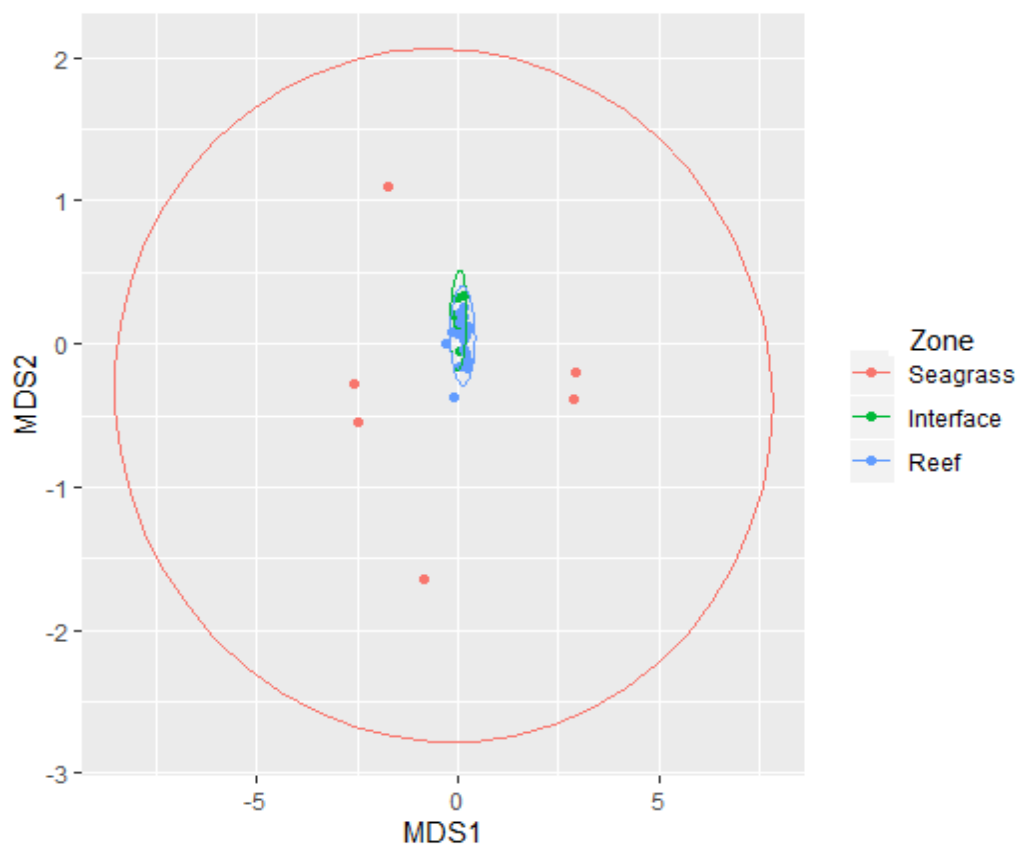


Figure 7: Differences in fish community composition across Seagrass, Interface and Reef zones (Stress = 0.09) within Malatapay MPA, Philippines. Data points represent fish surveys (n = 33) and Bray-Curtis distances represent dissimilarity in community composition. Ellipses indicate 95% confidence intervals for clusters for each zone.

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

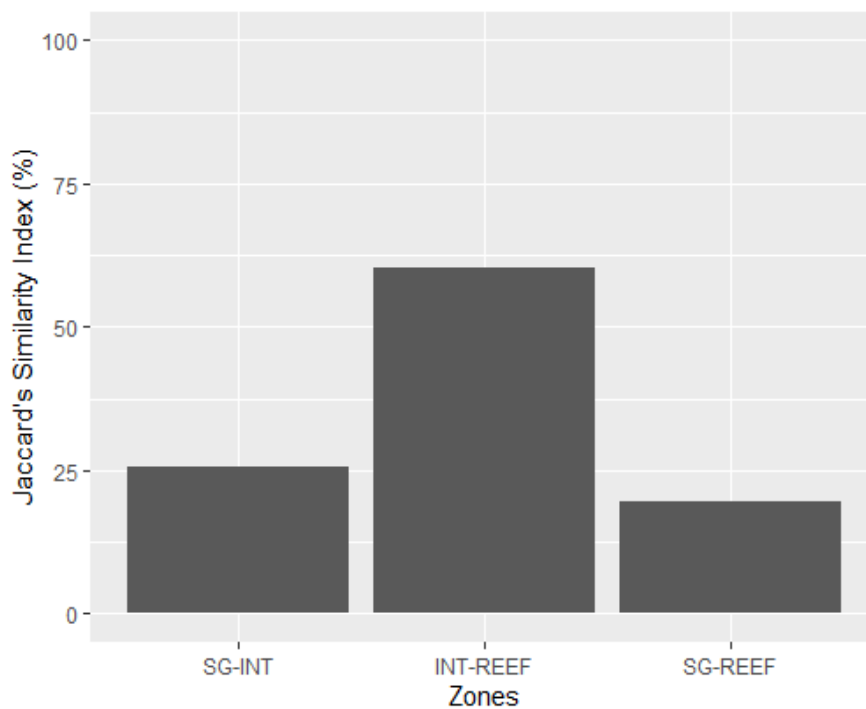


Figure 8: Jaccard's Similarity Indices for zone pairs within Malatapay MPA, Philippines. Higher values indicate a higher percentage of shared fish species.

Table 1: SIMPER results indicating which species are driving the observed dissimilarity in zonal fish communities within Malatapay MPA, Philippines. Average abundance in each zone, contribution to dissimilarity between groups (%), and the cumulative total of contributions (%) are provided for each species.

(a) Seagrass-Interface

Species	Average Abundance		Contribution %	Cumulative %
	Seagrass	Interface		
Goatfish	0.00	4.21	12.00	12.00
Rabbitfish	0.24	4.35	10.24	22.24
Butterflyfish	0.24	3.93	9.46	31.70
Sergeantfish	0.00	3.84	8.37	40.07
Bristletooth	0.00	2.84	7.28	47.35
Pearl-Scaled Angelfish	0.00	2.68	7.01	54.36
Surgeonfish	0.80	2.57	5.64	60.00
Bicolor Goatfish	0.24	1.44	3.51	63.51
Bream	0.00	1.34	3.21	66.72
Dash-Dot Goatfish	0.00	1.24	3.20	69.92
Triggerfish	0.00	1.08	2.65	72.57
Grouper	0.00	0.98	2.44	75.01
Soldierfish	0.00	0.59	1.88	76.89
Bleeker's Parrotfish	0.00	0.29	0.60	77.49
Red-Breasted Wrasse	0.00	0.14	0.41	77.90
Thumbprint Emperor	0.00	0.14	0.32	78.22
Blackeye Thicklip Wrasse	0.00	0.14	0.25	78.47

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

(b) Seagrass-Reef

Species	Average Abundance		Contribution %	Cumulative %
	Seagrass	Reef		
Fusiliers	0.00	5.36	10.08	10.08
Goatfish	0.00	4.28	9.85	19.93
Butterflyfish	0.24	3.24	6.97	26.90
Bristletooth	0.00	2.60	5.82	32.72
Pearl-Scaled Angelfish	0.00	2.24	4.99	37.71
Bicolor Angelfish	0.00	1.66	3.89	41.60
Cleaner Wrasse	0.17	1.68	3.65	45.25
Triggerfish	0.00	1.32	3.15	48.40
Bream	0.00	1.50	3.10	51.50
Parrotfish	0.50	1.40	2.82	54.32
Grouper	0.00	1.31	2.74	57.06
Dash-Dot Goatfish	0.00	1.03	2.07	59.13
Floral Wrasse	0.00	0.78	1.93	61.06
Angelfish	0.00	0.68	1.71	62.77
Keyhole Angelfish	0.00	0.65	1.34	64.11

(c) Interface-Reef

Species	Average Abundance		Contribution %	Cumulative %
	Interface	Reef		
Rabbitfish	4.35	0.81	8.29	8.29
Bleeker's Parrotfish	0.29	0.00	0.60	8.89

3.1.2 Lutoban South MPA

Simpson's fish species diversity did not differ across the three zones (one-way ANOVA, $F_{2,17} = 1.248$, $p > 0.05$). Zone had no effect on total fish abundance (one-way ANOVA, $F_{2,17} = 2.854$, $p > 0.05$; Figure 9a) or total fish biomass (one-way ANOVA, $F_{2,17} = 1.547$, $p > 0.05$; Figure 9b). Fish community composition was similar across all three zones, with Planktivores being the dominant group (Figures 10a-c). The Seagrass fish community consisted of no Top Predators at all (Figure 10a), and the Interface community had a higher percentage of Herbivores (21.5 %; Figure 10b) than the other two zones (2.6 % and 5.8 %; Figures 10a and 10c respectively). Dispersals differed between groups, and though zonal fish communities were not significantly different from one another, the Interface and Reef communities were more similar to one another than they were to the Seagrass community (Figure 11). Of all target fish species, 40 % were identified across the 20 fish surveys conducted in Lutoban South MPA, and while adjacent zones had higher percentages of shared fish species, the nonadjacent Seagrass and Reef zones still shared 22.22 % of species (Jaccard's Similarity Index; Figure 12). SIMPER analysis revealed that 13 species were responsible for driving the main community differences between the Seagrass and Interface zones (82 % variability overall; Table 2a), 11 species for the Seagrass and Reef zones (89 % variability overall; Table 2b), and that species were of equal abundance across the Interface and Reef zones (57 % variability overall).

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

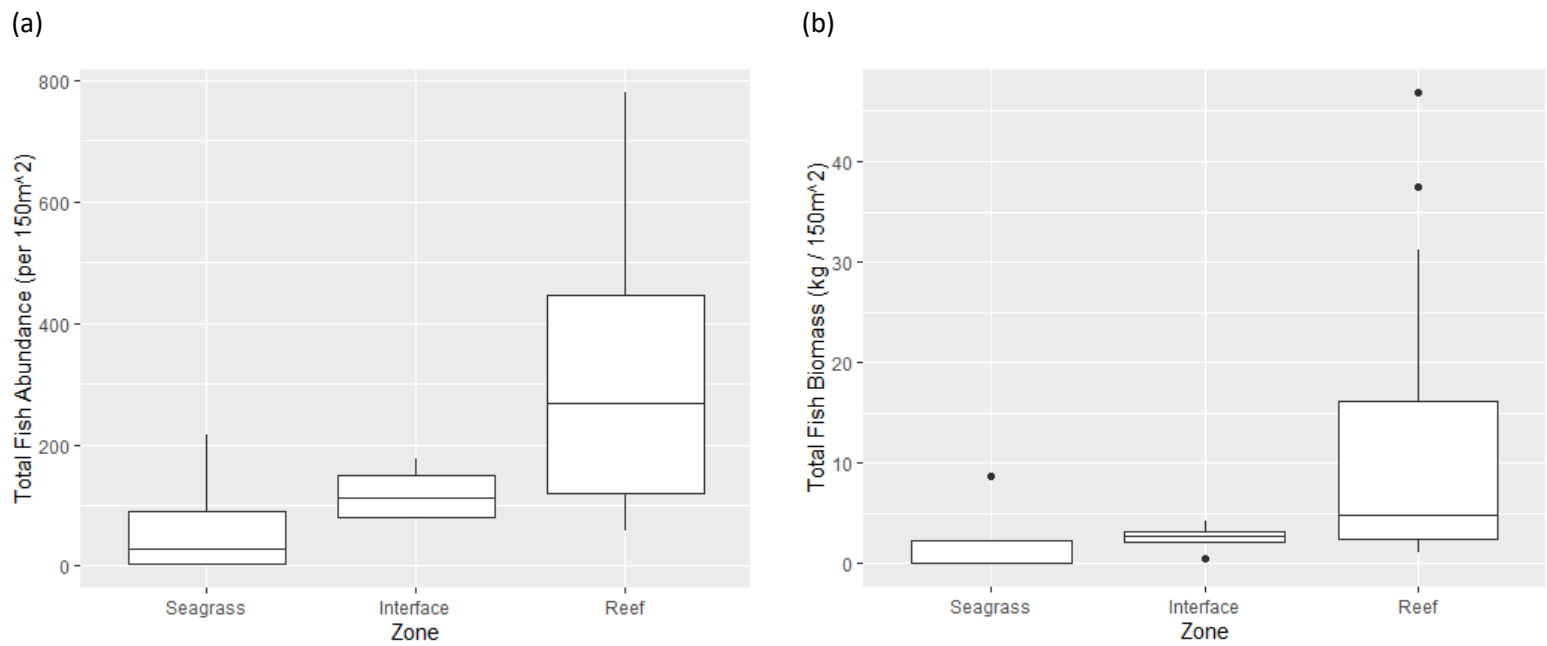


Figure 9: The effect of zone on total fish abundance (a) and total fish biomass (b) across 20 fish surveys (SG n = 4, INT n = 4, RF n = 12) conducted within Lutoban South MPA, Philippines.

Lutoban South MPA

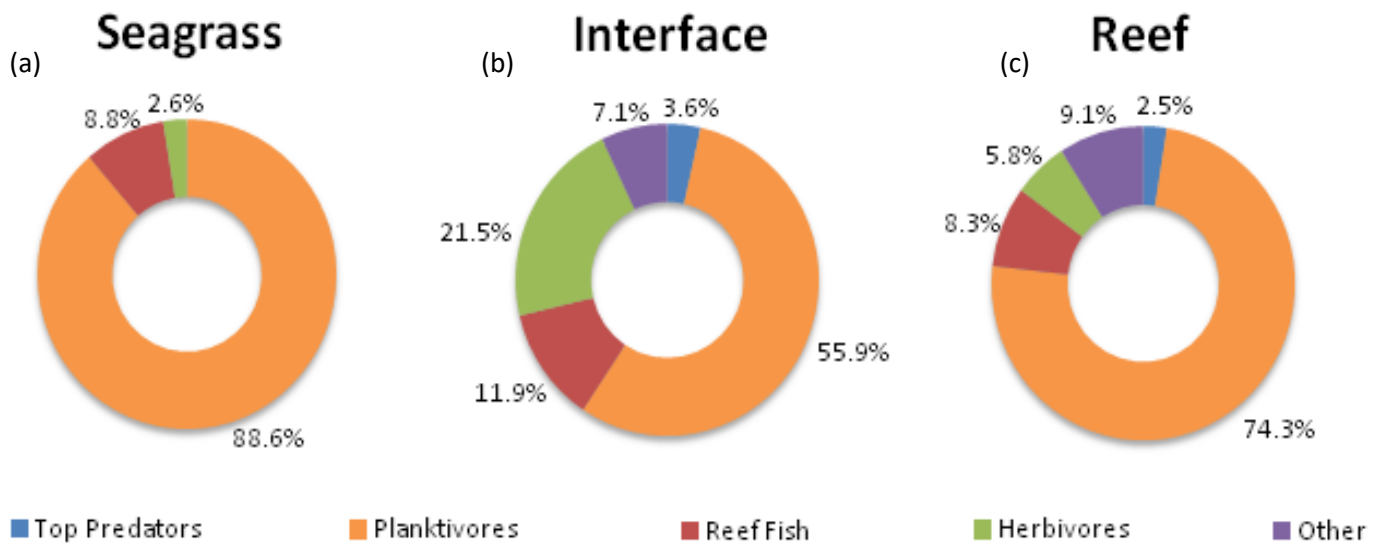


Figure 10: Composition of fish communities in Seagrass (a), Interface (b) and Reef (c) zones within Lutoban South MPA, Philippines. Fish species were categorised by primary function, and each chart is composed of all surveys combined from within the given zone (SG n = 4, INT n = 4, RF n = 12). Percentages indicate group contribution to the overall fish abundance within the zone (SG n = 273, INT n = 478, RF n = 3696).

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

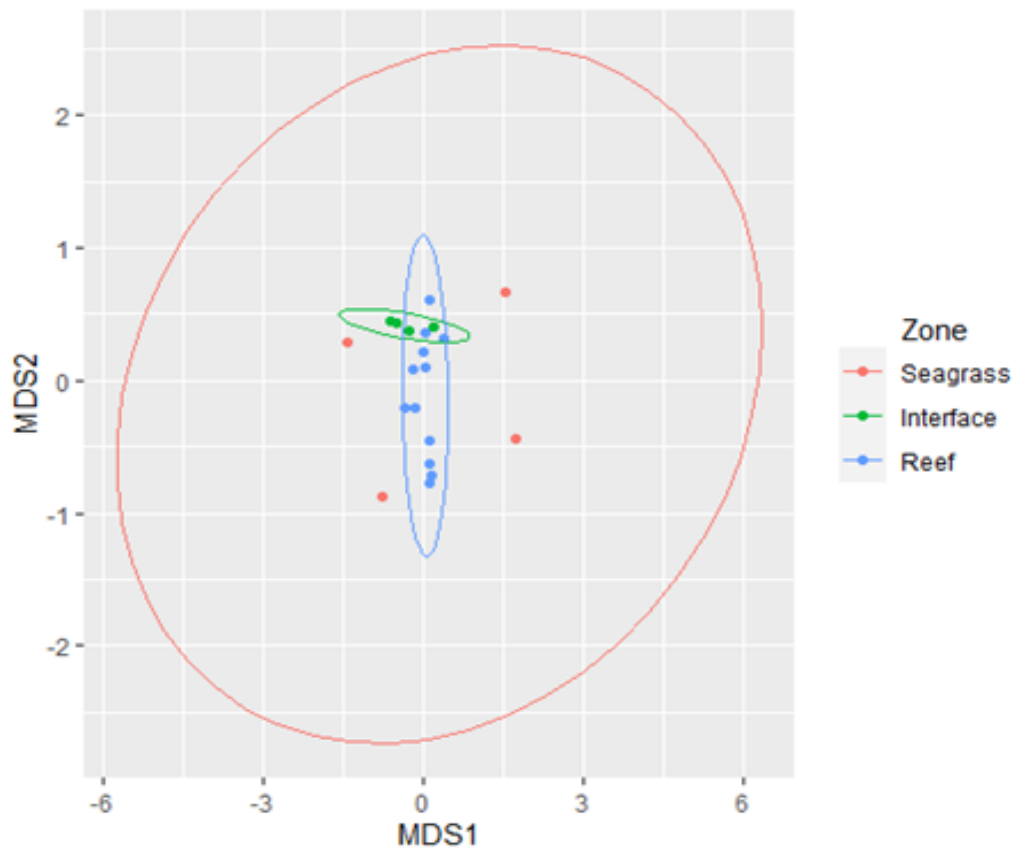


Figure 11: Differences in fish community composition across Seagrass, Interface and Reef zones (Stress = 0.12) within Lutoban South MPA, Philippines. Data points represent fish surveys ($n = 20$) and Bray-Curtis distances represent dissimilarity in community composition. Ellipses indicate 95% confidence intervals for clusters for each zone.

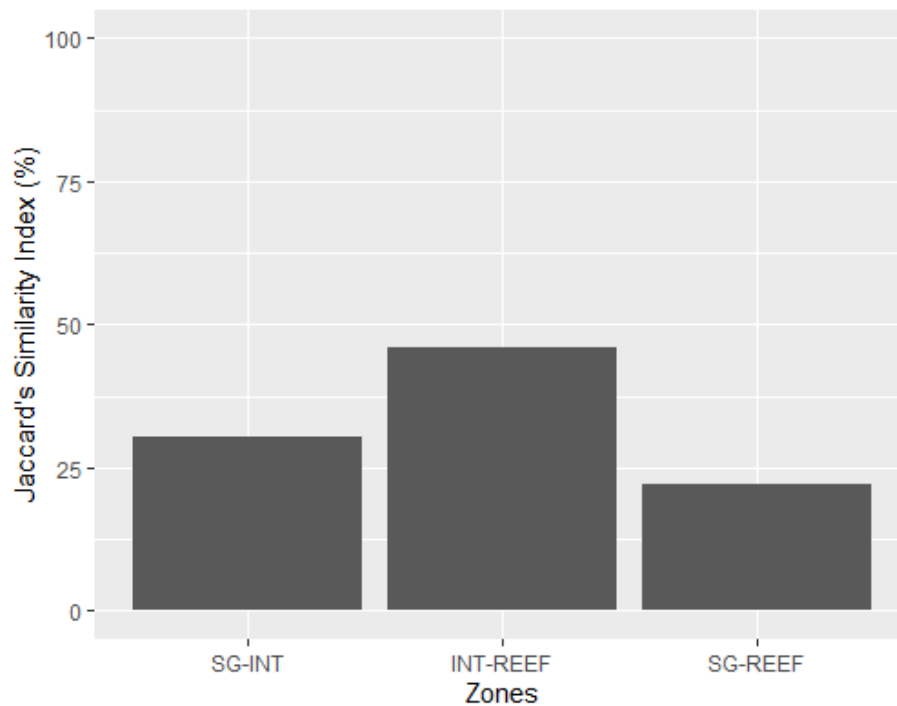


Figure 12: Jaccard's Similarity Indices for zone pairs within Lutoban South MPA, Philippines. Higher values indicate a higher percentage of shared fish species.

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Table 2: SIMPER results indicating which species are driving the observed dissimilarity in zonal fish communities within Lutoban South MPA, Philippines. Average abundance in each zone, contribution to dissimilarity between groups (%), and the cumulative total of contributions (%) are provided for each species.

(a) Seagrass-Interface

Species	Average Abundance		Contribution %	Cumulative %
	Seagrass	Interface		
Sergeantfish	3.54	7.32	18.06	18.06
Goatfish	0.25	3.36	10.00	28.06
Butterflyfish	0.00	2.99	9.84	37.90
Pearl-Scaled Angelfish	0.00	1.82	5.66	43.56
Bream	0.00	1.72	5.42	48.98
Cleaner Wrasse	0.00	1.46	4.74	53.72
Dash-Dot Goatfish	0.25	1.53	4.08	57.80
Cornetfish	0.00	0.93	3.17	60.97
Rabbitfish	0.35	0.90	2.52	63.49
Scrawled Filefish	0.60	0.00	2.38	65.87
White-Spotted Rabbitfish	0.56	0.71	2.32	68.19
Spadefish	0.00	0.25	0.85	69.04
Floral Wrasse	0.00	0.25	0.80	69.84

(b) Seagrass-Reef

Species	Average Abundance		Contribution %	Cumulative %
	Seagrass	Reef		
Butterflyfish	0.00	4.09	8.72	8.72
Goatfish	0.25	2.98	5.62	14.34
Bristletooth	0.00	2.12	4.52	18.86
Cleaner Wrasse	0.00	2.03	4.28	23.14
Pearl-Scaled Angelfish	0.00	1.73	4.14	27.28
Triggerfish	0.00	1.63	3.76	31.04
Grouper	0.00	1.17	2.60	33.64
Keyhole Angelfish	0.00	1.21	2.23	35.87
Bicolor Angelfish	0.00	1.24	2.21	38.08
Peacock Grouper	0.00	1.04	2.11	40.19
Parrotfish	0.00	0.93	1.94	42.13

3.1.3 Dalakit MPA

Simpson's fish species diversity was higher on the Reef than in the Seagrass (Wilcoxon Rank Sum test, $W = 1$, $p < 0.05$; Figure 13). Total fish abundance was lower in the Seagrass than on the Reef (t-test, $t = -4.301$, $df = 4.082$, $p < 0.05$; Figure 14a), and zone had no effect on total fish biomass (t-test, $t = -1.875$, $df = 5.224$, $p > 0.05$; Figure 14b). The Seagrass fish community consisted of only three functional groups, and was primarily dominated by Reef Fish (80 %; Figure 15a). The Reef community had a more even functional composition than the Seagrass zone, with a lower percentage of Top Predators (1.2 %; Figure 15b). Dispersals did not differ between groups, and zonal communities were significantly different from one another, with zone accounting for approximately 69 % of the total variability between communities (PERMANOVA, $R^2 = 0.69$, $F_{1,7} = 16.329$, $p < 0.01$; Figure 16). Of all target fish species, 38.95 % were identified across the nine fish

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

surveys conducted within Dalakit MPA, and Jaccard's Similarity Index confirmed that only 8.11 % of species were both reef- and seagrass-associated (Figure 17). SIMPER analysis revealed that ten species were responsible for driving the main community differences between the two zones (93 % variability overall; Table 3).

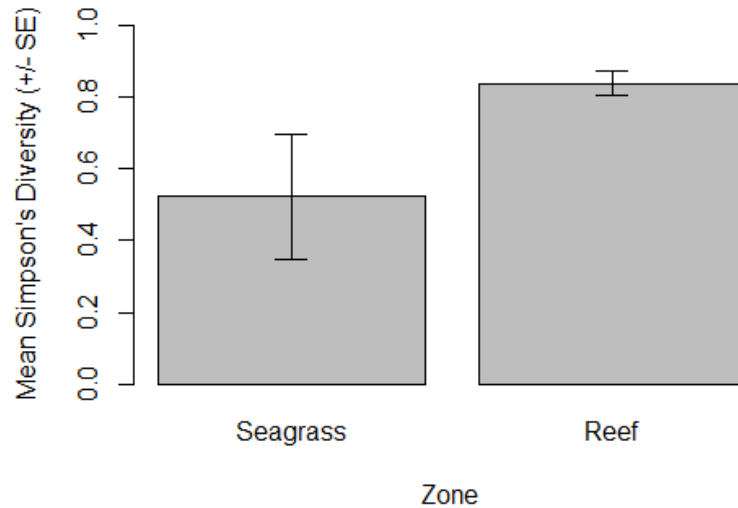


Figure 13: The effect of zone on Simpson's species diversity index across nine fish surveys (SG n = 4, RF n = 5) conducted within Dalakit MPA, Philippines.

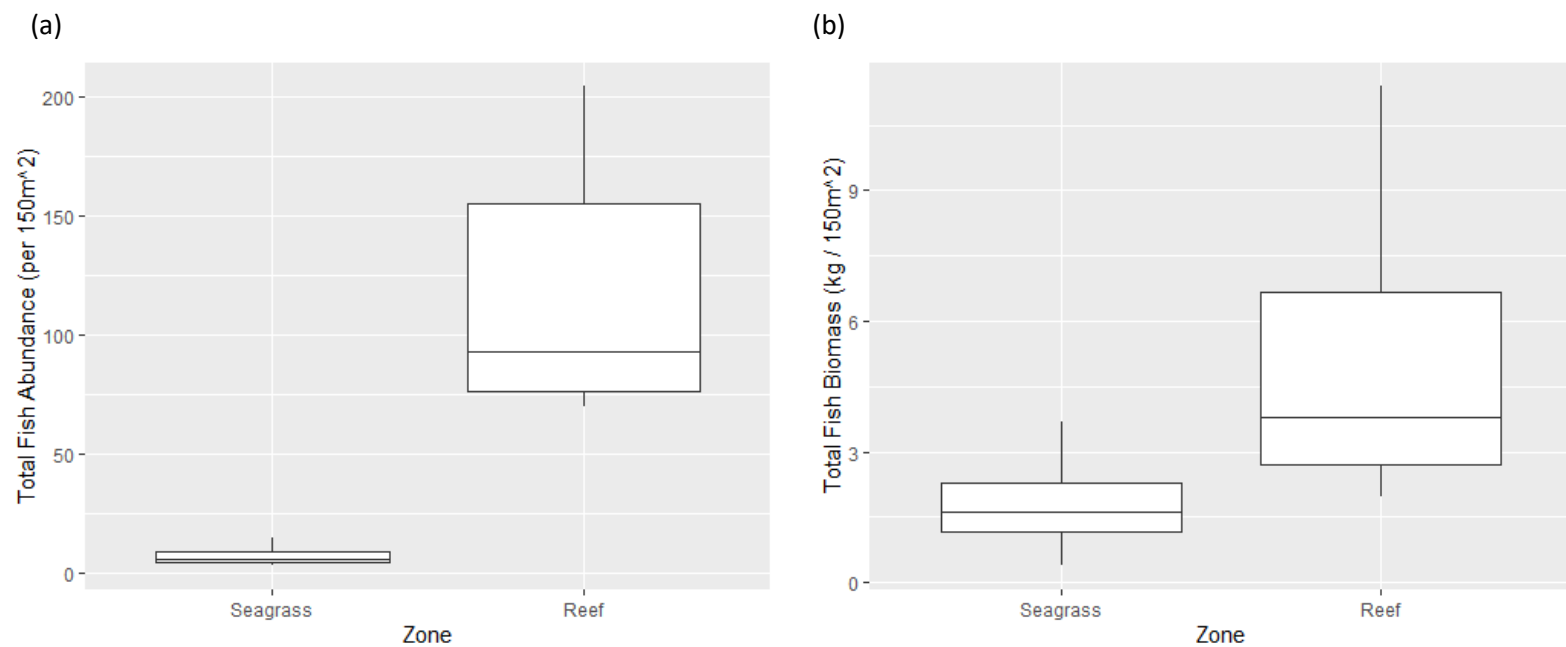


Figure 14: The effect of zone on total fish abundance (a) and total fish biomass (b) across nine fish surveys (SG n = 4, RF n = 4) conducted within Dalakit MPA, Philippines.

Dalakit MPA

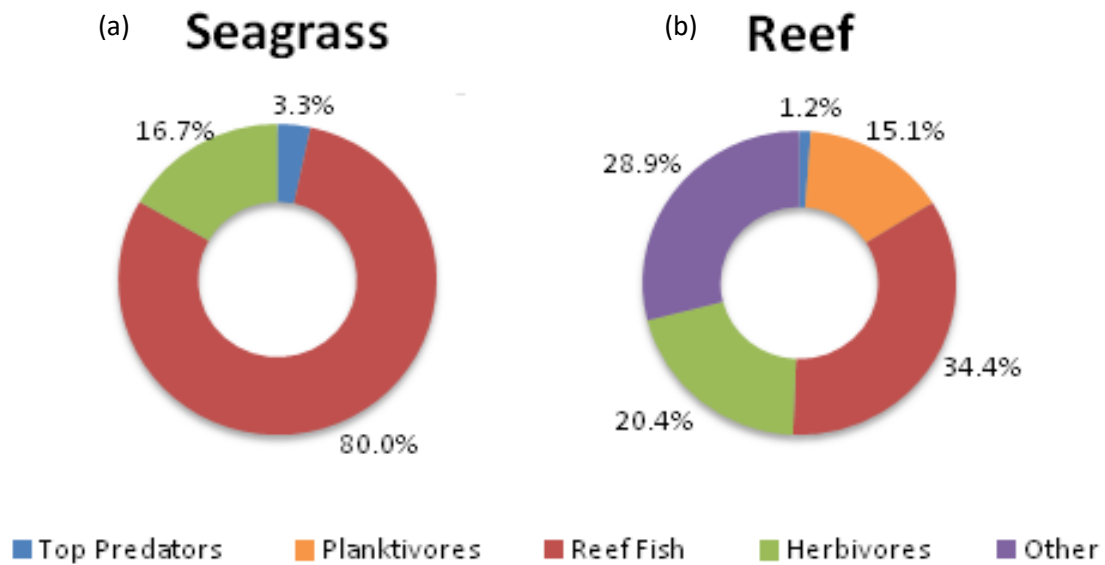


Figure 15: Composition of fish communities in Seagrass (a) and Reef (b) zones within Dalakit MPA, Philippines. Fish species were categorised by primary function, and each chart is composed of all surveys combined from within the given zone (SG n = 4, RF n = 5). Percentages indicate group contribution to the overall fish abundance within the zone (SG n = 30, RF n = 598).

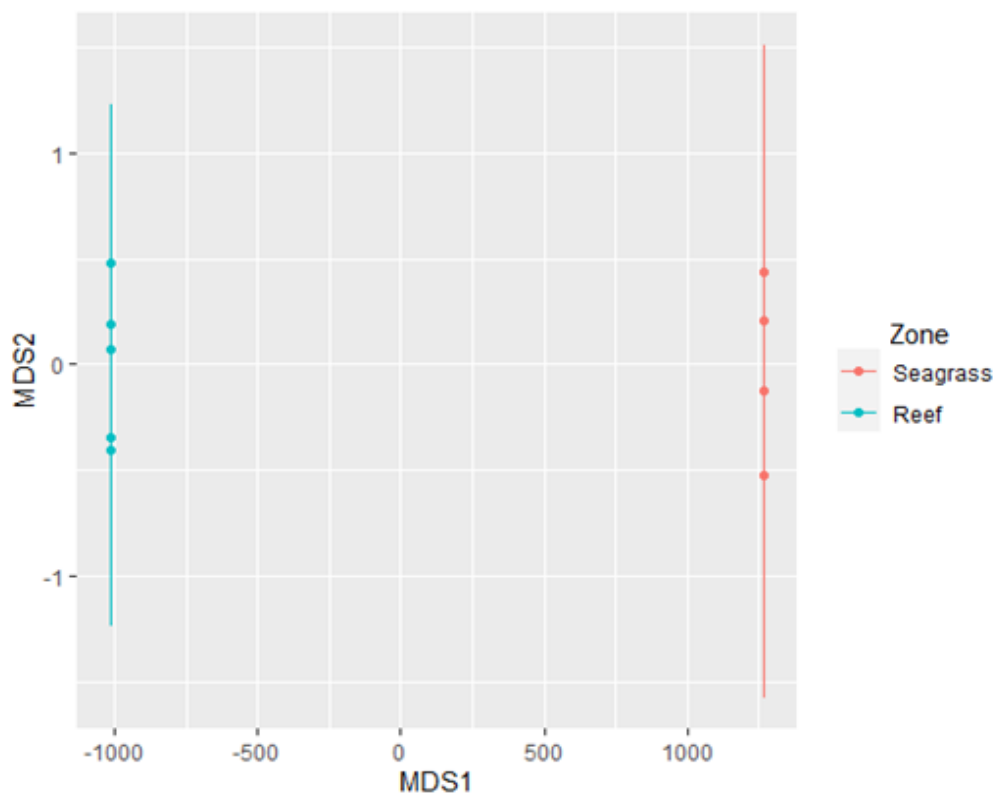


Figure 16: Differences in fish community composition across Seagrass and Reef zones (Stress < 0.0001) within Dalakit MPA, Philippines. Data points represent fish surveys (n = 9) and Bray-Curtis distances represent dissimilarity in community composition. Ellipses indicate 95% confidence intervals for clusters for each zone.

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

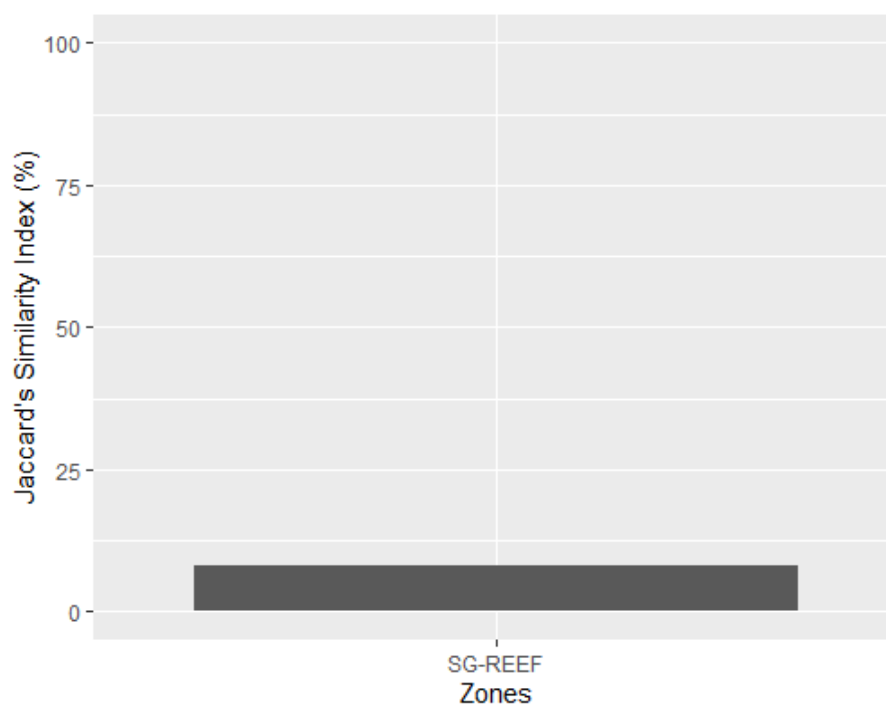


Figure 17: Jaccard's Similarity Index for Seagrass and Reef zones within Dalakit MPA, Philippines. Higher values indicate a higher percentage of shared fish species.

Table 3: SIMPER results indicating which species are driving the observed dissimilarity in zonal fish communities within Dalakit MPA, Philippines. Average abundance in each zone, contribution to dissimilarity between groups (%), and the cumulative total of contributions (%) are provided for each species.

Species	Average Abundance		Contribution %	Cumulative %
	Seagrass	Reef		
Butterflyfish	0.00	3.59	9.19	9.19
Bristletooth	0.00	3.54	9.05	18.24
Pearl-Scaled Angelfish	0.00	2.98	7.93	26.17
Cleaner Wrasse	0.00	2.81	7.29	33.46
Goatfish	0.00	2.76	7.18	40.64
Surgeonfish	0.00	2.33	6.05	46.69
Brushtail Tang	0.00	2.22	5.44	52.13
Grouper	0.00	1.93	4.88	57.01
Yellowstripe Goatfish	0.00	2.25	4.57	61.58
Honeycomb Grouper	0.00	1.33	3.52	65.10

3.2 Invertebrate Communities

3.2.1 Malatapay MPA

Simpson's invertebrate species diversity did not differ across the three zones (Welch's ANOVA, $F_{2,9.91} = 0.598$, $p > 0.05$) and dispersals did not differ between groups. The Seagrass zone was dominated by Generalist species (86.3 %), with Seagrass Specialists as the second most abundant group (11.2 %) and few

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Reef Specialists (2.5 %; Figure 18a). The Interface and Reef zones were similar in overall composition, consisting mainly of Generalists and Reef Specialists, and with very low percentages of Seagrass Specialists (0.2 % and 1.6 % respectively; Figures 18b and 18c). Zonal invertebrate communities were significantly different from one another, with zone accounting for approximately 26 % of the dissimilarity between communities (PERMANOVA, $R^2 = 0.260$, $F_{2,29} = 5.088$, $p \leq 0.001$; Figure 19). The Interface and Reef communities were more similar to one another than they were to the Seagrass community (Figure 19). Of all target invertebrate species, 47.83 % were identified across the 32 invertebrate surveys conducted within Malatapay MPA, with the nonadjacent Seagrass and Reef zones sharing a higher percentage of species than the adjacent Seagrass and Interface zones (30 % and 28.57 % respectively, Jaccard's Similarity Index; Figure 20). SIMPER analysis revealed that 12 species were responsible for driving the main community differences between the Seagrass and Interface zones (84 % variability overall; Table 4a), 11 species for the Seagrass and Reef zones (77 % variability overall; Table 4b), and only three species for the Interface and Reef zones (63 % variability overall; Table 4c).

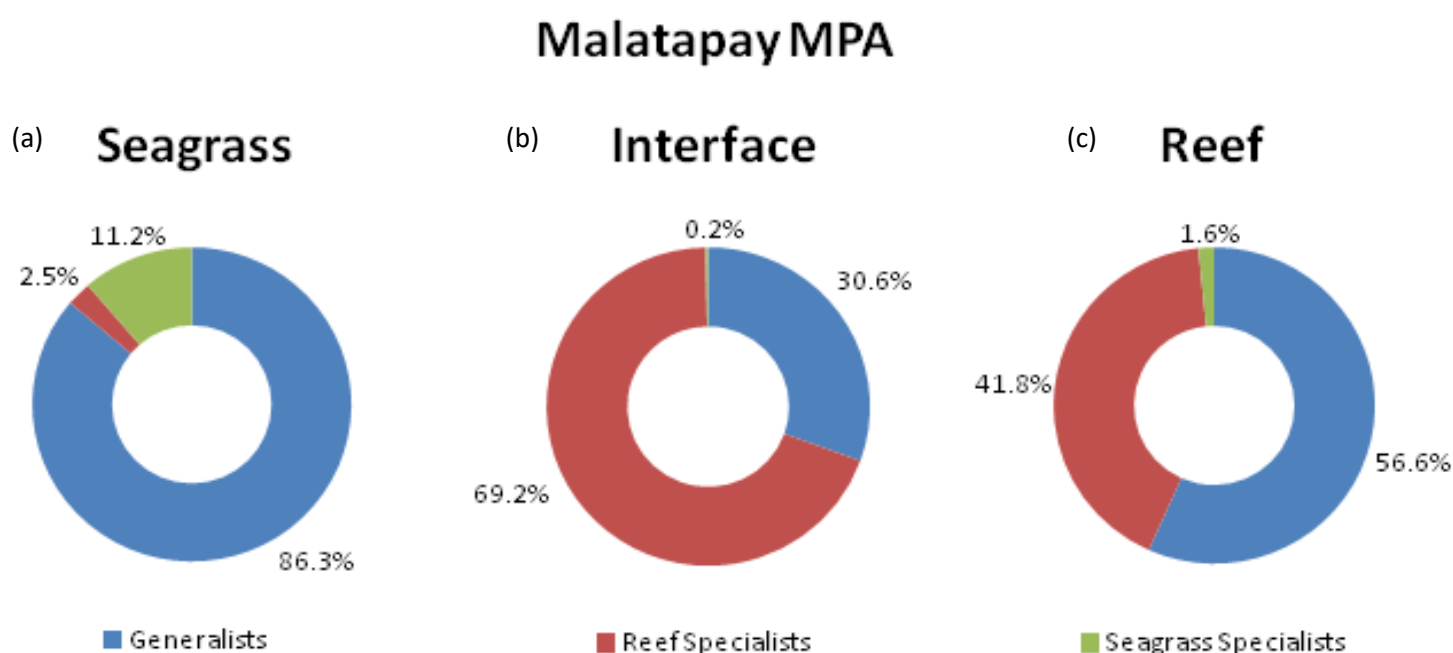


Figure 18: Composition of invertebrate communities in Seagrass (a), Interface (b) and Reef (c) zones within Malatapay MPA, Philippines. Invertebrate species were broadly categorised by ecological niche, and each chart is composed of all surveys combined from within the given zone (SG n = 6, INT n = 6, RF n = 20). Percentages indicate group contribution to the overall invertebrate abundance within the zone (SG n = 80, INT n = 396, RF n = 1017).

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

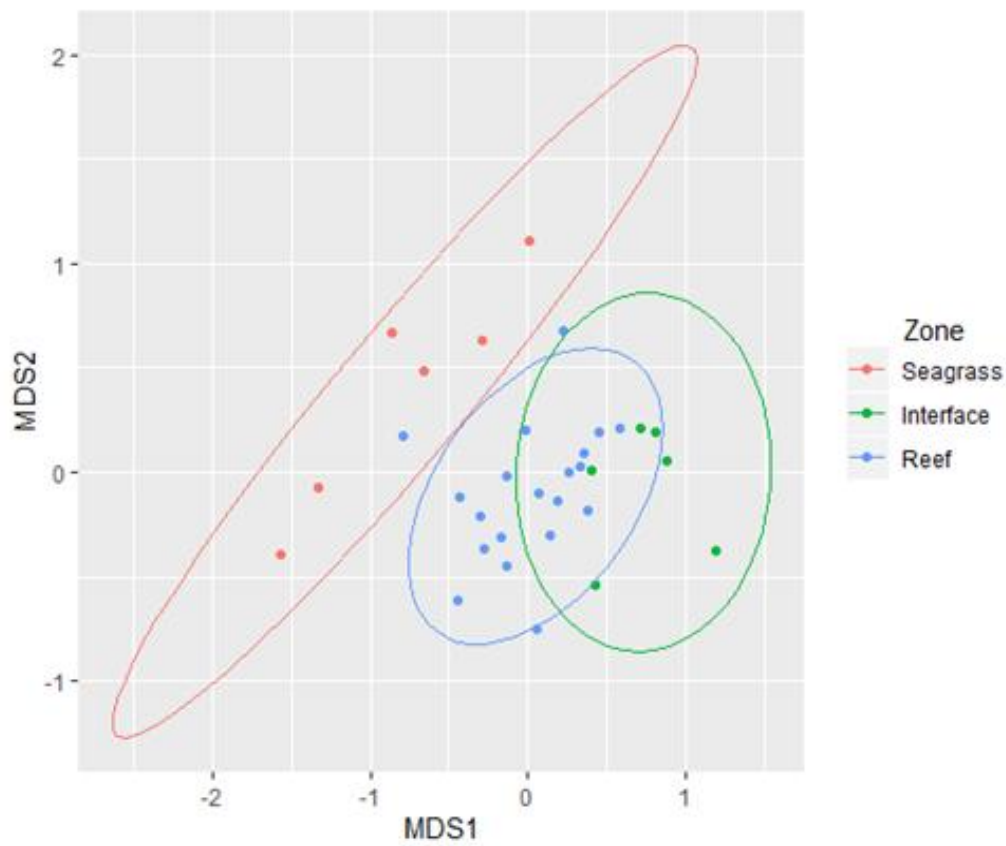


Figure 19: Differences in invertebrate community composition across Seagrass, Interface and Reef zones (Stress = 0.18) within Malatapay MPA, Philippines. Data points represent invertebrate surveys ($n = 32$) and Bray-Curtis distances represent dissimilarity in community composition. Ellipses indicate 95% confidence intervals for clusters for each zone.

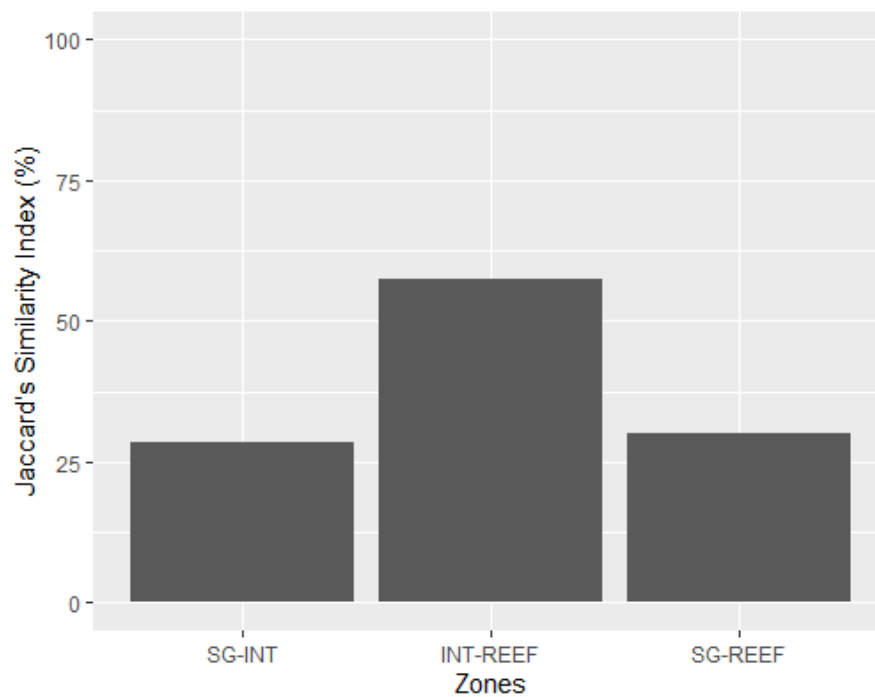


Figure 20: Jaccard's Similarity Indices for zone pairs within Malatapay MPA, Philippines. Higher values indicate a higher percentage of shared invertebrate species.

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Table 4: SIMPER results indicating which species are driving the observed dissimilarity in zonal invertebrate communities within Malatapay MPA, Philippines. Average abundance in each zone, contribution to dissimilarity between groups (%), and the cumulative total of contributions (%) are provided for each species.

(a) Seagrass-Interface

Species	Average Abundance		Contribution %	Cumulative %
	Seagrass	Interface		
<i>Drupella</i>	0.00	4.00	15.73	15.73
<i>Coralliophila</i>	0.00	3.47	12.32	28.05
Rock Murex	0.17	1.57	6.38	34.43
Other Shrimp	0.17	0.85	4.46	38.89
Rocky Turban	0.00	0.62	2.82	41.71
Olive Shell	0.64	0.17	2.77	44.48
Giant Clam	0.00	0.57	2.56	47.04
Mantis Shrimp	0.00	0.50	2.51	49.55
Other Topshell	0.00	0.46	1.87	51.42
Pearl Oyster	0.00	0.40	1.29	52.71
Big Lip Conch	0.00	0.17	1.00	53.71
Mimic Conch	0.00	0.17	0.50	54.21

(b) Seagrass-Reef

Species	Average Abundance		Contribution %	Cumulative %
	Seagrass	Reef		
<i>Diadema</i> Urchin	1.01	2.96	11.83	11.83
Sea Star	0.50	1.88	7.36	19.19
Banded Coral Shrimp	0.00	1.21	6.43	25.62
Cone Shell	1.04	1.08	4.59	30.21
Pinkfish Sea Cucumber	0.00	0.74	3.68	33.89
Other Cowrie	0.86	0.05	3.45	37.34
Olive Shell	0.64	0.05	3.17	40.51
Collector Urchin	0.73	0.00	3.11	43.62
Frog Shell	0.33	0.56	2.87	46.49
Small Conch	0.40	0.00	1.63	48.12
Scallop	0.33	0.00	1.37	49.49

(c) Interface-Reef

Species	Average Abundance		Contribution %	Cumulative %
	Interface	Reef		
<i>Coralliophila</i>	3.47	1.09	11.98	11.98
Rocky Turban	0.62	0.10	2.54	14.52
Giant Clam	0.57	0.00	2.32	16.84

3.2.2 Lutoban South MPA

Simpson's invertebrate species diversity was highest at the Interface (one-way ANOVA, $F_{2,28} = 5.698$, $p < 0.01$; Figure 21). Dispersals differed between groups, though post-hoc analyses (Tukey's HSD) revealed that variance only differed between the Seagrass and Interface zones. The Seagrass zone consisted largely of

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Seagrass Specialist species (66.9 %), with Generalists as the second most abundant group (32 %) and with very few Reef Specialists (1.1 %; Figure 22a). The Interface and Reef zones were very similar in overall composition: both zones consisted primarily of Generalists, with Reef Specialists being the second most abundant group, and had very low percentages of Seagrass Specialists (1.8 % and 1.7 % respectively; Figures 22b and 22c). The Seagrass community was significantly different to both the Interface and the Reef communities, which did not differ from one another (Figure 23), and zone accounted for approximately 29 % of the dissimilarity between groups (PERMANOVA, $R^2 = 0.290$, $F_{2,28} = 5.728$, $p \leq 0.001$). Of all target invertebrate species, 55.43 % were identified across the 31 invertebrate surveys conducted within Lutoban South MPA, and while adjacent zones had higher percentages of shared invertebrate species, the nonadjacent Seagrass and Reef zones still shared 25 % of species (Jaccard's Similarity Index; Figure 24). SIMPER analysis revealed that 11 species were responsible for driving the main community differences between the Seagrass and Interface zones (78 % variability overall; Table 5a), nine species for the Seagrass and Reef zones (79 % variability overall; Table 5b), and five species for the Interface and Reef zones (57 % variability overall; Table 5c).

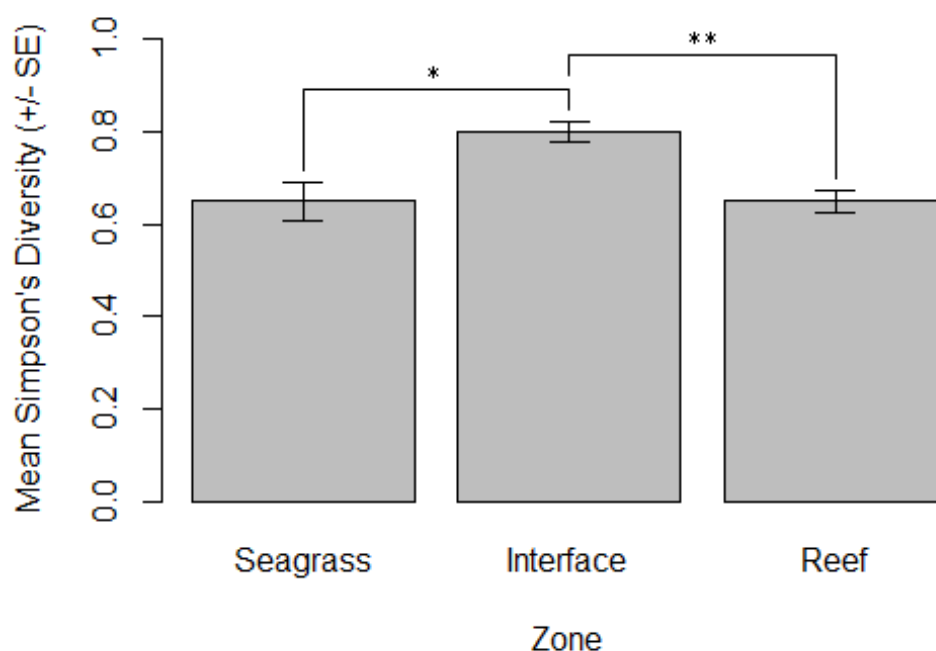


Figure 21: The effect of zone on Simpson's species diversity index across 31 invertebrate surveys (SG $n = 7$, INT $n = 6$, RF $n = 18$) conducted within Lutoban South MPA, Philippines. Connecting bars represent results of post-hoc analyses (Tukey's HSD), whereby asterisks indicate level of significance (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$).

Lutoban South MPA

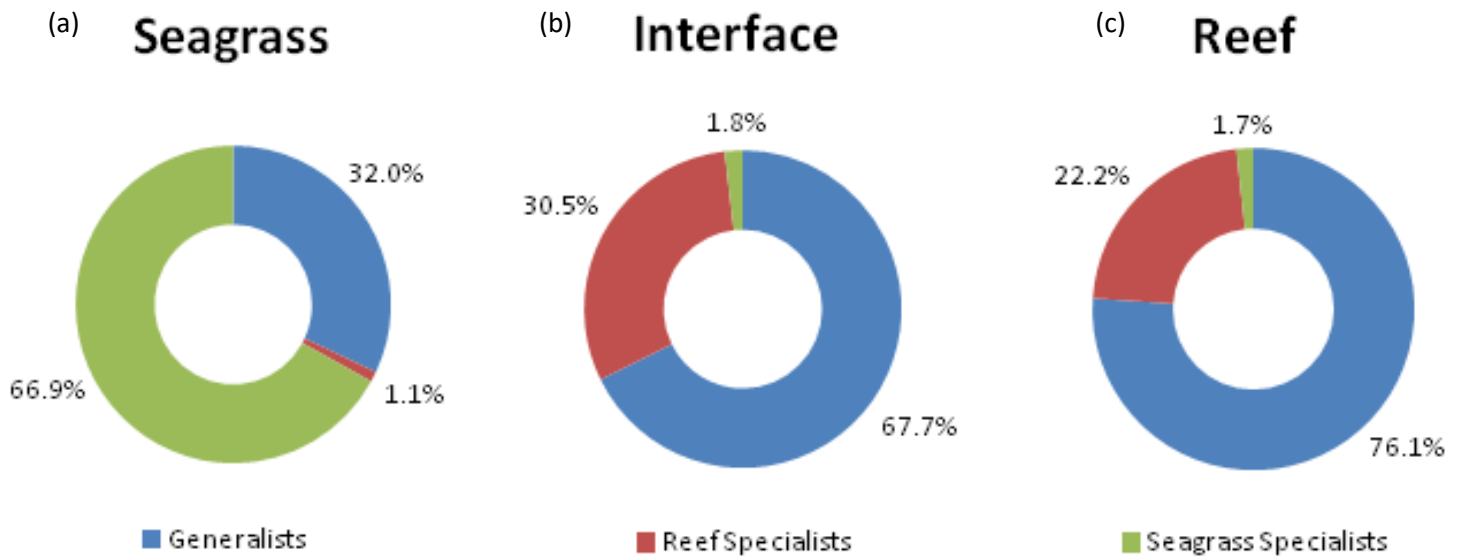


Figure 22: Composition of invertebrate communities in Seagrass (a), Interface (b) and Reef (c) zones within Lutoban South MPA, Philippines. Invertebrate species were broadly categorised by ecological niche, and each chart is composed of all surveys combined from within the given zone (SG n = 7, INT n = 6, RF n = 18). Percentages indicate group contribution to the overall invertebrate abundance within the zone (SG n = 562, INT n = 492, RF n = 1116).

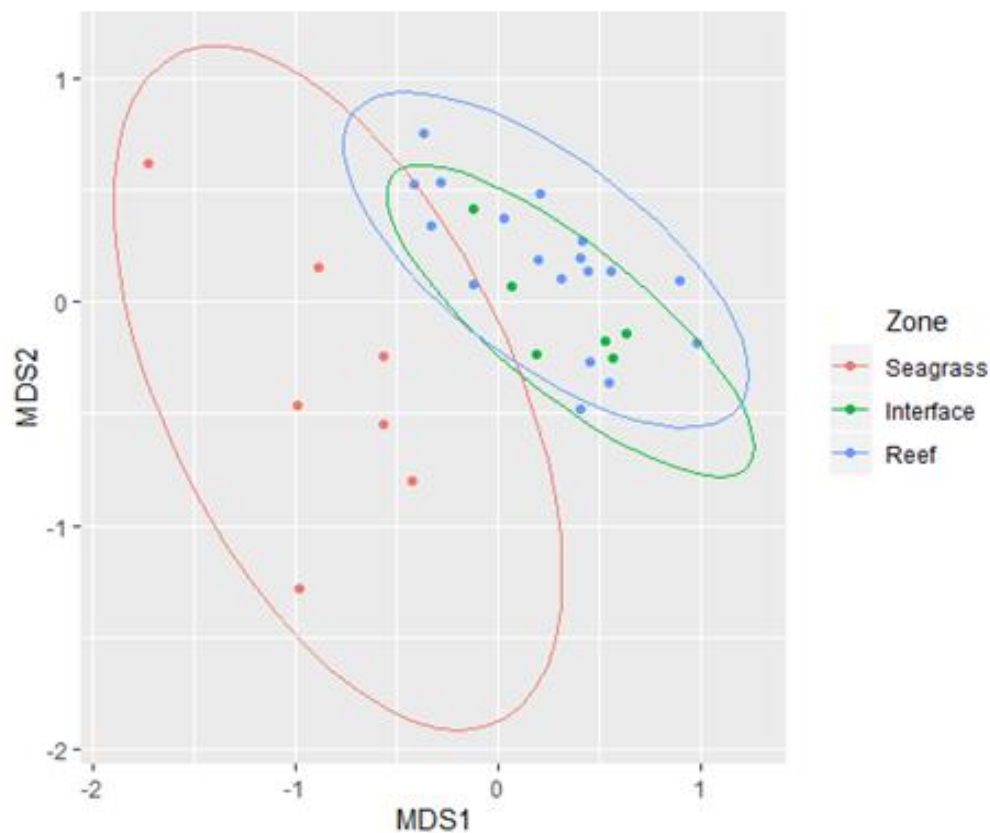


Figure 23: Differences in invertebrate community composition across Seagrass, Interface and Reef zones (Stress = 0.15) within Lutoban South MPA, Philippines. Data points represent invertebrate surveys (n = 31) and Bray-Curtis distances represent dissimilarity in community composition. Ellipses indicate 95% confidence intervals for clusters for each zone.

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

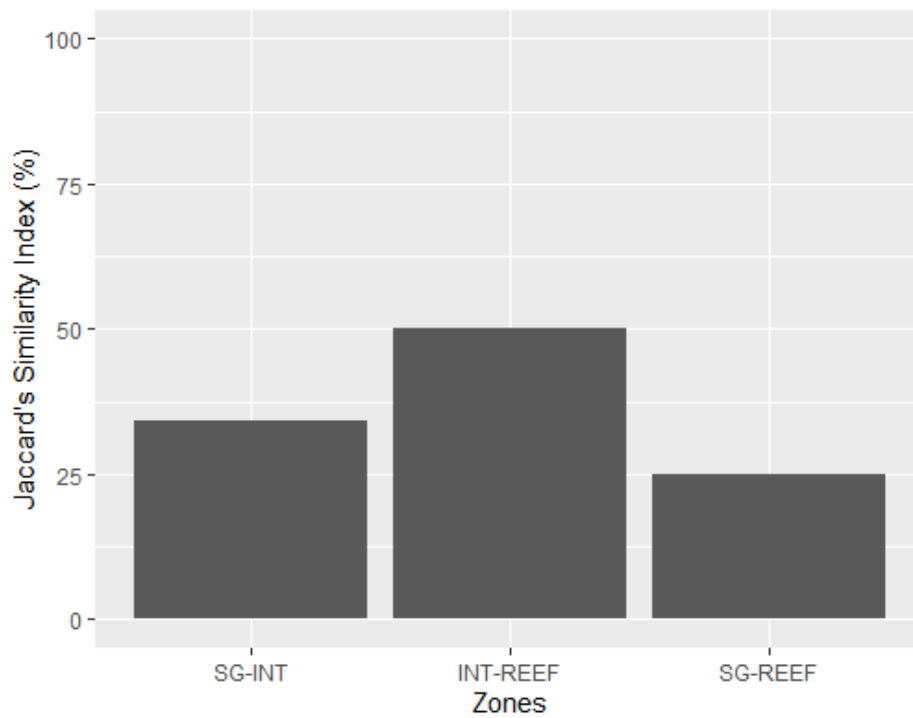


Figure 24: Jaccard's Similarity Indices for zone pairs within Lutoban South MPA, Philippines. Higher values indicate a higher percentage of shared invertebrate species.

Table 5: SIMPER results indicating which species are driving the observed dissimilarity in zonal invertebrate communities within Lutoban South MPA, Philippines. Average abundance in each zone, contribution to dissimilarity between groups (%), and the cumulative total of contributions (%) are provided for each species.

(a) Seagrass-Interface

Species	Average Abundance		Contribution %	Cumulative %
	Seagrass	Interface		
Rock Boring Urchin	0.00	2.38	6.75	6.75
<i>Coralliophila</i>	0.00	2.02	6.17	12.92
Pen Oyster	1.74	0.17	5.41	18.33
Sap-Sucking Slug	0.00	1.33	4.40	22.73
Cone Shell	0.53	1.60	4.09	26.82
Other Shell	0.29	1.11	3.09	29.91
Other Cowrie	0.14	0.74	2.21	32.12
Other Shrimp	0.00	0.33	1.27	33.39
Volute Shell	0.00	0.17	0.50	33.89
Common Egg Cowrie	0.00	0.17	0.49	34.38
Leopard Sea Cucumber	0.00	0.17	0.48	34.86

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

(b) Seagrass-Reef

Species	Average Abundance		Contribution %	Cumulative %
	Seagrass	Reef		
<i>Diadema</i> Urchin	0.74	5.31	16.85	16.85
Pen Oyster	1.74	0.00	7.74	24.59
Collector Urchin	2.16	0.21	7.66	32.25
Sea Star	2.57	2.11	6.25	38.50
Nudibranch	0.14	1.23	5.21	43.71
Banded Coral Shrimp	0.25	0.97	3.84	47.55
Other Bivalve	0.39	0.00	1.46	49.01
Scallop	0.29	0.00	1.17	50.18
Small Conch	0.29	0.00	1.11	51.29

(c) Interface-Reef

Species	Average Abundance		Contribution %	Cumulative %
	Interface	Reef		
Rock Boring Urchin	2.38	0.36	7.71	7.71
Sap-Sucking Slug	1.33	0.11	4.99	12.70
Cone Shell	1.60	0.58	4.91	17.61
Other Cowrie	0.74	0.00	2.90	20.51
Other Shrimp	0.33	0.00	1.52	22.03

3.2.3 Dalakit MPA

Simpson's invertebrate species diversity did not differ across the two zones ($t = -0.339$, $df = 12.835$, $p > 0.05$). The Seagrass zone was heavily dominated by Generalist species (92.3 %), with Seagrass Specialists being the second most abundant group (6.2 %), and with a very low percentage of Reef Specialists (1.5 %; Figure 25a). In contrast, the Reef zone was mainly comprised of Reef Specialists (68.4 %), with Generalists accounting for the remaining abundance (31.6 %, no Seagrass Specialists; Figure 25b). Dispersals did not differ between groups, and zonal communities were significantly different from one another, with zone accounting for approximately 57 % of the total variability between communities (PERMANOVA, $R^2 = 0.565$, $F_{1,13} = 16.89$, $p \leq 0.001$; Figure 26). Of all target invertebrate species, 36.96 % were identified across the 15 invertebrate surveys conducted in Dalakit MPA, and Jaccard's Similarity Index confirmed that 17.65 % of species were both reef- and seagrass-associated (Figure 27). SIMPER analysis revealed that 13 species were responsible for driving the main community differences between the two zones (89 % variability overall; Table 6).

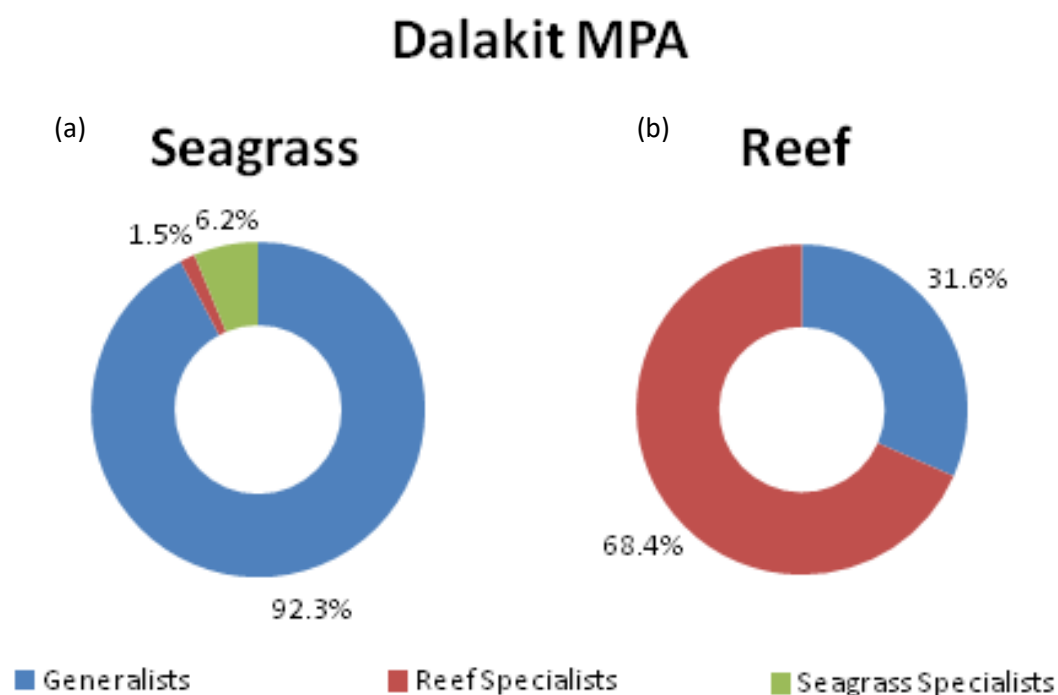


Figure 25: Composition of invertebrate communities in Seagrass (a) and Reef (b) zones within Dalakit MPA, Philippines. Invertebrate species were broadly categorised by ecological niche, and each chart is composed of all surveys combined from within the given zone (SG n = 9, RF n = 6). Percentages indicate group contribution to the overall invertebrate abundance within the zone (SG n = 274, RF n = 497).

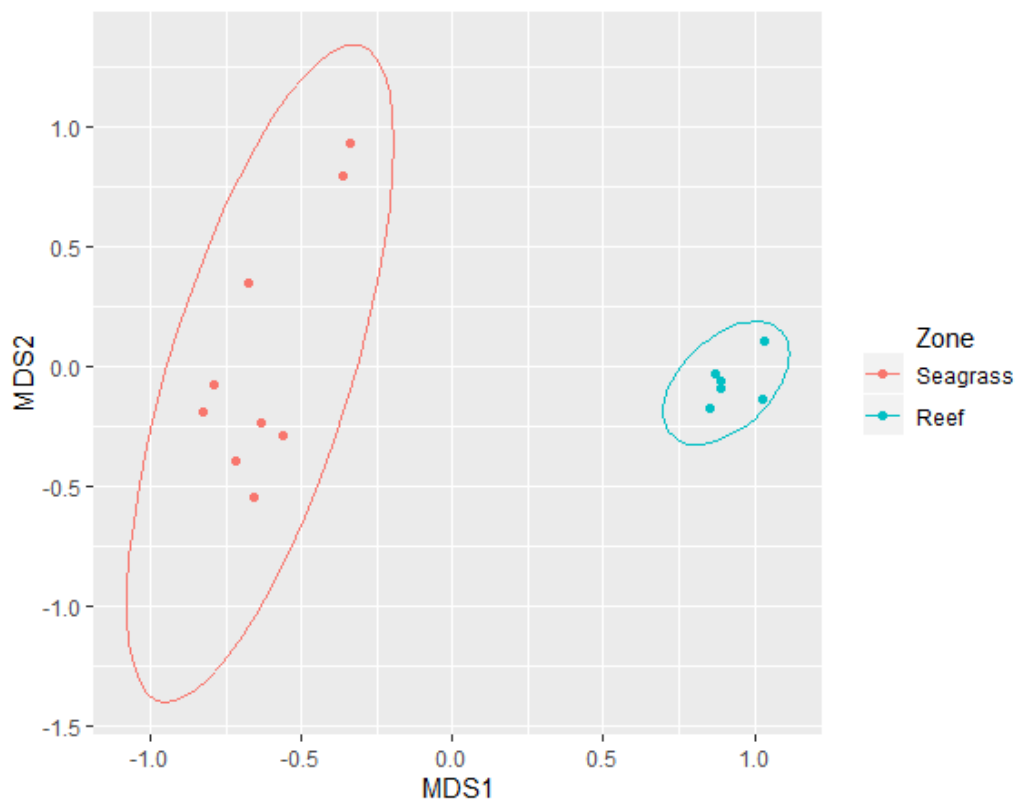


Figure 26: Differences in invertebrate community composition across Seagrass and Reef zones (Stress = 0.05) within Dalakit MPA, Philippines. Data points represent invertebrate surveys (n = 15) and Bray-Curtis distances represent dissimilarity in community composition. Ellipses indicate 95% confidence intervals for clusters for each zone.

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

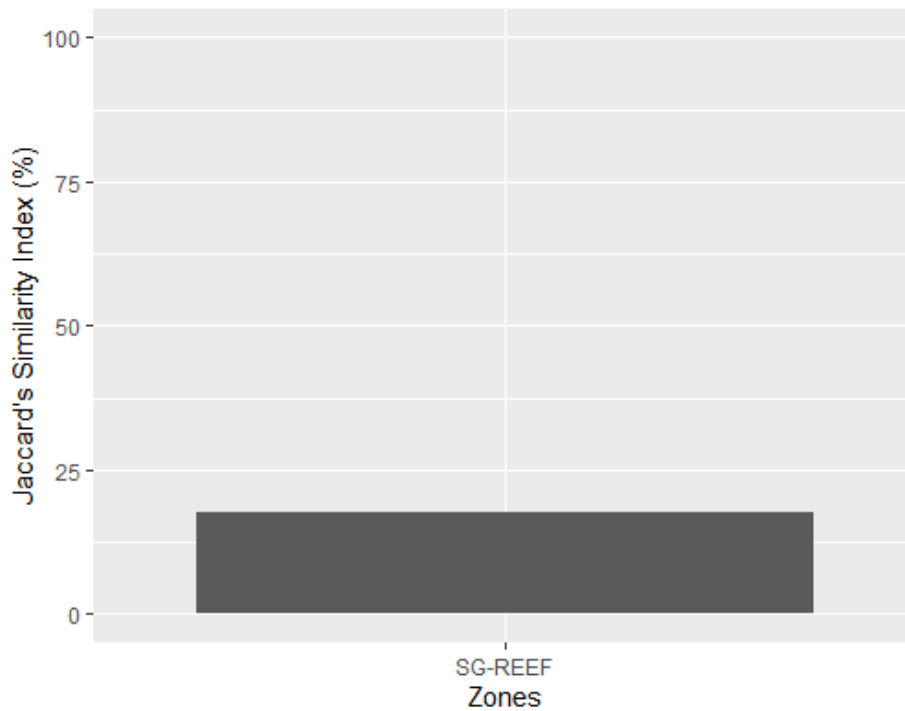


Figure 27: Jaccard's Similarity Index for Seagrass and Reef zones within Dalakit MPA, Philippines. Higher values indicate a higher percentage of shared invertebrate species.

Table 6: SIMPER results indicating which species are driving the observed dissimilarity in zonal invertebrate communities within Dalakit MPA, Philippines. Average abundance in each zone, contribution to dissimilarity between groups (%), and the cumulative total of contributions (%) are provided for each species.

Species	Average Abundance		Contribution %	Cumulative %
	Seagrass	Reef		
<i>Drupella</i>	0.00	5.32	17.18	17.18
<i>Diadema</i> Urchin	0.33	4.30	12.65	29.83
<i>Coralliophila</i>	0.00	3.89	12.41	42.24
Sea Star	0.27	1.65	4.75	46.99
Rock Boring Urchin	0.00	1.44	4.50	51.49
Rock Murex	0.16	1.48	4.34	55.83
Other Shell	1.44	0.57	3.11	58.94
Giant Clam	0.00	0.83	2.85	61.79
Boring Giant Clam	0.00	0.57	1.87	63.66
Banded Coral Shrimp	0.00	0.24	1.00	64.66
Honeycomb Oyster	0.00	0.17	0.71	65.37
Rocky Turban	0.00	0.17	0.48	65.85
Pearl Oyster	0.00	0.17	0.48	66.33

4. DISCUSSION

This study provides insight into seagrass-reef ecosystem connectivity within the Indo-Pacific region, though results appear to be both site-specific and taxon-specific: compositional variability occurred across all three sites, and connectivity trends appear to be driven by different phenomena for each taxon. Despite this variability, some consistent trends were observed across Malatapay MPA and Lutoban South MPA for both fish and invertebrate assemblages, whereas Dalakit MPA only showed similarities to other sites for invertebrates. In terms of wider application, this key combination of site-specificity and consistent connectivity trends can be used to inform future MPA management within Negros Oriental, Philippines.

4.1 Fish Communities

4.1.1 Malatapay MPA

Within Malatapay MPA, fish community composition patterns were inconsistent with my predictions. The Reef community was as equally diverse as the Interface community, contradicting previous studies that found species diversity to be highest at the ecotone between neighbouring habitats (Denys & Tschardtke 2002, Magura 2002, Kark 2013). Though fish abundance was lowest in the Seagrass zone, it did not significantly differ between the Interface and Reef zones, a trend that was driven at least in part by the presence of schooling species (sergeantfish and goatfish) in both zones. Fish biomass trends within Malatapay MPA were particularly interesting, as no significant differences occurred across all three zones; this seems to contradict previous studies that detail biomass increasing with habitat complexity (Smith et al. 2014, Casartelli & Ferragut 2018), including for reef fish assemblages (Charbonnel et al. 2002). This trend was driven by the combination of large numbers of small planktivorous fish being observed in the Reef zone, and a high percentage of top predators being observed in the Seagrass zone, some of which were very large. Interestingly, the Seagrass zone had a considerably higher percentage of top predators (12.7 %) than the other two zones (both 0.5 %). Of the nine top predators observed, three were trevallies (Carangidae), with one large 40-50 cm individual observed on one occasion and a pair of 20-30 cm individuals on another occasion. Many other studies conducted within the Indo-Pacific region have reported the occurrence of trevallies foraging in seagrass beds, both as adults and as juveniles (Unsworth et al. 2008, 2009, Morrison et al. 2014), so this was not unexpected. Of the other top predators observed in the Seagrass zone, four were cornetfish (*Fistularia commersonii*), which are also known to occur and forage over seagrass meadows (Bariche et al. 2009).

Surprisingly, the two remaining top predators observed in the Seagrass zone were longface emperors (*Lethrinus olivaceus*), both of which were very large in size (50-60 cm and 90-100 cm), and which were observed as a pair. Current literature offers little information in terms of why these longface emperors may have been situated in the Seagrass zone, with very few studies having previously reported sightings in seagrass beds. Longface emperors often spend their juvenile stages in seagrass beds (Tomascik et al. 1997), but based on the large size categories that were observed in the Malatapay MPA Seagrass zone, the individuals appeared to be adults. In lethrinids, protogynous hermaphroditism is the typical mode of sexuality, meaning females predominate at smaller sizes and males at larger sizes (Young & Martin 1982). This has recently been confirmed in *L. olivaceus*, and it was further found that females dominated in young age classes (1-8 years) and males in older age

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

classes (> 9 years) (Shimose 2021). Therefore, it is very likely that the smaller individual observed in the Seagrass zone was female, and that the larger individual observed was male. In terms of their purpose for being in the Seagrass zone, it could be presumed that as a top predator, the longface emperors were there to hunt. However, for the duration of the survey, the pair moved very slowly and didn't travel very far, which suggests that they were not hunting. This is supported by the fact that when excited (i.e. hunting), longface emperors often show mottled colour patterns or markings of deep red, which may disappear in a moment according to emotional state (FAO 1974, Carpenter & Allen 1989, see Jang 2020 for video footage). This mottled colouration was not seen in the individuals observed in the Malatapay MPA Seagrass zone. Furthermore, longface emperors are usually solitary (Carpenter & Allen 1989, Kuitert & Tono-zuka 2001), and can often be found schooling in large numbers to hunt, or forming large aggregations for spawning (Carpenter & Allen 1989): interestingly, no literature has detailed otherwise as of yet. Therefore, this sighting of a probable male-female pair seems to be a rare occurrence, and begs the question whether they were in fact a breeding pair. Very little is known about the spawning behaviour of lethrinids, which is not surprising as it is thought that most species spawn after dark (Carpenter & Allen 1989). Though individuals of *L. olivaceus* are known to be dioecious and to carry out external fertilisation (Currey et al. 2013), spawning periods vary across populations. For instance, preliminary data indicates that the peak spawning period for longface emperor populations on the Great Barrier Reef is from September to October, on an annual basis (Currey et al. 2013). In contrast, populations in Palau are known to be serial spawners, spawning throughout the year on the first few days of each lunar month (Carpenter & Allen 1989). In this study, the longface emperors were seen in the Seagrass zone on 5th February 2020, 11 days after the new moon according to an online database (25th January 2020; *Ver Calendario* 2018). While this does not align with previous studies, the variability in reproductive timing that has been reported across different *L. olivaceus* populations means that it is not possible to definitively reject reproduction as an explanation for the sighting. Additionally, lethrinid spawning occurs whilst individuals swim in circles either near the surface, or at the bottom of reef slopes (Carpenter & Allen 1989). Though this usually occurs in large aggregations, the longface emperors observed in the Seagrass zone within Malatapay MPA were seen at a fairly shallow depth (approximately 5 m), and so once again, reproduction cannot be conclusively ruled out as an explanation for the sighting. To further this, large males of *L. olivaceus* may develop a crimson-red cast on their face and fins when they are courting (Myers 1991). However, if this red colouration were present on the larger longface emperor observed during our survey, it is very unlikely that the divers would have been able to see it: as well as observing the fish from a distance, the divers did not have torches, without which their colour perception would have been altered by the loss of red light with depth, even at just 5 m. Hence, this courting behaviour remains a possibility. Overall, though some inferences point towards breeding, the reason for why the two longface emperors were in the Seagrass zone ultimately remains ambiguous.

Fish community connectivity trends within Malatapay MPA aligned with my prediction that fish assemblages would not differ across zone, indicating high ecosystem connectivity. This trend was driven by high percentages of shared species across zones (between 19 % and 61 %), with fish communities in neighbouring zones sharing more species than nonadjacent zones, which also aligned with predictions. Main differences between the adjacent Interface and Reef communities were driven by higher rabbitfish (Siganidae) abundances being observed in the Interface zone. Based on available size data (Woodland 2001), 164 of the 167 rabbitfish individuals seen in the Interface zone appeared to be juveniles (total length < 20 cm); in contrast, only 12 rabbitfish juveniles were observed on the Reef. This indicates a strong preference for the Interface zone, perhaps as it

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

provides individuals with greater accessibility to the Seagrass zone, which juvenile siganids use as foraging grounds (Erftemeijer & Allen 1993) and for refuge (Simanjuntak et al. 2020). This is supported by the fact that juvenile rabbitfish were often seen moving across the Seagrass-Interface boundary whilst often forming small schools consisting of multiple species, presumably for protection (Kasumyan & Pavlov 2018). An alternative explanation for this may be that juvenile rabbitfish transition from seagrass interiors to seagrass near reefs (i.e. the Interface) as they age, so they are appropriately located in the vicinity of their adult habitats (i.e. the Reef) - a trend that has been reported for the parrotfish species *Sparisoma cretense* (Espino et al. 2014). Furthermore, though higher connectivity was observed between neighbouring zones, nonadjacent Seagrass and Reef communities still shared almost 20 % of species. With the exception of the longface emperors, the top predator species seen in the Seagrass zone (trevally and cornetfish) were also Reef-associated, highlighting the use of seagrasses as foraging grounds by these species (Unsworth et al. 2008, 2009, Bariche et al. 2009, Morrison et al. 2014). Other shared species between the Seagrass and Reef zones included cleaner wrasse, butterflyfish, surgeonfish, goatfish, rabbitfish and parrotfish, with almost all individuals of the latter three families observed in the Seagrass zone appearing to be juveniles. As such, my results align with previous reports of these families using seagrass beds as nursery grounds within the Indo-Pacific (Erftemeijer & Allen 1993, Vijay Anand & Pillai 2005, Unsworth et al. 2007, Simanjuntak et al. 2020). Thus, it appears that, as predicted, the high connectivity observed between fish communities within Malatapay MPA was driven by the high interzonal mobility of certain fish groups (i.e. top predators and juveniles). Despite there being limited literature on seagrass-reef ecosystem connectivity within the Indo-Pacific, my findings show some consistencies with that of an earlier seagrass-reef connectivity study conducted within Malatapay, prior to its demarcation as an MPA in 2018: Kochzius (1997) also found goatfish (Mullidae), rabbitfish (Siganidae) and parrotfish (Scaridae) species to exhibit seagrass-reef connectivity, though of these families, only Mullidae appeared to use the seagrass as a nursery area. In addition to this, my findings are consistent with that of a more recent study conducted by Unsworth et al. (2008) within eastern Indonesia, which also documented high connectivity of fish communities between seagrass and reef habitats; seagrass beds acted as an important habitat for juvenile fishes (including goatfish), and top predators (including trevallies) were seen in seagrass beds close to reefs.

4.1.2 Lutoban South MPA

As with Malatapay MPA, fish communities within Lutoban South MPA showed composition patterns that contradicted my predictions. Fish species diversity values for the Seagrass zone and, to a lesser extent, for the Reef zone were unexpectedly high, resulting in all three zones being equally diverse. This not only contradicts previous studies that detail species diversity being highest within ecotones (Denys & Tschardtke 2002, Magura 2002, Kark 2013), but also those that show diversity to be higher on coral reefs than in seagrass beds (Bosire et al. 2012, Liu 2018). Fish abundance trends within Lutoban South MPA were particularly similar to that of Malatapay MPA in that it did not differ across zone, and that it appeared to be driven at least in part by the presence of schools in all three zones; the abundant schooling species included those at Malatapay MPA (i.e. sergeantfish and goatfish), with the addition of unicornfish and fusiliers. These findings are not only inconsistent with my prediction, but also with that of other studies, which frequently report higher fish abundance on coral reefs than in seagrass beds (Honda et al. 2013, Liu 2018), though the inverse has also been documented (Liu 2018). Interestingly, as with Malatapay MPA, fish biomass did not differ across the three zones within Lutoban South MPA. This yet again contradicts my prediction, as well as previous

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

work that details biomass increasing with habitat complexity (Smith et al. 2014, Casartelli & Ferragut 2018), including for reef fish assemblages (Charbonnel et al. 2002). This appears to be driven by primarily small planktivorous fish being observed on the Reef, skewing data towards low biomass, reaching levels similar to that of the other two zones.

Similarly to Malatapay MPA, fish community connectivity trends within Lutoban South MPA were consistent with my predictions. Once again, fish assemblages were similar across all three zones, indicating high ecosystem connectivity, and this was driven in part by high percentages of shared species across zones (between 22 % and 46 %). Fish communities in neighbouring zones shared more species than nonadjacent zones, yet again aligning with my predictions. Interestingly, no top predators were present in the Seagrass zone at all, which contrasts strongly to results for Malatapay MPA; this suggests that the Seagrass zone does not act as such an important foraging ground for top predators at this site. A unique observation within Lutoban South MPA was the presence of three scrawled filefish (*Aluterus scriptus*) juveniles in the Seagrass zone. This aligns with the findings of León et al. (2004), who documented low biomass of *A. scriptus* within algal-seagrass beds in the Dominican Republic. Though adults of *A. scriptus* were not seen on the Reef at Lutoban South MPA, they were seen on coral reefs at other sites within the region during training, and are known to be typically reef-associated (Floeter et al. 2006, 2007, Izzo et al. 2010, Aguilar-Medrano et al. 2018, Cortés-Useche et al. 2018). As such, *A. scriptus* is likely to show an ontogenetic habitat shift from Seagrass to Reef zones within Lutoban South MPA. Though higher connectivity was observed between neighbouring zones, nonadjacent Seagrass and Reef communities still shared approximately 22 % of species, which is very similar to the percentage seen within Malatapay MPA (19.57 %). Shared species included sergeantfish, fusiliers and unicornfish, all of which are schooling planktivores, and thus accounted for almost 90 % of the total abundance seen within the Seagrass zone. The remaining shared species included the goatfish and rabbitfish families, and as with Malatapay MPA, almost all individuals of these families appeared to be juveniles according to available size data (goatfish TL < 20 cm; Randall 2001, rabbitfish TL < 20 cm; Woodland 2001). Once again, these findings are consistent with those of many other studies conducted within the Indo-Pacific that report these families using seagrass beds as nursery ground within the region (Erftemeijer & Allen 1993, Vijay Anand & Pillai 2005, Unsworth et al. 2007, Simanjuntak et al. 2020), including in Negros Oriental, Philippines (Kochzius 1997). Therefore, as concluded for Malatapay MPA and in line with predictions, it seems that the high interzonal mobility of certain fish groups (i.e. planktivorous schooling fish and juveniles) is responsible for the high ecosystem connectivity observed between Lutoban South MPA fish communities. This aligns with the findings of Unsworth et al.'s (2008) connectivity study, which reported juvenile fish (including goatfish) using seagrass beds as a nursery habitat, as well as high seagrass abundances of the unicornfish *Naso vlamingii*, which is a schooling planktivorous species (Marine Research Section 1997, Quimpo et al. 2019). Interestingly, the individuals of *N. vlamingii* seen during this study were reported to be juveniles. Based on available size data for five *Naso* species (Randall 1984, Marine Research Section 1997), it appears that the unicornfish seen within the Seagrass zone at Lutoban South MPA may have also been juveniles (10-20 cm total length); however, with the limited availability of size data for the *Naso* genus, and without identification to the species level, it is not possible to firmly conclude this.

4.1.3 Dalakit MPA

Unlike for the other two sites, some fish community composition trends within Dalakit MPA were consistent with my hypotheses: both fish species diversity and abundance were higher on the Reef

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

than in the Seagrass zone, which aligns with available literature (Honda et al. 2013, Bosire et al. 2012, Liu 2018). Fish species diversity was unexpectedly high on the Reef (Figure 13), especially given its small size and single depth range (Shallow). In addition, the fish species accumulation curve for the Reef zone at Dalakit MPA did not plateau after just four surveys (Appendix E), suggesting that a greater number of Reef surveys would have provided a more accurate representation of the fish community. Having said this, it is unlikely that additional Reef surveys would have altered the overall trends seen within Dalakit MPA, except perhaps for fish biomass, as the Seagrass fish community appears to be well-represented (Appendix E). As with the other two sites, fish biomass did not differ across the two zones, yet again contradicting my prediction, as well as previous literature that details biomass increasing with habitat complexity (Smith et al. 2014, Casartelli & Ferragut 2018), including for reef fish assemblages (Charbonnel et al. 2002). This trend seems to be driven by a combination of larger reef fish (up to 30 cm total length) being consistently observed in the Seagrass zone, and high numbers of small and juvenile fish (up to 10 cm total length) being observed on the Reef.

In contrast to the other two MPA sites, Dalakit MPA fish community connectivity trends strongly contradicted my predictions. Zonal fish assemblages differed significantly from one another, with zone accounting for almost 70 % of the total dissimilarity between communities. Combined with the unexpectedly low percentage of shared fish species observed across the Seagrass and Reef zones (8.11 %, 3 species), this indicates very low ecosystem connectivity. Only one individual of a single top predator species (cornetfish) was shared across the two zones, suggesting that the Seagrass zone does not act as an important foraging ground for top predators within Dalakit MPA. The two remaining shared species included porcupinefish (Diodontidae), which are habitat generalists known to frequent seagrass beds (Leis 2001, Sambrook et al. 2019), and the sweetlips family (Haemulidae). A single juvenile sweetlips (0-5 cm) was observed in a shallow pit covered with biological debris within the Seagrass zone, which is consistent with previous studies that detail sweetlips species depending on seagrass meadows during their juvenile stages (McKenzie 2014, McKenzie & Yoshida 2014). In addition, three older sweetlips individuals (20-30 cm) were observed within the Reef zone at Dalakit MPA, aligning with studies that describe sweetlips as being typically reef-associated species (McKay 2001). Hence, my findings suggest that sweetlips show an ontogenetic habitat shift from seagrass beds to reefs, though they seem to be the only group to do so at this site. Thus, in contradiction with the findings of many other studies (Erftemeijer & Allen 1993, Kochzius 1997, Dorenbosch et al. 2005, Vijay Anand & Pillai 2005, Unsworth et al. 2007, 2008, Verweij et al. 2008, Campbell et al. 2011, Jaxion-Harm et al. 2012, Morrison et al. 2014, Simanjuntak et al. 2020), and unlike for the other two sites, the Seagrass zone does not appear to act as an important fish nursery ground within Dalakit MPA.

According to available literature, it appears that the unexpectedly low connectivity between zonal fish communities within Dalakit MPA was most likely driven by the specific configuration of the site. Compared with reefs directly adjacent to seagrasses, greater distances between reef and seagrass beds have been known to lower juvenile biomass in the seagrass (Espino et al. 2014), and significantly reduce seagrass fish densities, often to the point of species absence (Dorenbosch et al. 2005). As such, the lack of a seagrass-reef interface at Dalakit MPA, and instead the existence of rocky area between the two zones, likely alters fish assemblages by inherently increasing the distance between the Seagrass and Reef zones. Similarly, Dorenbosch et al. (2007) found fish assemblage composition, species richness, fish density and fish size within both seagrass and reef habitats to be related to the configuration of seagrass habitats in relation to the coral reef. This was

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

thought to have been driven by varying levels of habitat accessibility, which can affect short distance migration by reef-associated fishes or predators, and ontogenetic migration over larger distances (Dorenbosch et al. 2007). Thus, the rocky area between the Seagrass and Reef zones within Dalakit MPA may also reduce fish accessibility to the Seagrass from the Reef, and vice versa, lowering community connectivity. Another possible explanation for the low connectivity seen between zonal fish communities at Dalakit MPA may be the seagrass species composition and abundances within the Seagrass zone. Attributes of seagrass structure, including seagrass canopy height, seagrass cover and shoot density have been found to influence juvenile fish densities (Gullström et al. 2008), fish species richness and dominant fish species (Pogoreutz et al. 2012). Similarly, Dorenbosch et al. (2007) suggested that differences in fish assemblages may be explained by varying levels of habitat complexity, which can affect shelter possibilities of a habitat with respect to predation. On the other hand, Campbell et al. (2011) found no evidence at all to suggest that high fish densities in seagrass habitat were influenced by seagrass structural characteristics, whilst many other studies have found the presence or absence of seagrass to be a more important determinant of fish density and structure than seagrass species composition (Jenkins & Wheatley 1998, Nakamura & Sano 2004a, Webster 2004, Dorenbosch et al. 2005). Unfortunately, within Dalakit MPA, seagrass species composition and relative abundances within the Seagrass zone remain unknown; hence, while it is possible that these factors influence connectivity between zonal fish assemblages, this cannot be explored in detail for this site.

4.1.4 Fish ecosystem connectivity across all sites

Overall, fish connectivity trends for Malatapay MPA and Lutoban South MPA were extremely similar: both sites showed high seagrass-reef ecosystem connectivity across the three zones, which appeared to be driven by the high interzonal mobility of certain fish groups. Based on previous literature (Dorenbosch et al. 2007, Gullström et al. 2008, Pogoreutz et al. 2012), it seems likely that these similarities in connectivity may be driven by similarities in site configuration, and in seagrass species composition and abundances within the Seagrass zones: both sites have a very large plateau at 5 m depth and a steep reef slope from 9 m to 16 m, with *Syringodium isoetifolium* and *Thalassia hemprichii* being the most abundant seagrass species within both Seagrass zones. Despite these striking consistencies in connectivity, different fish groups were responsible for driving the ecosystem connectivity observed within Malatapay MPA (juveniles and top predators) and Lutoban South MPA (juveniles and schooling planktivores). Furthermore, fish seagrass-reef ecosystem connectivity was very low within Dalakit MPA, which strongly contradicted the trends seen for the other two MPAs, where connectivity was approximately 2.5 times higher. As discussed, previous literature suggests that this is likely due to the very different habitat configuration of Dalakit MPA compared with the other two sites (i.e. no Interface zone, Reef zone closer to the shoreline than the Seagrass zone; Dorenbosch et al. 2005, 2007, Espino et al. 2014), as well as potential differences in seagrass species composition and abundance (Dorenbosch et al. 2007, Gullström et al. 2008, Pogoreutz et al. 2012). Other factors that may have played a role in this between-site variability is the comparatively shallow depth of the Reef zone within Dalakit MPA (3 m - 7 m), and local setting (e.g. artificial reef near to Dalakit MPA) (Pogoreutz et al. 2012, Morrison et al. 2014). Across all fish surveys, 16 of the total 95 target fish species (16.8 %) were both seagrass- and reef-associated. This aligns with the findings of a similar study conducted within the Indo-Pacific that reported shared seagrass-reef species accounting for approximately 15 % of all coral reef fishes (Nakamura & Sano 2004b). It is important to note, however, that none of the 16 seagrass-reef fish species in the present study were shared across all three MPA sites. Taking all of this into account, the results of

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

this study indicate that ecosystem connectivity trends are site-specific, aligning with studies that report habitat value and seascape connectivity as being contextual (Dorenbosch et al. 2007, Morrison et al. 2014, Henderson et al. 2017).

4.2 Invertebrate Communities

Invertebrate community composition trends varied depending on the site. Within Lutoban South MPA, invertebrate species diversity was highest at the Interface; this aligns with the findings of other studies that found species diversity to be highest at the ecotone (Denys & Tschardt 2002, Magura 2002, Kark 2013), and was the only instance during this study where species diversity trends met my prediction. In contrast, species diversity values for the Seagrass and Reef zones within Malatapay MPA were unexpectedly high, resulting in all three zones being equally diverse. Similarly, species diversity did not differ across zone within Dalakit MPA. These findings not only contradict my prediction and the studies detailed above, but also studies that report species diversity differing across habitats (Bosire et al. 2012, Liu 2018). Interestingly, this trend of equal diversity across all three zones was the same for both fish and invertebrate communities within Malatapay MPA, whereas species diversity trends varied across taxa for the other two sites. A unique observation within Lutoban South MPA was the presence of 343 bell's urchins (*Salmacis spp.*) on a single survey within the Seagrass zone; individuals were seen in dense clusters, often forming stacks with individuals situated on top of others. This suggests that the transect line for this survey may have been positioned within a bell's urchin breeding ground. Though there is no literature available for whether spawning aggregation occurs in *Salmacis spp.*, this observation appears to be consistent with the findings of Gaudette et al. (2006) and Hawaii Association for Marine Education & Research (2017), who document mass spawning occurring in large, dense populations for other sea urchin species. Another key finding was that during the three invertebrate surveys conducted within the Dalakit MPA Seagrass zone at night time, four 'new' target species were observed that had not yet been seen at Dalakit MPA (i.e. during the day). These included other cleaner shrimp, moon shell, swimming crab and squid (bobtail squid *Euprymna sp.* and either Idiosepiidae or Loliginidae). In fact, three of these species (moon shell, swimming crab, bobtail squid) had not been seen on any survey at any site prior to this. This suggests that these species may be primarily nocturnal, which is supported by available literature (Takahashi & Kawaguchi 2001, Jones & Nishiguchi 2004, Pastorino 2005). Not only did this increase the accuracy of species richness at Dalakit MPA, but this also highlighted the need to conduct night surveys, to account for the species diversity or connectivity contributions of nocturnal species.

Though invertebrate community connectivity trends were fairly consistent across all three MPA sites, there was some between-site variability. Within Lutoban South MPA, the Seagrass assemblage was significantly different to that of the Interface and Reef zones, which did not differ from one another. Though this indicates low ecosystem connectivity between the Seagrass community and that of the other two zones, there appeared to be higher connectivity between the Interface and Reef communities; this was reinforced by the high percentage of shared species (50 %) and extremely similar community composition of the two zones (Figures 22b-c) at this site. This trend somewhat contradicted my prediction that all zonal communities would differ, and varied slightly from the connectivity trends seen at the other two sites: invertebrate assemblages significantly differed across all three zones within both Malatapay MPA and Dalakit MPA, indicating low ecosystem connectivity, as predicted. Similarly to species diversity trends, Jaccard's similarity trends were also site-specific to a degree. Within Lutoban South MPA, neighbouring zones shared more

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

species than the nonadjacent Seagrass and Reef zones, as predicted; however, as this trend was as equally strong as that for fish communities, this contradicted my prediction that it would be weaker for invertebrates. In contrast, the Malatapay MPA Seagrass community unexpectedly shared more species with the Reef community (30 %) than with that of the Interface (28.57 %). Though this somewhat contradicted my hypothesis that neighbouring zones would share more species than nonadjacent zones, the neighbouring Interface and Reef zones still shared the highest percentage of species (57.5 %) at this site. Hence, this finding aligns with my prediction that this trend would be weaker for invertebrate communities compared with fish communities. Despite these site differences, percentages of shared species across the Seagrass and Reef zones were similar for Lutoban South MPA (25 %) and Malatapay MPA (30 %), which in fact amounted to the same number of shared species (12) at each site. Dalakit MPA had a lower percentage of invertebrate species shared across the Seagrass and Reef zones (17.6 %) than the other two sites, with half the number of shared species. As with the fish communities at Dalakit MPA, this may be due to differences in seagrass community composition or habitat configuration (i.e. rocky area, increased distance between Seagrass and Reef zones) compared with the other two sites (Heck 1977, Lanham et al. 2021).

Once again, though overall connectivity trends were relatively consistent across all three MPAs, the invertebrate species driving these trends were somewhat site-dependent. Of the total number of species that were found in both the Seagrass and Reef zones within each site, four, five and one species were unique to Malatapay MPA, Lutoban South MPA and Dalakit MPA respectively. Having said this, Malatapay MPA had two seagrass-reef shared species (collector urchin, frog shell) in common with Lutoban South MPA, and one other (rock murex) in common with Dalakit MPA. Furthermore, five seagrass-reef shared species were common across all three sites (*Diadema* urchin, cone shell, other shell, nudibranch, sea star). Most of the connectivity observed between the Seagrass and Reef zones at each site was driven by generalist species: eight of the 12 shared species at Malatapay MPA, nine of the 12 at Lutoban South MPA, and five of the six within Dalakit MPA were habitat generalists. Across all three sites, these generalist species accounted for between 94 % and 96 % of the total connectivity that was observed between the Seagrass and Reef zones. For instance, within Malatapay MPA, 611 individuals of the seagrass-reef shared species were seen across all Seagrass and Reef surveys, and 575 of these were habitat generalists (94.11 %). Interestingly, for all three sites, several of the shared generalist species were also responsible for driving community differences between the Seagrass and Reef zones; this demonstrates that although they were found (and often abundant) in both habitats, their overall abundance still significantly differed across the two zones. The remaining 4-6 % of the total seagrass-reef connectivity for each site was driven by habitat specialists. For both Malatapay MPA and Dalakit MPA, only one individual of each specialist species was recorded in their non-specialist habitat across all invertebrate surveys, resulting in their limited contribution to the total connectivity. With habitat generalists accounting for the vast majority of the limited connectivity observed between the Seagrass and Reef communities at all three sites, my findings support my prediction that invertebrate connectivity trends would be driven by ecological niche requirements. This is further supported by the fact that invertebrate community composition also appeared to be driven by ecological niche across all sites: Seagrass zones were consistently dominated by generalists and seagrass specialists, with reef specialists accounting for just 1.1 % to 2.5 % of the total abundance at each site (Figures 18a, 22a, 25a). In contrast, the reverse trend was seen within the Interface (where present) and Reef zones, with these zones consisting primarily of generalists and reef specialists, and with seagrass specialists responsible for 0 % (none within the Dalakit Reef zone) to 1.8 % of the total abundance (Figures 18b-c, 22b-c, 25b).

There are very few studies that assess seagrass-reef ecosystem connectivity for invertebrate communities. Having said this, my findings for invertebrate communities appear to align with that of Heck (1977), who found that invertebrate community composition within seagrass meadows varied across site, with differences being driven by habitat preferences of individual species. This study also reported some reef-associated invertebrate species "spilling over" into the neighbouring seagrass habitat (Heck 1977) which, once again, aligns with the ecosystem connectivity observed across all sites in this study. My results are also consistent with that of another study conducted by Nakamura & Sano (2005), who described habitat suitability and complexity as being determinants of invertebrate community composition within seagrass beds, whilst also finding some invertebrate taxa to be present in both seagrass and adjacent reef habitats. Based on the limited mobility of most, if not all, of the seagrass-reef species seen across the three sites, it can be assumed that connectivity does not exist on the organismal level, as for fish (i.e. nursery or foraging grounds). On the other hand, for many of these shared species, studies have documented long-distance larval dispersal and high gene flow between populations within the Indo-Pacific (collector urchin; Malay et al. 2000, *Diadema* urchin; Lessios et al. 2001, cone shell; Duda et al. 2012, crown of thorns; Vogler et al. 2013, pen oyster; Lemer et al. 2016, thorny oyster; Lodeiros et al. 2016) or the East-Atlantic (frog shell; Crocetta et al. 2020). Therefore, given the vast distances that their larvae are able to disperse, and the limited distance between the Seagrass, Interface and Reef zones within Malatapay MPA, it is likely that these species show gene flow across zones, and thus connectivity at the population level rather than at the organismal level.

4.3 Management Implications

Despite being a key component of marine ecosystems, seagrass meadows are largely understudied and underdocumented in South-East Asia (Waycott et al. 2009); hence, it is likely that they are currently receiving inadequate protection. First and foremost, my findings illustrate the importance of incorporating seagrass beds into Marine Protected Areas. Of MCP's 95 target fish species, 21 were observed within the Seagrass zone at one or more of the MPA sites, with 19 of these species being commercially important to local communities within Negros Oriental, and 16 species showing connections to the Reef. The Seagrass zones appeared to act as a temporary habitat for many of these species; by acting as foraging, nursery and potentially breeding grounds, the seagrass beds support the growth and survival of these species, and thus local fish fisheries. The Seagrass zones also act as a habitat for many invertebrate species, though this is likely to be on a permanent basis for these taxa. Of MCP's 91 target invertebrate species, 36 were seagrass-associated; 28 of these species were commercially important to local communities, either as a food source (including gleaning for local consumption) or for the shell trade, and 17 species showed connections to the Reef, though this was most likely in the form of genetic connectivity. In addition, 10 of the 36 seagrass-associated invertebrate species (eg, crabs, sea urchins, sea stars) are known to form the diet of many commercial fish species in the region. Hence, once again, the Seagrass zones support the growth and survival of many important invertebrate species, and thus local fish and invertebrate fisheries. Through the current protection of the seagrass beds within the Zamboanguita MPAs, the Zamboanguita municipal government unit is not only protecting these valuable species, but is also inherently protecting the connectivity, or lack thereof, associated with Reef communities, meaning: reef fish species remain protected during important seagrass-reef migrations; entirely different invertebrate assemblages are being protected within the seagrass beds compared with those protected on the reefs; and the genetic diversity of many invertebrate species is being maintained

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

across seagrass and reef communities, which is important for population health. Furthermore, through protection, the species diversity associated with these seagrass communities is being preserved. Given that high species diversity can increase ecosystem stability (Tilman 1996, McCann 2000, Lamy et al. 2020), and that species diversity generally increases with habitat diversity (Roberts et al. 2003), protecting the diversity of multiple habitats may increase ecosystem stability within Negros Oriental. This is especially important within South-East Asia as the number of natural disturbances occurring within the region is increasing, a trend that is expected to continue (Asian Development Bank 2013). Finally, though it was not investigated in this study, inclusion of the seagrass beds within the MPAs studied here has likely mitigated certain threats, such as mechanical damage, by regulating marine activities (eg, forcing boat traffic to relocate parking to the sandy area south of Malatapay MPA). Therefore, it becomes apparent that by protecting seagrasses, local governments are able to support local food security and local livelihoods, but also the overall health and stability of entire seagrass-reef ecosystems. This is particularly beneficial in South-East Asia, as millions of people heavily rely on the resources and employment associated with marine capture fisheries (Bailey & Pomeroy 1996).

My findings are similar to that of another seagrass-reef connectivity study conducted by Sambrook et al. (2019) within the Indo-Pacific region; these authors found that almost 20 % of the 2642 fish species present in the highly diverse Coral Triangle region (Allen 2015) are likely to occur in both reef and non-reef habitats (including seagrass beds). Though MCP do not monitor all fish species, this finding is similar to the degree of fish connectivity observed in this study, whereby 16 (16.84 %) of the 95 fish species monitored by MCP were observed in both the Seagrass and Reef zones. Many other connectivity studies have advocated for the protection or restoration of Indo-Pacific seagrass beds based on the support they provide to adjacent fisheries (Unsworth & Cullen 2010, Blandon & zu Ermgassen 2014, Unsworth et al. 2014, Cullen-Unsworth & Unsworth 2018, Unsworth et al. 2019). Interestingly, there are also several instances where researchers have demonstrated the benefits of using ecosystem connectivity information to inform MPA management decisions. For instance, Magris et al. (2018) found that the best strategy for enhancing biodiversity persistence in fish populations was to combine both representation and connectivity objectives. Similarly, De Leo & Micheli (2015) demonstrated how knowledge of species connectivity can be used to inform reserve sizing decisions: for larval dispersal > 10 km, one or two large reserves were found to be more efficient in terms of fisheries gains than 10 or 20 small reserves covering the same area. As demonstrated by my own findings, decision-makers can also use information about ecosystem connectivity to optimise reserve habitat composition. McLeod et al. (2009) argue that connectivity between functionally linked habitats is essential for maintaining ecosystem function and resilience, and that this should be incorporated into marine reserve planning. For instance, to account for self-seeding through larval dispersal, and for the movement of adults and juveniles of mobile species, these authors recommend that areas in close proximity to a zone of interest should also be protected. Hence, consistent with my own findings, these authors advocate for the inclusion of entire ecological units (as well as buffer zones) within MPA network design (McLeod et al. 2009).

Another key finding from my study is that MPAs should be managed independently, on a site-by-site basis. Though some consistent trends were observed, these were often driven by different groups depending on the site. For instance, the high connectivity between zonal fish communities within Malatapay MPA appeared to be driven by top predators and juveniles, whereas for Lutoban South MPA, the same trend was instead driven by schooling planktivores and juveniles. Furthermore, fish connectivity trends within Dalakit MPA strongly contrasted those observed for the other two sites,

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

most likely due to differences in habitat configuration, and perhaps seagrass species composition. This between-site variability illustrates the importance of considering each site as its own ecological unit, as well as the inability of management bodies to make broad assumptions about ecosystem connectivity. These findings align with many other studies that advocate for site-specific management of MPAs for similar reasons. Jaxion-Harm et al. (2012) found that the nursery value of seagrasses could not be generalised at the family level for fish species, and that nursery value varied between islands and sites. Thus, these authors argue that seagrass-reef connectivity at both the species- and site-level should be taken into consideration when implementing policy and conservation practices (Jaxion-Harm et al. 2012). Similarly, Dorenbosch et al. (2007) found that the value of seagrasses as a juvenile habitat should not be generalised *a priori*, since habitat configuration may interact with the degree of connectivity between seagrasses and coral reefs, and argue that accounting for both habitat type and habitat configuration can shape and increase the efficiency of MPA management actions. During yet another seagrass-reef connectivity study, researchers not only advocated for ecosystem-level management of shallow water tropical habitats, but also argued that management bodies require local-level knowledge of habitat interactions in order for fish assemblages to be successfully enhanced or conserved (Unsworth et al. 2008). Therefore, as site-specific results appear to be a frequent phenomenon within seagrass-reef connectivity research, including for the current study, each MPA should be considered as an independent unit, and managed as such.

With the combination of particularly vulnerable seagrass populations in South-East Asia, and the amplified threat that seagrass losses pose to livelihoods within the region, seagrass ecosystem management within the region is extremely important. Incorporating seagrass meadows into MPAs is an efficient approach towards preserving current seagrass populations as it concentrates efforts into a specific area, whilst offering several benefits in a single management move. However, it has been argued that, in isolation, incorporating seagrass meadows into MPAs is unlikely to effectively preserve them. McLeod et al. (2009) suggest that future connectivity patterns should be modelled in order to identify any areas at risk of losing ecosystem function, so that appropriate measures can be taken to protect these areas now. These authors also argue that MPA management should be integrated with coastal management regimes to enable effective control of threats, especially when an MPA is surrounded by intensively used land and water (McLeod et al. 2009). Furthermore, proper enforcement and adequate funding are required for an MPA to be effective, and means of monitoring the area are needed to track conservation success; fortunately, these appear to be available for the Zamboanguita MPAs in this study, at least for the time being. In addition to preserving current seagrass populations, restoration strategies may also prove to be useful in South-East Asia. Previous studies have found that both the installation of eco-moorings and seagrass replanting efforts in other regions have successfully allowed for the recovery of seagrass populations and their associated epifaunal communities (Orth & McGlathery 2012, Lefcheck et al. 2017, Luff et al. 2019); these methods could be explored for South-East Asia. Whilst the optimal approach would likely be a combination of all of these strategies, effective management fundamentally relies on community and government engagement. Thus, both citizen science (Jones et al. 2018) and widespread accessibility to literature should remain at the centre of management strategies. This is especially important within South-East Asia, where large-scale seagrass management is highly complex (Kirkman & Kirkman 2002): up to 11 countries may be involved, with Indonesia and the Philippines covering more than 25,000 islands in total. Therefore, though incorporation of seagrass beds into MPAs and site-by-site MPA management are encouraged, further action may be required to properly enforce and maintain protection of these vital ecosystems within South-East Asia.

4.4 Future Research

This study demonstrates the importance of monitoring the seagrass-reef interface as a separate zone during connectivity studies. Though the Interface and Reef zones were occasionally very similar in composition (eg, Lutoban South fish and invertebrate communities; Figures 10b-c and 22b-c respectively), this was often not the case. Furthermore, this study found evidence of some fish species showing a preference for a certain area along the seagrass-reef continuum: at Malatapay MPA, rabbitfish juveniles were found in highest abundance in the Interface zone, perhaps as it allows greater accessibility to the Seagrass zone or to the Reef zone, or both. Similar results have also been reported by Espino et al. (2014), whereby biomass of juvenile parrotfish was found to be higher in seagrass adjacent to reefs (< 10 m away from reefs) compared to seagrass interiors (< 200 m away). Thus, future seagrass-reef connectivity studies should consider the system as a continuum and account for the transition zone separately, as opposed to only monitoring the two habitats.

To gain a greater overview of seagrass-reef ecosystem connectivity, future research should also account for nocturnal fish and invertebrate activity, by surveying communities at night. During recreational night dives carried out on the Malatapay MPA reef within the study period, divers observed very different communities compared to those seen during the day. For instance, divers reported seeing at least two target species (Spanish dancer nudibranch *Hexabranhus sanguineus*, dwarf cuttlefish *Sepia bandensis*) that were not observed on any daytime dives during this study, as well as much higher abundances of cryptic target species (eg, scorpion spider conch) than were ever seen during the day. As these species do not tend to travel large distances, it can be presumed that these species were present on the reef during the day, though well-hidden within crevices or buried in the sand; this is supported by literature that details these taxa as being less active during the day (Francis 1980, Boneka et al. 1994, Cooke et al. 2019). Another three target species (moon shell, swimming crab, bobtail squid *Euprymna sp.*) were observed during the Seagrass zone night surveys at Dalakit MPA that were not recorded on any daytime surveys during the study period, which suggests they are typically nocturnal, and in turn is supported by available literature (Takahashi & Kawaguchi 2001, Jones & Nishiguchi 2004, Pastorino 2005). In addition, eggs of typically nocturnal species (moon shell and squid or cuttlefish) were observed within Seagrass zones during this study, either positioned on the seabed or attached to seagrass blades. Though this indicates that adults of these species were present at the respective site, additional night surveys may have confirmed this. To further this, many studies have reported nocturnal foraging migrations of fish species in seagrass beds that are in close proximity to coral reefs (Robblee & Zieman 1984, Nagelkerken et al. 2000, Kopp et al. 2007, Shoji et al. 2017), including within Malatapay prior to the MPA being demarcated in 2018 (Kochzius 1997). Hence, it is important that future survey efforts, including those by MCP, account for nocturnal activity as it will allow for a more accurate representation of total seagrass-reef connectivity.

Finally, my findings illustrate the importance of site-specific monitoring techniques within ecosystem management. In order for organisations (including MCP) and government bodies to be able to effectively monitor progress within established MPAs, they must first gain an accurate overview of the communities living there. In this study, fish species accumulation curves for Dalakit MPA showed that the Reef zone was under-surveyed (Appendix E), indicating that MCP's approach of conducting four fish surveys within each Reef depth zone (i.e. only Shallow for Dalakit MPA) was not optimal for this site. Though it is perhaps unlikely that additional Reef surveys would have affected overall

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

connectivity trends, they may have altered compositional trends such as species diversity. As high species diversity can increase ecosystem stability (Tilman 1996, McCann 2000, Lamy et al. 2020), and given that coastal habitats within South-East Asia are expected to experience greater disturbance in the future due to climate change (Asian Development Bank 2013, Sinha et al. 2017), monitoring and preserving species diversity within Negros Oriental (including Dalakit MPA) may be vitally important, especially in terms of local food security. Hence, assessment of species accumulation curves for Dalakit MPA allowed for this recognition of suboptimal monitoring techniques, providing the opportunity for improvements to be made by MCP, and should allow for better-informed management decisions to be made for this site in the future. In line with this, future management efforts are encouraged to incorporate site-specific optimisation of monitoring techniques into their approach, by means of species accumulation curves and other similar methods.

4.5 Conclusions

In conclusion, seagrass-reef ecosystem connectivity within fish and invertebrate communities in Negros Oriental MPAs supports local fisheries, and thus local food security. Fish trends appeared to be driven by their high interzonal mobility, whereas ecological niche requirements seemed to drive invertebrate trends. Though overall patterns were largely consistent, between-site variability meant that results were also partly site-specific; marked differences in connectivity trends were likely driven, at least in part, by differences in habitat configuration and seagrass bed composition across sites. This research illustrates the importance of incorporating seagrass beds into Marine Protected Areas within the Negros Oriental region, as well as managing MPAs on a site-by-site basis. By doing so, governments are not only able to support local food security and livelihoods, but also the overall health and stability of entire seagrass-reef ecosystems. In order to effectively protect seagrass-reef ecosystems within this region, management bodies should consider using connectivity information to optimise MPA placing and composition, as well as combining MPA management with other conservation strategies. Additional seagrass-reef connectivity studies should be carried out within the Indo-Pacific region and worldwide, with future research efforts (1) monitoring the seagrass-reef interface as its own zone, (2) accounting for nocturnal activity through night surveys, and (3) incorporating site-specific optimisation of monitoring techniques into their approach, by means of species accumulation curves and other similar methods.

ACKNOWLEDGEMENTS

This work was supported by Marine Conservation Philippines and the University of Plymouth. I would like to thank Dr Stacey DeAmicis and Alan Kavanagh for their continued support, and for their contributions towards the write-up of this report. I am also very grateful to Alan Kavanagh, Jesper Løf and Kristina Sjögren for their considerable contributions towards data collection. Finally, I would like to thank Raffy Casinares, Laura Schram and Ernst de Vries for their assistance in my fish and invertebrate identification training, as well as all the other volunteers and staff members at MCP who made this research possible.

REFERENCES

- Aguilar-Medrano R, Arias-González, J (2018) Functional reef fish groups of the Mexican Caribbean: implications of habitat complexity. *Revista Mexicana de Biodiversidad* 89:1138-1153
- Allen G (2015) Review of Indo-Pacific coral reef fish systematics: 1980 to 2014. *Ichthyological Research* 62:2-8
- Armstrong A, Armstrong A, McGregor F, Richardson A, Bennett M, Townsend K, Hays G, van Keulen M, Smith J, Dudgeon C (2020) Satellite tagging and photographic identification reveal connectivity between two UNESCO World Heritage Areas for reef manta rays. *Frontiers in Marine Science* 7:1-18
- Arthur K, Boyle M, Limpus C (2008) Ontogenetic changes in diet and habitat use in green sea turtle (*Chelonia mydas*) life history. *Marine Ecology Progress Series* 362:303-311
- Asian Development Bank (2013) The rise of natural disasters in Asia and the Pacific: learning from ABD's experience. <https://www.adb.org/sites/default/files/evaluation-document/36114/files/rise-natural-disasters-asia-pacific.pdf> (accessed 11 Mar 2021)
- Bailey C, Pomeroy C (1996) Resource dependency and development options in coastal South-East Asia. *Society and Natural Resources* 9:191-199
- Bariche M, Alwan N, El-Assi H, Zurayk R (2009) Diet composition of the Lessepsian bluespotted cornetfish *Fistularia commersonii* in the eastern Mediterranean. *Journal of Applied Ichthyology*, 25:460-465
- Birkeland C, Amesbury S (1988) Fish-transect surveys to determine the influence of neighboring habitats on fish community structure in the tropical Pacific. In: Dahl A (ed) *Regional co-operation on environmental protection of the marine and coastal areas in the Pacific*. UNEP Regional Seas Reports and Studies 195-202
- Blandon A, zu Ermgassen P (2014) Quantitative estimate of commercial fish enhancement by seagrass habitat in southern Australia. *Estuarine, Coastal and Shelf Science* 141:1-8
- Bloor I, Attrill M, Jackson E (2013) A review of the factors influencing spawning, early life stage survival and recruitment variability in the common cuttlefish (*Sepia officinalis*). *Advances in Marine Biology* 65:1-65
- Bologna P, Heck Jr K (1999) Macrofaunal associations with seagrass epiphytes: relative importance of trophic and structural characteristics. *Journal of Experimental Marine Biology and Ecology* 242:21-39
- Boneka F, Ompi M, Andaki J (1994) Occurrence of the common spider shell, *Lambis lambis* (L.)(Gastropoda: Strombidae) in the intertidal zone of Karatung, Sangihe Island, Indonesia. *Phuket Marine Biological Center Special Publication* 13:159-161
- Bosire J, Okemwa G, Ochiwo J (2012) Mangrove linkages to coral reef and seagrass ecosystem services in Mombasa and Takaungu, Kenya. In: *Participatory modelling frameworks to understand wellbeing trade-offs in coastal ecosystem services: mangrove sub-component*. https://www.researchgate.net/profile/Gladys_Okemwa/publication/338116734_Mangrove_linkages_to_coral_reef_and_seagrass_ecosystem_services_in_Mombasa_and_Takaungu_Kenya/links/5e00602f299bf10bc371970b/Mangrove-linkages-to-coral-reef-and-seagrass-ecosystem-services-in-Mombasa-and-Takaungu-Kenya.pdf (accessed 30 Mar 2021), p 13

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Brewer D, Blaber S, Salini J, Farmer M (1995) Feeding ecology of predatory fishes from Groote Eylandt in the Gulf of Carpentaria, Australia, with special reference to predation on penaeid prawns. *Estuarine, Coastal and Shelf Science* 40:577-600

Burkholder J, Tomasko D, Touchette B (2007) Seagrasses and eutrophication. *Journal of Experimental Marine Biology and Ecology* 350:46-72

Campbell S, Kartawijaya T, Sabarini E (2011) Connectivity in reef fish assemblages between seagrass and coral reef habitats. *Aquatic Biology* 13:65-77

Carpenter K, Allen G (1989) FAO Species Catalogue, Vol. 9, Emperor fishes and large-eye brems of the world (family Lethrinidae). FAO Fisheries Synopsis 9:75-77

Casartelli M, Ferragut C (2018) The effects of habitat complexity on periphyton biomass accumulation and taxonomic structure during colonization. *Hydrobiologia* 807:233-246

Charbonnel E, Serre C, Ruitton S, Harmelin J, Jensen A (2002) Effects of increased habitat complexity on fish assemblages associated with large artificial reef units (French Mediterranean coast). *ICES Journal of Marine Science* 59:S208-S213

Cooke G, Tonkins B, Mather J (2019) Chapter 8, Care and Enrichment for Captive Cephalopods. In: Carere C, Mather J (eds) *The welfare of invertebrate animals*. Springer Nature Switzerland AG, Cham/Switzerland, p 179-208

Cortés-Useche C, Calle-Triviño J, Sellares-Blasco R, Luis-Báez A, Arias-González J (2018) An updated checklist of the reef fishes of the Southeastern Reefs Marine Sanctuary of the Dominican Republic. *Revista Mexicana de Biodiversidad* 89:382-392

Crocetta F, Caputi L, Paz-Sedano S, Tanduo V, Vazzana A, Oliverio M (2020) High genetic connectivity in a gastropod with long-lived planktonic larvae. *Journal of Molluscan Studies* 86:42-55

Cullen-Unsworth L, Unsworth R (2018) A call for seagrass protection. *Science* 361:446-448

Currey L, Williams A, Mapstone B, Davies C, Carlos G, Welch D, Simpfendorfer C, Ballagh A, Penny A, Grandcourt E, Mapleston A (2013) Comparative biology of tropical *Lethrinus* species (Lethrinidae): challenges for multi-species management. *Journal of Fish Biology* 82:764-788

DeAmicis S (2012) The long-term effects of *Sargassum muticum* (Yendo) fenestrated invasion on *Zostera marina* L. and its associated epibiota. PhD thesis, University of Plymouth, UK

DeAmicis S, Foggo A (2015) Long-term field study reveals subtle effects of the invasive alga *Sargassum muticum* upon the epibiota of *Zostera marina*. *PLoS One* 10:e0137861

De Jonge V, De Jong D (1992) Role of tide, light and fisheries in the decline of *Zostera marina* L. in the Dutch Wadden Sea. In: Dankers N, Smit C, Scholl M (eds) *Present and future conservation of the Wadden Sea: Proceedings of the 7th International Wadden Sea Symposium, Ameland 1990*. Netherlands Institute for Sea Research Publication Series, Texel/Netherlands, p 161-176

De Leo G, Micheli F (2015) The good, the bad and the ugly of marine reserves for fishery yields. *Philosophical Transactions of the Royal Society B: Biological Sciences* 370:20140276

Denys C, Tschardt T (2002) Plant-insect communities and predator-prey ratios in field margin strips, adjacent crop fields, and fallows. *Oecologia* 130:315-324

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Dibacco C, Levin L, Sala E (2006) Connectivity in marine ecosystems: the importance of larval and spore dispersal. In: Crooks K, Sanjayan M (eds) Connectivity Conservation (Conservation Biology 14). Cambridge University Press, Cambridge/UK, p 184-212

Dorenbosch M, Grol M, Christianen M, Nagelkerken I, Van Der Velde G (2005) Indo-Pacific seagrass beds and mangroves contribute to fish density and diversity on adjacent coral reefs. Marine Ecology Progress Series 302:63-76

Dorenbosch M, Verberk W, Nagelkerken I, Van der Velde G (2007) Influence of habitat configuration on connectivity between fish assemblages of Caribbean seagrass beds, mangroves and coral reefs. Marine Ecology Progress Series 334:103-116

Doropoulos C, Hyndes G, Lavery P, Tuya F (2009) Dietary preferences of two seagrass inhabiting gastropods: allochthonous vs autochthonous resources. Estuarine, Coastal and Shelf Science 83:13-18

Duarte C, Cebrián J (1996) The fate of marine autotrophic production. Limnology and Oceanography 41:1758-1766

Duarte C, Chiscano C (1999) Seagrass biomass and production: a reassessment. Aquatic Botany 65:159-174

Duda Jr T, Terbio M, Chen G, Phillips S, Olenzek A, Chang D, Morris D (2012) Patterns of population structure and historical demography of *Conus* species in the tropical Pacific. American Malacological Bulletin 30:175-187

Duffy C, Francis M, Manning M, Bonfil R (2012) Regional population connectivity, oceanic habitat, and return migration revealed by satellite tagging of white sharks, *Carcharodon carcharias*, at New Zealand aggregation sites. In: Domeier M (ed) Global Perspectives on the Biology and Life History of the White Shark. CRC Press, Boca Raton/Florida, p 301-318

Erftemeijer P, Allen G (1993) Fish fauna of seagrass beds in south Sulawesi, Indonesia. Records of the Western Australian Museum 16:269-277

Erftemeijer P, Lewis III R (2006) Environmental impacts of dredging on seagrasses: a review. Marine Pollution Bulletin 52:1553-1572

Espino F, González J, Haroun R, Tuya F (2014) Abundance and biomass of the parrotfish *Sparisoma cretense* in seagrass meadows: temporal and spatial differences between seagrass interiors and seagrass adjacent to reefs. Environmental Biology of Fishes 98:121-133

FAO (1974) Lethrinidae, Emperors, Scavengers. FAO Species Identification Sheets. <http://www.fao.org/3/e9163e/E9163e2k.pdf> (accessed 26 Mar 2021)

Firth L, Mieszkowska N, Thompson R, Hawkins S (2013) Climate change and adaptational impacts in coastal systems: the case of sea defences. Environmental Science: Processes & Impacts 15:1665-1670

Floeter S, Halpern B, Ferreira C (2006) Effects of fishing and protection on Brazilian reef fishes. Biological Conservation 128:391-402

Floeter S, Krohling W, Gasparini J, Ferreira C, Zalmon I (2007) Reef fish community structure on coastal islands of the southeastern Brazil: the influence of exposure and benthic cover. Environmental Biology of Fishes 78:147-160

Fortes M (1988) Mangrove and seagrass beds of East Asia: habitats under stress. Ambio 17:207-213

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

- Francis M (1980) Habitat, food and reproductive activity of the nudibranch *Hexabranhus sanguineus* on Tongatapu Island. *The Veliger* 22:252-258
- Gaudette J, Wahle R, Himmelman J (2006) Spawning events in small and large populations of the green sea urchin *Strongylocentrotus droebachiensis* as recorded using fertilization assays. *Limnology and Oceanography* 51:1485-1496
- Gerland P, Raftery A, Ševčíková H, Li N, Gu D, Spoorenberg T, Alkema L, Fosdick B, Chunn J, Lalic N, Bay G (2014) World population stabilization unlikely this century. *Science* 346:234-237
- Gillanders B, Able K, Brown J, Eggleston D, Sheridan P (2003) Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. *Marine Ecology Progress Series* 247:281-295
- Grober-Dunsmore R, Pittman S, Caldow C, Kendall M, Frazer T (2009) Chapter 14, A landscape ecology approach for the study of ecological connectivity across tropical marine seascapes. In: Nagelkerken I (ed) *Ecological connectivity among tropical coastal ecosystems*. Springer, Dordrecht/Netherlands, p 493-530
- Gullström M, Bodin M, Nilsson P, Öhman M (2008) Seagrass structural complexity and landscape configuration as determinants of tropical fish assemblage composition. *Marine Ecology Progress Series* 363:241-255
- Hamisi M, Lyimo T, Muruke M (2004) Cyanobacterial Occurrence and Diversity in Seagrass Meadows in Coastal Tanzania. *Western Indian Ocean Journal of Marine Science* 3:113-122
- Hawaii Association for Marine Education & Research (2017) Sea Urchin Orgy Uncut. <https://vimeo.com/227394581> (accessed 9 April 2021)
- Heck Jr K (1977) Comparative species richness, composition, and abundance of invertebrates in Caribbean seagrass (*Thalassia testudinum*) meadows (Panamá). *Marine Biology* 41:335-348
- Heithaus M, Dill L, Marshall G, Buhleier B (2002) Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. *Marine Biology* 140:237-248
- Henderson C, Gilby B, Lee S, Stevens T (2017) Contrasting effects of habitat complexity and connectivity on biodiversity in seagrass meadows. *Marine Biology* 164:117
- Hemminga M, Duarte C (2000) *Seagrass Ecology*. Cambridge University Press, Cambridge/UK
- Henriques M, Almada V (1998) Juveniles of non-resident fish found in sheltered rocky subtidal areas. *Journal of Fish Biology* 52:1301-1304
- Hitt S, Pittman S, Nemeth R (2011) Diel movements of fishes linked to benthic seascape structure in a Caribbean coral reef ecosystem. *Marine Ecology Progress Series* 427:275-291
- Holon F, Boissery P, Guilbert A, Freschet E, Deter J (2015) The impact of 85 years of coastal development on shallow seagrass beds (*Posidonia oceanica* L.(Delile)) in South Eastern France: a slow but steady loss without recovery. *Estuarine, Coastal and Shelf Science* 165:204-212
- Honda K, Nakamura Y, Nakaoka M, Uy W, Fortes M (2013) Habitat use by fishes in coral reefs, seagrass beds and mangrove habitats in the Philippines. *PLoS One* 8:e65735

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

- Izzo P, Milessi A, Ortega L, Segura A (2010) First record of *Aluterus scriptus* (Monacanthidae) in Mar del Plata, Argentina. *Marine Biodiversity Records* 3
- Jang T (2020) Longface emperor fish hunting in camouflage mode. It changes color before hunting, circling their prey from all sides to block/catch from escape out of hiding place. 2020. <https://www.picuki.com/media/2186171007294078268> (accessed 26 Mar 2021)
- Jaxion-Harm J, Saunders J, Speight M (2012) Distribution of fish in seagrass, mangroves and coral reefs: life-stage dependent habitat use in Honduras. *Revista de Biología Tropical* 60:683-698
- Jenkins G, Wheatley M (1998) The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: comparison of shallow seagrass, reef-algal and unvegetated sand habitats, with emphasis on their importance to recruitment. *Journal of Experimental Marine Biology and Ecology* 221:147-172
- Jiang Z, Huang D, Fang Y, Cui L, Zhao C, Liu S, Wu Y, Chen Q, Ranvilage C, He J, Huang X (2020) Home for marine species: seagrass leaves as vital spawning grounds and food source. *Frontiers in Marine Science* 7:194
- Jinks K, Brown C, Rasheed M, Scott A, Sheaves M, York P, Connolly R (2019) Habitat complexity influences the structure of food webs in Great Barrier Reef seagrass meadows. *Ecosphere* 10:e02928
- Jones B, Nishiguchi M (2004) Counterillumination in the Hawaiian bobtail squid, *Euprymna scolopes* Berry (Mollusca: Cephalopoda). *Marine Biology* 144:1151-1155
- Jones B, Unsworth R, McKenzie L, Yoshida R, Cullen-Unsworth L (2018) Crowdsourcing conservation: The role of citizen science in securing a future for seagrass. *Marine Pollution Bulletin* 134:210-215
- Kark S (2013) Effects of ecotones on biodiversity. In: Levin S (ed) *Encyclopedia of Biodiversity* (Second Edition). Elsevier, New Jersey/USA, p 142-148
- Kasumyan A, Pavlov D (2018) Evolution of schooling behavior in fish. *Journal of Ichthyology* 58:670-678
- Kirkman H, Kirkman J (2002) The management of seagrasses in Southeast Asia. *Bulletin of Marine Science* 71:1379-1390
- Kochzius M (1997) Interrelation of ichthyofauna from a seagrass meadow and coral reef in the Philippines. In: Sérel B, Sire J (eds) *Proceedings of the 5th Indo-Pacific Fisheries Conference, Nouméa. Société Française d'Ichtyologie, Paris/France*, p 517-535
- Kopp D, Bouchon-Navaro Y, Louis M, Bouchon C (2007) Diel differences in the seagrass fish assemblages of a Caribbean island in relation to adjacent habitat types. *Aquatic Botany* 87:31-37
- Krupp L, Cortés J, Wolff M (2009) Growth dynamics and state of the seagrass *Thalassia testudinum* in the Gandoca-Manzanillo National Wildlife Refuge, Caribbean, Costa Rica. *Revista de Biología Tropical* 57:187-201
- Kuiter R, Tono-zuka T (2001) Pictorial guide to Indonesian reef fishes, Part 1. Zoonetics, Australia, p 1-302
- Lamy T, Koenigs C, Holbrook S, Miller R, Stier A, Reed D (2020) Foundation species promote community stability by increasing diversity in a giant kelp forest. *Ecology* 101:e02987

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

- Lanham B, Poore A, Gribben P (2021) Fine-scale responses of mobile invertebrates and mesopredatory fish to habitat configuration. *Marine Environmental Research* 168:105319
- Lefcheck J, Marion S, Orth R (2017) Restored eelgrass (*Zostera marina* L.) as a refuge for epifaunal biodiversity in mid-Western Atlantic coastal bays. *Estuaries and Coasts* 40:200-212
- Leis J (2001) Diodontidae, Porcupinefishes (burrfishes). In: Carpenter K, Niem V (eds) *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Volume 6. Bony fishes part 4 (Labridae to Latimeriidae), estuarine crocodiles, sea turtles, sea snakes and marine mammals*. FAO, Rome/Italy, p 3958-3965
- Lemer S, Combosch D, Sotto F, Giribet G, Dumale D, Soliman V (2016) The family Pinnidae (Bivalvia) in the Philippine archipelago: observations on its distribution and phylogeography. *Nautilus* 130:137-145
- León Y, Pugibet E, Sluka R (2004) The abundance of fishes in shallow, algal/seagrass habitats in the waters surrounding Parque Nacional del Este, Dominican Republic. *Proceedings of the 48th Gulf and Caribbean Fisheries Institute*, p 259-271
- Lessios H, Kessing B, Pearse J (2001) Population structure and speciation in tropical seas: global phylogeography of the sea urchin *Diadema*. *Evolution*, 55:955-975
- Liu K (2018) Fish diversity and distribution in the seagrass-coral reef continuum at two sites off the western coast of Isla Bastimentos, Bocas del Toro, Panama. Independent Study Project (ISP) Collection 2945
- Lodeiros C, Soria G, Valentich-Scott P, Munguía-Vega A, Cabrera J, Cudney-Bueno R, Looor A, Márquez A, Sonnenholzner S (2016) Spondylids of eastern pacific ocean. *Journal of Shellfish Research* 35:279-293
- Lotze H, Lenihan H, Bourque B, Bradbury R, Cooke R, Kay M, Kidwell S, Kirby M, Peterson C, Jackson J (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806-1809
- Luff A, Sheehan E, Parry M, Higgs N (2019) A simple mooring modification reduces impacts on seagrass meadows. *Scientific Reports* 9:1-10
- Magris R, Andrello M, Pressey R, Mouillot D, Dalongeville A, Jacobi M, Manel S (2018) Biologically representative and well-connected marine reserves enhance biodiversity persistence in conservation planning. *Conservation Letters* 11:e12439
- Magura T (2002) Carabids and forest edge: spatial pattern and edge effect. *Forest Ecology and Management* 157:23-37
- Malay M, Juinio-Meñez M, Villanoy C (2000) Population genetic structure of the sea urchin *Tripneustes gratilla* from selected sites in Western Luzon and Eastern Philippines. In: *Proceedings of the 9th International Coral Reef Symposium*. Ministry of Environment, Indonesian Institute of Sciences, and International Society for Reef Studies, Bali/Indonesia, p 1-5
- Manzanera M, Pérez M, Romero J (1998) Seagrass mortality due to oversedimentation: an experimental approach. *Journal of Coastal Conservation* 4:67-70
- Marine Research Section (1997) Bony Fishes, Acanthuridae. In: *Fishes of the Maldives*. Marine Research Section - Ministry of Fisheries and Agriculture, Republic of Maldives, p 319-322

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

- Marsden I, Hart D, Reid C, Gomez C (2016) Earthquake Disturbances. In: Kennish M (ed) Encyclopedia of Estuaries. Springer, Dordrecht/Netherlands, p 207-214
- McCann K (2000) The diversity–stability debate. *Nature* 405:228-233
- McKay R (2001) Haemulidae (= Pomadasyidae), Grunts (also sweetlips, rubberlips, hotlips and velvetchins). In: Carpenter K, Niem V (eds) FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Volume 5. Bony fishes part 3 (Menidae to Pomacentridae). FAO, Rome/Italy, p 2961-2976
- McKenzie L (2014) Australian pastures of the sea. *Wildlife Australia* 51:18-21
- McKenzie L, Yoshida R (2014) Seagrass-Watch. In: Proceedings of a workshop for monitoring seagrass habitats in the Burdekin and Wet Tropics regions, Queensland. Seagrass-Watch HQ (James Cook University), Cardwell/Australia, p 13
- McLeod E, Salm R, Green A, Almany J (2009) Designing marine protected area networks to address the impacts of climate change. *Frontiers in Ecology and the Environment* 7:362-370
- Morrison M, Lowe M, Grant C, Smith P, Carbines G, Reed J, Bury S, Brown J (2014) Seagrass meadows as biodiversity and productivity hotspots. Ministry for Primary Industries, Wellington/New Zealand
- Myers R (1991) Micronesian reef fishes: a practical guide to the identification of the coral reef fishes of the tropical and Western Pacific. Coral Graphics, Guam
- Nakamura Y, Sano M (2004a) Is there really lower predation risk for juvenile fishes in a seagrass bed compared with an adjacent coral area?. *Bulletin of Marine Science* 74:477-482
- Nakamura Y, Sano M (2004b) Overlaps in habitat use of fishes between a seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan: importance of the seagrass bed as juvenile habitat. *Fisheries Science* 70:788-803
- Nakamura Y, Sano M (2005) Comparison of invertebrate abundance in a seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan. *Fisheries Science* 71:543-550
- Nagelkerken I, Dorenbosch M, Verberk W, De La Morinière E, Van Der Velde G (2000) Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. *Marine Ecology Progress Series* 194:55-64
- Odum E (1953) *Fundamentals of Ecology*. W. B. Saunders Company, Philadelphia/USA
- Ogden J, Zieman J (1977) Ecological aspects of coral reef-seagrass bed contacts in the Caribbean. *Proceedings of the Third International Coral Reef Symposium* 1:377-382
- Orth R, Heck K, van Montfrans J (1984) Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* 7:339-350
- Orth R, McGlathery K (2012) Eelgrass recovery in the coastal bays of the Virginia Coast Reserve, USA. *Marine Ecology Progress Series* 448:173-176
- Parrish J (1989) Fish communities of interacting shallow-water habitats in tropical oceanic regions. *Marine Ecology Progress Series* 58:143-160

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

- Pastorino G (2005) Recent Naticidae (Mollusca: Gastropoda) from the Patagonian coast. *The Veliger* 47:225-228
- Pogoreutz C, Kneer D, Litaay M, Asmus H, Ahnelt H (2012) The influence of canopy structure and tidal level on fish assemblages in tropical Southeast Asian seagrass meadows. *Estuarine, Coastal and Shelf Science* 107:58-68
- Poiner I, Walker D, Coles R (1989) Regional studies – seagrasses of tropical Australia. In: Larkum A, McComb A, Shepherd S (eds) *Biology of Seagrasses*. Elsevier, Amsterdam/Netherlands, p 279-303
- Preen A, Lee Long W, Coles R (1995) Flood and cyclone related loss, and partial recovery, of more than 1000km² of seagrass in Hervey Bay, Queensland, Australia. *Aquatic Botany* 52:3-17
- Quimpo T, Cabaitan P, Olavides R, Dumalagan Jr E, Munar J, Siringan F (2019) Spatial variability in reef-fish assemblages in shallow and upper mesophotic coral ecosystems in the Philippines. *Journal of Fish Biology* 94:17-28
- R Core Team (2019) R: A language and environment for statistical computing (Version 3.6.2). R Foundation for Statistical Computing. Vienna/Austria. <https://www.R-project.org>
- Ralph P, Tomasko D, Moore K, Seddon S, Macinnis-Ng C (2007) Human impacts on seagrasses: eutrophication, sedimentation and contamination. In: Larkum A, Orth R, Duarte C (eds) *Seagrasses: Biology, Ecology and Conservation*. Springer, Dordrecht/Netherlands, p 567-593
- Randall J (1984) Acanthuridae. In: Fischer W, Bianchi G (eds) *FAO species identification sheets for fishery purposes. Western Indian Ocean (Fishing Area 51). Volume 1*. FAO, Rome/Italy
- Randall J (2001) Mullidae, Goatfishes (surmullets). In: Carpenter K, Niem V (eds) *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Volume 5. Bony fishes part 3 (Menidae to Pomacentridae)*. FAO, Rome/Italy, p 3175-3186
- Robblee M, Zieman J (1984) Diel variation in the fish fauna of a tropical seagrass feeding ground. *Bulletin of Marine Science* 34:335-345
- Roberts C, Andelman S, Branch G, Bustamante R, Carlos Castilla J, Dugan J, Halpern B, Lafferty K, Leslie H, Lubchenco J, McArdle D (2003) Ecological criteria for evaluating candidate sites for marine reserves. *Ecological Applications* 13:S199-S214
- Sambrook K, Hoey A, Andréfouët S, Cumming G, Duce S, Bonin M (2019) Beyond the reef: the widespread use of non-reef habitats by coral reef fishes. *Fish and Fisheries* 20:903-920
- Shanks A (2009) Pelagic larval duration and dispersal distance revisited. *The Biological Bulletin* 216:373-385
- Shimose T (2021) Age, growth, and reproductive traits of two large emperor fishes, *Lethrinus olivaceus* and *L. xanthochilus*, around Yaeyama Islands, Okinawa, southern Japan. *Environmental Biology of Fishes* 104:181-194
- Shoji J, Mitamura H, Ichikawa K, Kinoshita H, Arai N (2017) Increase in predation risk and trophic level induced by nocturnal visits of piscivorous fishes in a temperate seagrass bed. *Scientific Reports* 7:1-10
- Short F, Mathieson A, Nelson J (1986) Recurrence of the eelgrass wasting disease at the border of New Hampshire and Maine, USA. *Marine Ecology Progress Series* 29:89-92

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Short F, Polidoro B, Livingstone S, Carpenter K, Bandeira S, Bujang J, Calumpong H, Carruthers T, Coles R, Dennison W, Erftemeijer P (2011) Extinction risk assessment of the world's seagrass species. *Biological Conservation* 144:1961-1971

Simanjuntak C, Putri A, Rahardjo M, Syafei L, Abdillah D (2020) Species composition and abundance of small fishes in seagrass beds of the Karang Congkak Island, Kepulauan Seribu National Park, Indonesia. In: IOP Conference Series: Earth and Environmental Science (Volume 404). IOP Publishing, p 012063

Sinha E, Michalak A, Balaji V (2017) Eutrophication will increase during the 21st century as a result of precipitation changes. *Science*, 357:405-408

Small C, Nicholls R (2003) A global analysis of human settlement in coastal zones. *Journal of Coastal Research* 584-599

Smith R, Johnston E, Clark G (2014) The role of habitat complexity in community development is mediated by resource availability. *PLoS One* 9:e102920

Stevick P, Neves M, Johansen F, Engel M, Allen J, Marcondes M, Carlson C (2011) A quarter of a world away: female humpback whale moves 10 000 km between breeding areas. *Biology Letters* 7:299-302

Sullivan M (1979) Epiphytic diatoms of three seagrass species in Mississippi Sound. *Bulletin of Marine Science* 29:459-464

Takahashi K, Kawaguchi K (2001) Nocturnal occurrence of the swimming crab *Ovalipes punctatus* in the swash zone of a sandy beach in northeastern Japan. *Fishery Bulletin* 99:510-515

Talbot M, Knoop W, Bate G (1990) The dynamics of estuarine macrophytes in relation to flood/siltation cycles. *Botanica Marina* 33:159-164

Tanaka Y, Go G, Watanabe A, Miyajima T, Nakaoka M, Uy W, Nadaoka K, Watanabe S, Fortes M (2014) 17-year change in species composition of mixed seagrass beds around Santiago Island, Bolinao, the northwestern Philippines. *Marine Pollution Bulletin* 88:81-85

Taylor P, Fahrig L, Henein K, Merriam G (1993) Connectivity is a vital element of landscape structure. *Oikos* 68:571-573

Terrados J, Borum J (2004) Why are seagrasses important? - Goods and services provided by seagrass meadows. In: Borum J, Duarte C, Krause-Jensen D, Greve T (eds) *European seagrasses: an introduction to monitoring and management*. The M&MS Project, p 8-10

Terrados J, Duarte C, Fortes M, Borum J, Agawin N, Bach S, Thampanya U, Kamp-Nielsen L, Kenworthy W, Geertz-Hansen O, Vermaat J (1998) Changes in community structure and biomass of seagrass communities along gradients of siltation in SE Asia. *Estuarine, Coastal and Shelf Science* 46:757-768

Tide Forecast (2021) Tide times for Zamboanguita. <https://www.tide-forecast.com/locations/Zamboanguita/tides/latest> (accessed 8 Feb 2021)

Tilman D (1996) Biodiversity: population versus ecosystem stability. *Ecology* 77:350-363

Tomascik T, Mah A, Nontji A, Moosa M (1997) *The ecology of the Indonesian seas, part II*. Oxford University Press, Oxford/UK

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Toonen R, Andrews K, Baums I, Bird C, Concepcion G, Daly-Engel T, Eble J, Faucci A, Gaither M, Iacchei M, Puritz J (2011) Defining boundaries for ecosystem-based management: a multispecies case study of marine connectivity across the Hawaiian Archipelago. *Journal of Marine Biology* 2011:1-13

Unsworth R, Cullen L (2010) Recognising the necessity for Indo-Pacific seagrass conservation. *Conservation Letters* 3:63-73

Unsworth R, Garrard S, De León P, Cullen L, Smith D, Sloman K, Bell J (2009) Structuring of Indo-Pacific fish assemblages along the mangrove–seagrass continuum. *Aquatic Biology* 5:85-95

Unsworth R, De León P, Garrard S, Jompa J, Smith D, Bell J (2008) High connectivity of Indo-Pacific seagrass fish assemblages with mangrove and coral reef habitats. *Marine Ecology Progress Series* 353:213-224

Unsworth R, Hinder S, Bodger O, Cullen-Unsworth L (2014) Food supply depends on seagrass meadows in the coral triangle. *Environmental Research Letters* 9:094005

Unsworth R, Nordlund L, Cullen-Unsworth L (2019) Seagrass meadows support global fisheries production. *Conservation Letters* 12:e12566

Unsworth R, Taylor J, Powell A, Bell J, Smith D (2007) The contribution of scarid herbivory to seagrass ecosystem dynamics in the Indo-Pacific. *Estuarine, Coastal and Shelf Science* 74:53-62

Van der Velde G, Gorissen M, Den Hartog C, van't Hoff T, Meijer G (1992) Importance of the Lagoon (Bonaire, Netherlands Antilles) for a selected number of reef fish species. In: Jaccarini V, Martens E (eds) *The ecology of mangrove and related ecosystems*. Springer, Dordrecht/Netherlands, p 139-140

Ver *Calendario* (2018) <https://www.vercalendario.info/en/moon/philippines-month-january-2020.html> (accessed 26 Mar 2021)

Verweij M, Nagelkerken I, Hans I, Ruseler S, Mason P (2008) Seagrass nurseries contribute to coral reef fish populations. *Limnology and Oceanography* 53:1540-1547

Vijay Anand P, Pillai N (2005) Occurrence of juvenile fishes on the seagrass beds of Kavaratti Atoll, Lakshadweep, India. *Indian Journal of Fisheries* 52:459-468

Virnstein R, Nelson W, Lewis F, Howard R (1984) Latitudinal patterns in seagrass epifauna: do patterns exist, and can they be explained?. *Estuaries* 7:310-330

Vogler C, Benzie J, Tenggardjaja K, Barber P, Wörheide G (2013) Phylogeography of the crown-of-thorns starfish: genetic structure within the Pacific species. *Coral Reefs* 32:515-525

Vrijenhoek R (2010) Genetic diversity and connectivity of deep-sea hydrothermal vent metapopulations. *Molecular Ecology* 19:4391-4411

Walker D, Lukatelich R, Bastyan G, McComb A (1989) Effect of boat moorings on seagrass beds near Perth, Western Australia. *Aquatic Botany* 36:69-77

Waycott M, Duarte C, Carruthers T, Orth R, Dennison W, Olyarnik S, Calladine A, Fourqurean J, Heck K, Hughes A, Kendrick G (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences* 106:12377-12381

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Webster M (2004) Density dependence via intercohort competition in a coral-reef fish. *Ecology* 85:986-994

Weinstein M, Heck K (1979) Ichthyofauna of seagrass meadows along the Caribbean coast of Panamá and in the Gulf of Mexico: composition, structure and community ecology. *Marine Biology* 50:97-107

Woodland D (2001) Siganidae, Rabbitfishes (spinefoots). In: Carpenter K, Niem V (eds) *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Volume 6. Bony fishes part 4 (Labridae to Latimeriidae), estuarine crocodiles, sea turtles, sea snakes and marine mammals*. FAO, Rome/Italy, p 3627-3641

Young P, Martin R (1982) Evidence for protogynous hermaphroditism in some lethrinid fishes. *Journal of Fish Biology* 21:475-484

Zimmerman R, Kohrs D, Alberte R (1996) Top-down impact through a bottom-up mechanism: the effect of limpet grazing on growth, productivity and carbon allocation of *Zostera marina* L. (eelgrass). *Oecologia* 107:560-567

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

APPENDICES

Appendix A: MPA Coordinates

Malatapay MPA		Lutoban South MPA		Dalakit MPA	
Latitude	Longitude	Latitude	Longitude	Latitude	Longitude
9° 07' 20" N	123° 12' 45" E	9° 04' 27" N	123° 09' 36" E	9° 05' 37" N	123° 11' 27" E
9° 07' 18" N	123° 12' 46" E	9° 04' 23" N	123° 09' 41" E	9° 05' 40" N	123° 11' 26" E
9° 07' 16" N	123° 12' 48" E	9° 04' 14" N	123° 09' 27" E	9° 05' 40" N	123° 11' 35" E
9° 07' 22" N	123° 12' 53" E	9° 04' 05" N	123° 08' 58" E	9° 05' 40" N	123° 11' 42" E
9° 07' 23" N	123° 12' 51" E	9° 04' 11" N	123° 08' 56" E	9° 05' 40" N	123° 11' 29" E
9° 07' 21" N	123° 12' 46" E	9° 04' 19" N	123° 09' 24" E	9° 05' 51" N	123° 11' 37" E

N.B. These co-ordinates were taken from an official municipal ordinance document. However, due to lack of accessibility to accurate satellite information, the Zamboanguita municipal government detail several co-ordinates that are situated on land. Therefore, in reality, the placement of these MPAs varies slightly from the co-ordinates detailed above, with local communities treating the area directly seaward from the shore as the MPA, and following demarcation where applicable.

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Appendix B: Seagrass Species List

Seagrass Species	Estimated Abundance		
	Malatapay MPA	Lutoban South MPA	Dalakit MPA
<i>Cymodocea rotundata</i>	High	Medium	Unknown
<i>Cymodocea serrulata</i>	Medium	Low	Unknown
<i>Enhalus acoroides</i>	Low	High	Unknown
<i>Halodule pinifolia</i>	Low	Medium	Unknown
<i>Halodule uninervis</i>	Medium	Low	Unknown
<i>Halophila</i> spp. (<i>ovalis</i> , <i>decipiens</i> , <i>minor</i>)	None / Rare	High	Unknown
<i>Syringodium isoetifolium</i>	High	High	Unknown
<i>Thalassia hemprichii</i>	High	High	Unknown

N.B. These species abundance estimates are based on a combination of local knowledge, and the results of a low-accuracy seagrass monitoring project conducted by MCP in 2018, which involved divers surveying seagrass species along 50m fixed transects. Though the project was discontinued, MCP staff were still able to collect information on species presence at certain sites, and were able to make rough estimations of their overall abundance. These data were later refined using local knowledge, and adapted into a 'SACFOR'-style abundance scale, as detailed above.

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Appendix C: Fish Species List

Common Name	Species	Family	Primary Role	Importance
Angelfish	Pomacanthidae	Pomacanthidae	Reef Fish	Commercially important (>20cm)
Barracuda	Sphyraenidae	Sphyraenidae	Reef Fish	Commercially important
Barramundi Cod	<i>Cromileptes altivelis</i>	Serranidae	Reef Fish	Commercially important
Barred Thicklip Wrasse	<i>Hemigymnus fasciatus</i>	Labridae	Reef Fish	Reef health indicator (<i>Drupella</i> predator); commercially important
Bicolor Angelfish	<i>Centropyge bicolor</i>	Pomacanthidae	Herbivore (Grazer / Detritivore)	Reef health indicator
Bicolor Goatfish	<i>Parupeneus barberinoides</i>	Mullidae	Reef Fish	Commercially important
Blackeye Thicklip Wrasse	<i>Hemigymnus melapterus</i>	Labridae	Reef Fish	Commercially important
Blackfin Barracuda	<i>Sphyraena quenie</i>	Sphyraenidae	Top Predator	Commercially important
Blacktail Snapper	<i>Lutjanus fulvus</i>	Lutjanidae	Reef Fish	Commercially important
Bleeker's Parrotfish	<i>Chlorurus bleekeri</i>	Scaridae	<35cm: Herbivore (Small Excavator / Scraper) >35cm: Herbivore (Large Excavator / Bioeroder)	Reef health indicator; commercially important
Blubberlip Snapper	<i>Lutjanus rivulatus</i>	Lutjanidae	Reef Fish	Reef health indicator (<i>Drupella</i> predator); commercially important
Bluefin Trevally	<i>Caranx melampygus</i>	Carangidae	Top Predator	Commercially important
Blue-Spine Unicornfish	<i>Naso unicornis</i>	Acanthuridae	Herbivore (Browser)	Reef health indicator; commercially important
Bluespotted Grouper	<i>Cephalopholis cyanostigma</i>	Serranidae	Reef Fish	Commercially important
Bower's Parrotfish	<i>Chlorurus bowersi</i>	Scaridae	<35cm: Herbivore (Small Excavator / Scraper) >35cm: Herbivore (Large Excavator / Bioeroder)	Reef health indicator; commercially important
Bream	Nemipteridae	Nemipteridae	Reef Fish	Commercially important
Bristletooth	<i>Ctenochaetus spp.</i>	Acanthuridae	Other (Detritivore)	Reef health indicator (reef cleaner)
Brown-Marbled Grouper	<i>Epinephelus fuscoguttatus</i>	Serranidae	Reef Fish	Commercially important
Brushtail Tang	<i>Zebрасoma scopas</i>	Acanthuridae	Herbivore (Grazer / Detritivore)	Reef health indicator
Bullethead Parrotfish	<i>Chlorurus sordidus</i>	Scaridae	<35cm: Herbivore (Small Excavator / Scraper) >35cm: Herbivore (Large Excavator / Bioeroder)	Reef health indicator; commercially important
Bumphead Parrotfish	<i>Bolbometopon muricatum</i>	Scaridae	<35cm: Herbivore (Small Excavator / Scraper) >35cm: Herbivore (Large Excavator / Bioeroder)	Reef health indicator; commercially important
Butterflyfish	Chaetodontidae	Chaetodontidae	Other (Corallivore)	Reef health indicator (coral predator)
Checkered Snapper	<i>Lutjanus decussatus</i>	Lutjanidae	Reef Fish	Commercially important
Chub	Kyphosidae	Kyphosidae	Herbivore (Browser)	Reef health indicator; commercially important
Cleaner Wrasse	<i>Labrioides dimidiatus</i> , <i>Labroides bicolor</i>	Labridae	Other (Parasitivore)	Reef health indicator
Coral Grouper	<i>Cephalopholis miniata</i>	Serranidae	Reef Fish	Commercially important
Cornetfish	<i>Fistularia commersonii</i>	Fistulariidae	Top Predator	Commercially important
Crocodile Needlefish	<i>Tylosurus crocodilus</i>	Belonidae	Top Predator	Commercially important
Dark Surgeonfish	<i>Acanthurus nubilus</i>	Acanthuridae	Planktivore	Reef health indicator; commercially important
Dash-Dot Goatfish	<i>Parupeneus barberinus</i>	Mullidae	Reef Fish	Commercially important
Emperor	Lethrinidae	Lethrinidae	Reef Fish	Commercially important

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Floral Wrasse	<i>Cheilinus chlorourus</i>	Labridae	Reef Fish	Commercially important
Fusiliers	Caesionidae	Caesionidae	Planktivore	Commercially important
Goatfish	Mullidae	Mullidae	Reef Fish	Commercially important
Golden Rabbitfish	<i>Siganus guttatus</i>	Siganidae	Herbivore (Grazer / Detritivore)	Commercially important
Great Barracuda	<i>Sphyraena barracuda</i>	Sphyraenidae	Top Predator	Commercially important
Grouper	Serranidae	Serranidae	Reef Fish	Commercially important
Honeycomb Grouper	<i>Epinephelus merra</i>	Serranidae	Reef Fish	Commercially important
Humpback Red Snapper	<i>Lutjanus gibbus</i>	Lutjanidae	Reef Fish	Commercially important
Humphead Wrasse	<i>Cheilinus undulatus</i>	Labridae	Reef Fish	Reef health indicator (<i>Drupella</i> predator, Crown of Thorns predator); commercially important
Humpnose Big-Eye Bream	<i>Monotaxis grandoculis</i>	Nemipteridae	Reef Fish	Commercially important
Japanese Parrotfish	<i>Chlorurus japensis</i>	Scaridae	<35cm: Herbivore (Small Excavator / Scraper) >35cm: Herbivore (Large Excavator / Bioeroder)	Reef health indicator; commercially important
Keyhole Angelfish	<i>Centropyge tibicen</i>	Pomacanthidae	Herbivore (Grazer / Detritivore)	Reef health indicator
Long-Jawed Mackerel	<i>Rastrelliger kanagurta</i>	Scombridae	Planktivore	Commercially important
Longface Emperor	<i>Lethrinus olivaceus</i>	Lethrinidae	Top Predator	Commercially important
Lyretail	<i>Variola albimarginata</i> , <i>Variola louti</i>	Serranidae	Reef Fish	Commercially important
Mackerel	Scombridae	Scombridae	Top Predator	Commercially important
Mangrove Snapper	<i>Lutjanus argentimaculatus</i>	Lutjanidae	Reef Fish	Commercially important
Map Pufferfish	<i>Arothron mappa</i>	Tetraodontidae	Reef Fish	Commercially important
Midnight Angelfish	<i>Centropyge nox</i>	Pomacanthidae	Herbivore (Grazer / Detritivore)	Reef health indicator
Midnight Snapper	<i>Macolor macularis</i>	Lutjanidae	Reef Fish	Reef health indicator (<i>Drupella</i> predator); commercially important
Mullet	Mugilidae	Mugilidae	Reef Fish	Commercially important
One-Spot Snapper	<i>Lutjanus monostigma</i>	Lutjanidae	Reef Fish	Commercially important
Orange-Striped Emperor	<i>Lethrinus obsoletus</i>	Lethrinidae	Top Predator	Commercially important
Orange-Spine Unicornfish	<i>Naso lituratus</i>	Acanthuridae	Herbivore (Browser)	Reef health indicator; commercially important
Ornate Emperor	<i>Lethrinus ornatus</i>	Lethrinidae	Reef Fish	Commercially important
Parrotfish	Scaridae	Scaridae	Herbivore (Small Excavator, Scraper)	Reef health indicator; commercially important
Peacock Grouper	<i>Cephalopholis argus</i>	Serranidae	Reef Fish	Commercially important
Pearl-Scaled Angelfish	<i>Centropyge vroliki</i>	Pomacanthidae	Herbivore (Grazer / Detritivore)	Reef health indicator
Porcupinefish	Diodontidae	Diodontidae	Reef Fish	Reef health indicator (<i>Drupella</i> predator); commercially important
Rabbitfish	Siganidae	Siganidae	Herbivore (Grazer / Detritivore)	Reef health indicator; commercially important
Raggedtooth Parrotfish	<i>Calotomus spinidens</i>	Scaridae	Herbivore (Browser)	Reef health indicator; commercially important
Rainbow Runner	<i>Elagatis bipinnulatus</i>	Carangidae	Top Predator	Commercially important
Red Snapper	<i>Lutjanus bohar</i>	Lutjanidae	Reef Fish	Reef health indicator (<i>Drupella</i> predator); commercially important
Red-Breasted Wrasse	<i>Cheilinus fasciatus</i>	Labridae	Reef Fish	Reef health indicator (<i>Drupella</i> predator); commercially important

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Redfin Bream	<i>Monotaxis heterodon</i>	Nemipteridae	Reef Fish	Commercially important
Redtooth Triggerfish	<i>Odonus niger</i>	Balistidae	Reef Fish	Commercially important
Scad	Carangidae	Carangidae	Planktivore	Commercially important
Schooling Snapper	<i>Lutjanus rufolineatus</i> , <i>Lutjanus lutjanus</i> , <i>Lutjanus madras</i>	Lutjanidae	Reef Fish	Reef health indicator (<i>Drupella</i> predator); commercially important
Scrawled Filefish	<i>Aluterus scriptus</i>	Monacanthidae	Reef Fish	Commercially important
Sergeantfish	<i>Abudefduf</i> spp.	Pomacentridae	Planktivore	Commercially important
Slender Grouper	<i>Anyperodon leucogrammicus</i>	Serranidae	Reef Fish	Commercially important
Snapper	Lutjanidae	Lutjanidae	Reef Fish	Reef health indicator (<i>Drupella</i> predator); commercially important
Soldierfish	Myripristinae	Holocentridae	Reef Fish	Commercially important
Spadefish	Ephippidae	Ephippidae	Herbivore (Browser)	Reef health indicator; commercially important
Spotted Parrotfish	<i>Cetoscarus ocellatus</i>	Scaridae	<35cm: Herbivore (Small Excavator / Scraper) >35cm: Herbivore (Large Excavator / Bioeroder)	Reef health indicator; commercially important
Star Pufferfish	<i>Arothron stellatus</i>	Tetraodontidae	Reef Fish	Commercially important
Stareye Parrotfish	<i>Calotomus carolinus</i>	Scaridae	Herbivore (Browser)	Reef health indicator; commercially important
Steephead Parrotfish	<i>Chlorurus microrhinos</i>	Scaridae	<35cm: Herbivore (Small Excavator / Scraper) >35cm: Herbivore (Large Excavator / Bioeroder)	Reef health indicator; commercially important
Surgeonfish	<i>Acanthurus</i> spp.	Acanthuridae	Herbivore (Grazer / Detritivore)	Reef health indicator; commercially important
Sweetlips	Haemulidae	Haemulidae	Reef Fish	Commercially important
Thumbprint Emperor	<i>Lethrinus harak</i>	Lethrinidae	Reef Fish	Commercially important
Titan Triggerfish	<i>Balistoides viridescens</i>	Balistidae	Reef Fish	Reef health indicator (Crown of Thorns predator); commercially important
Trevally	Carangidae	Carangidae	Top Predator	Commercially important
Triggerfish	Balistidae	Balistidae	Reef Fish	Reef health indicator (<i>Drupella</i> predator)
Tripletail Wrasse	<i>Cheilinus trilobatus</i>	Labridae	Reef Fish	Reef health indicator (<i>Drupella</i> predator); commercially important
Tuna	Scombridae	Scombridae	Top Predator	Commercially important
Two-Spot Snapper	<i>Lutjanus biguttatus</i>	Lutjanidae	Reef Fish	Reef health indicator (<i>Drupella</i> predator); commercially important
Two-Spined Angelfish	<i>Centropyge bispinosa</i>	Pomacanthidae	Herbivore (Grazer / Detritivore)	Reef health indicator; commercially important
Unicornfish	<i>Naso</i> spp.	Acanthuridae	Planktivore	Commercially important
Virgate Rabbitfish	<i>Siganus virgatus</i>	Siganidae	Herbivore (Grazer / Detritivore)	Commercially important
White-Spotted Rabbitfish	<i>Siganus canaliculatus</i>	Siganidae	Herbivore (Browser)	Reef health indicator; commercially important
Whitetail Surgeonfish	<i>Acanthurus thompsoni</i>	Acanthuridae	Planktivore	Reef health indicator; commercially important
Yellowstripe Goatfish	<i>Mulloidichthys flavolineatus</i>	Mullidae	Reef Fish	Commercially important
Yellowtail Barracuda	<i>Sphyræna flavicauda</i>	Sphyrænidae	Reef Fish	Commercially important

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Appendix D: Invertebrate Species List

Common Name	Species	Family	Phylum	Ecological Niche	Importance
Abalone	<i>Haliotis spp.</i>	Haliotidae	Mollusca	Reef Specialist	Reef health indicator (herbivore); commercially important (food; shell trade; permit required)
Amberfish Sea Cucumber	<i>Thelenota anax</i>	Stichopodidae	Echinodermata	Generalist	Reef health indicator (cleaner organism); commercially important (food); local consumption
Banded Coral Shrimp	<i>Stenopus hispidus</i>	Stenopodidae	Arthropoda	Reef Specialist	Reef health indicator (cleaner organism)
Bell's Urchin	<i>Salmacis spp.</i>	Cidaridae, Temnopleuridae	Echinodermata	Seagrass Specialist	Reef health indicator (herbivore; diet of commercial fish); local consumption
Big Lip Conch	<i>Canarium spp.</i> (excluding <i>microurceus</i> , <i>mutabile</i>), <i>Conomurex spp.</i> (excluding <i>luhuanus</i>), <i>Dolomena spp.</i> (excluding <i>variabilis</i>) <i>Euprotomus spp.</i> , <i>Lentigo lentiginosus</i> , <i>Strombus spp.</i>	Strombidae	Mollusca	Generalist	Reef health indicator (herbivore); commercially important (food); local consumption
Black Fringed Sea Cucumber	<i>Holothuria leucospilota</i>	Holothuriidae	Echinodermata	Generalist	Reef health indicator (cleaner organism); commercially important (food); local consumption
Blackspotted Sea Cucumber	<i>Pearsonothuria graeffei</i>	Holothuriidae	Echinodermata	Generalist	Reef health indicator (cleaner organism); commercially important (food); local consumption
Blue-Ringed Octopus	<i>Hapalochlaena lunulata</i> , <i>Hapalochlaena spp.</i>	Octopodidae	Mollusca	Generalist	High touristic value
Bonnet Shell	<i>Casmaria ponderosa</i> , <i>Phalium angasi</i> , <i>Phalium bandatum</i> , <i>Phalium bulla</i> , <i>Phalium flammiferum</i> , <i>Phalium spp.</i> , <i>Semicassis bisulcata</i>	Cassidae	Mollusca	Generalist	Reef health indicator (Crown of Thorns predator); commercially important (shell trade); local consumption
Boring Giant Clam	<i>Tridacna crocea</i>	Cardiidae	Mollusca	Reef Specialist	Not commercially important - identified separately to Giant Clam (protected status)
Box Crab	<i>Calappa spp.</i>	Calappidae	Arthropoda	Generalist	Reef health indicator (diet of commercial fish); commercially important (food)
Broadclub Cuttlefish	<i>Sepia latimanus</i>	Sepiidae	Mollusca	Generalist	Commercially important (food)
Brown Sandfish Sea Cucumber	<i>Bohadschia vitiensis</i>	Holothuriidae	Echinodermata	Generalist	Reef health indicator (cleaner organism); commercially important (food); local consumption

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Chocolate Chip Sea Cucumber	<i>Bohadschia sp.</i>	Holothuriidae	Echinodermata	Generalist	Reef health indicator (cleaner organism); commercially important (food); local consumption
Coconut Octopus	<i>Amphioctopus marginatus</i>	Octopodidae	Mollusca	Generalist	Local consumption
Collector Urchin	<i>Tripneustes gratilla</i>	Toxopneustidae	Echinodermata	Generalist	Reef health indicator (herbivore; diet of commercial fish); commercially important (food); local consumption
Common Egg Cowrie	<i>Ovula ovum</i>	Ovulidae	Mollusca	Reef Specialist	Commercially important (shell trade)
Cone Shell	<i>Conus arenatus, Conus aulicus, Conus capitaneus, Conus geographus, Conus striatus, Conus textile, Conus spp.</i>	Conidae	Mollusca	Generalist	Commercially important (shell trade; permit required); local consumption
<i>Coralliophila</i>	<i>Coralliophila violacea</i>	Muricidae	Mollusca	Reef Specialist	Reef health indicator (corallivore; diet of commercial fish)
Crown of Thorns	<i>Acanthaster planci</i>	Acanthasteridae	Echinodermata	Reef Specialist	Reef health indicator (corallivore; diet of commercial fish)
Curryfish Sea Cucumber	<i>Stichopus vastus</i>	Stichopodidae	Echinodermata	Generalist	Reef health indicator (cleaner organism); commercially important (food); local consumption
Cushion Star	<i>Culcita novaeguineae</i>	Oreasteridae	Echinodermata	Reef Specialist	Reef health indicator (corallivore)
Day Octopus	<i>Octopus cyanea</i>	Octopodidae	Mollusca	Generalist	Commercially important (food)
<i>Diadema</i> Urchin	<i>Diadema spp.</i>	Diadematidae	Echinodermata	Generalist	Reef health indicator (herbivore; diet of commercial fish); local consumption
<i>Drupella</i>	<i>Drupella cornus</i>	Muricidae	Mollusca	Reef Specialist	Reef health indicator (corallivore; diet of commercial fish)
Dwarf Cuttlefish	<i>Sepia bandensis</i>	Sepiidae	Mollusca	Generalist	High touristic value
Eye-Spotted Sea Cucumber	<i>Stichopus ocellatus</i>	Stichopodidae	Echinodermata	Generalist	Reef health indicator (cleaner organism); commercially important (food); local consumption
Fire Urchin	<i>Asthenosoma spp.</i>	Echinothuriidae	Echinodermata	Generalist	Reef health indicator (herbivore; diet of commercial fish)
Flamboyant Cuttlefish	<i>Metasepia pfefferi</i>	Sepiidae	Mollusca	Generalist	High touristic value
Flat Turban	<i>Angaria spp.</i>	Angariidae	Mollusca	Reef Specialist	Reef health indicator (herbivore); local consumption
Flatworm	Polycladida	Polycladida (Order)	Platyhelminthes	Generalist	High touristic value; aquarium trade
Flower Urchin	<i>Toxopneustes pileolus</i>	Toxopneustidae	Echinodermata	Generalist	Reef health indicator (herbivore; diet of commercial fish); local consumption

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Frog Shell	Bursidae	Bursidae	Mollusca	Generalist	Reef health indicator (>10cm used as bait for commercial fish); local consumption
Giant Clam	<i>Tridacna spp.</i> (except for <i>crocea</i>)	Cardiidae	Mollusca	Reef Specialist	Commercially important (food; shell trade; protected status)
Giant Turban	<i>Turbo marmoratus</i>	Turbinidae	Mollusca	Reef Specialist	Reef health indicator (herbivore); commercially important (shell trade; protected status); local consumption
Globe Urchin	<i>Mespila globulus</i>	Temnopleuridae	Echinodermata	Reef Specialist	Reef health indicator (herbivore; diet of commercial fish); not commercially important or consumed locally - identified separately to Collector Urchin
Golden Sandfish Sea Cucumber	<i>Holothuria lessoni</i>	Holothuriidae	Echinodermata	Generalist	Reef health indicator (cleaner organism); commercially important (food); local consumption
Greenfish Sea Cucumber	<i>Stichopus chloronotus</i>	Stichopodidae	Echinodermata	Generalist	Reef health indicator (cleaner organism); commercially important (food); local consumption
Hammer Oyster	<i>Malleus spp.</i>	Malleidae	Mollusca	Seagrass Specialist	Commercially important (food)
Harlequin Shrimp	<i>Hymenocera elegans</i>	Hymenoceridae	Arthropoda	Reef Specialist	Reef health indicator (Crown of Thorns predator)
Harp Shell	<i>Harpa articularis</i> , <i>Harpa major</i> , <i>Harpa spp.</i>	Harpidae	Mollusca	Seagrass Specialist	Commercially important (shell trade; permit required)
Headshield Slug	Cephalaspidea	Cephalaspidea (Order)	Mollusca	Generalist	High touristic value; aquarium trade
Honeycomb Oyster	<i>Hyotissa hyotis</i>	Gryphaeidae	Mollusca	Reef Specialist	Commercially important (food)
Horned Helmet	<i>Cassis cornuta</i>	Cassidae	Mollusca	Generalist	Reef health indicator (Crown of Thorns predator); commercially important (food; shell trade; protected status); local consumption
Leopard Sea Cucumber	<i>Bohadschia argus</i>	Holothuriidae	Echinodermata	Generalist	Reef health indicator (cleaner organism); commercially important (food); local consumption
Lobster	Nephropidae, Palinuridae, Scyllaridae	Nephropidae, Palinuridae, Scyllaridae	Arthropoda	Generalist	Commercially important (food)
Lollyfish Sea Cucumber	<i>Holothuria atra</i>	Holothuriidae	Echinodermata	Generalist	Reef health indicator (cleaner organism); commercially important (food); local consumption

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Magnum Sea Cucumber	<i>Neothyonidium spp.</i>	Phylloporidae	Echinodermata	Generalist	Reef health indicator (cleaner organism); high touristic value
Mantis Shrimp	<i>Lysiosquilla maculata</i> , <i>Odontodactylus scyllarus</i>	Lysiosquillidae, Odontodactylidae	Arthropoda	Generalist	Commercially important (food)
Mimic Conch	<i>Conomurex luhuanus</i>	Strombidae	Mollusca	Generalist	Reef health indicator (herbivore); commercially important (food); local consumption
Mimic Octopus	<i>Thaumoctopus mimicus</i>	Octopodidae	Mollusca	Generalist	Local consumption; high touristic value
Moon Shell	<i>Cernina fluctuata</i> , <i>Natica fasciata</i> , <i>Natica stellata</i> , <i>Natica spp.</i> , <i>Naticarius onca</i> , <i>Naticarius spp.</i> , <i>Polinices albumen</i> , <i>Polinices aurantius</i> , <i>Polinices cumingianus</i> , <i>Polinices spp.</i> , <i>Tanea undulata</i> , <i>Tanea spp.</i> , <i>Tectonatica violacea</i> , <i>Tectonatica spp.</i>	Ampullinidae, Naticidae	Mollusca	Seagrass Specialist	Commercially important (shell trade); local consumption
Nilo Topshell	<i>Trochus niloticus</i>	Tegulidae	Mollusca	Reef Specialist	Reef health indicator (herbivore; >10cm used as bait for commercial fish); commercially important (shell trade; protected status); local consumption
Nudibranch	Nudibranchia (further identified)	Nudibranchia (Order)	Mollusca	Generalist (occasionally Reef Specialist)	All: high touristic value; aquarium trade Some: reef health indicators (corallivores; eg, <i>Phestilla spp.</i> , <i>Phyllodesmium briareum</i>)
Olive Shell	<i>Oliva sericea</i> , <i>Oliva spp.</i>	Olividae	Mollusca	Seagrass Specialist	Commercially important (shell trade; permit required); local consumption; used as bait for other species
Other Bivalve	Bivalvia >5cm (must be accessible and excluding any species monitored separately)	Bivalvia (Class)	Mollusca	Generalist	>10cm commercially important (food); local consumption
Other Cleaner Shrimp	<i>Lysmata amboinensis</i> , <i>Lysmata debelius</i> , <i>Stenopus pyronotus</i> , <i>Urocaridella antonbruunii</i> <i>Urocaridella spp.</i>	Lysmatidae, Palaemonidae, Stenopodidae	Arthropoda	Reef Specialist	Reef health indicator (cleaner organism)
Other Cowrie	<i>Leporicypraea valentia</i> , <i>Lyncina vitellus</i> , <i>Talparia talpa</i> , Cypraeidae (excluding <i>Cypraea tigris</i>)	Cypraeidae	Mollusca	Generalist (occasionally Reef Specialist)	Commercially important (shell trade; some species have protected status; eg, <i>Ipsa childreni</i> , <i>Raybaudia porteri</i> , <i>Ransoniella martini</i>)

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Other Crab	Xanthidae, Brachyura >5cm (excluding Box Crabs, Decorator Crabs, Hermit Crabs and Swimming Crabs)	Brachyura (Infraorder)	Arthropoda	Generalist	All: reef health indicator (diet of commercial fish) Some: commercially important (food)
Other Cuttlefish	<i>Sepia spp.</i> (excluding <i>bandensis</i> and <i>latimanus</i>)	Sepiidae	Mollusca	Generalist	Local consumption
Other Octopus	<i>Abdopus aculeatus</i> , Octopodidae (excluding any species monitored separately)	Octopodidae	Mollusca	Generalist	Local consumption
Other Sea Cucumber (identified and recorded as its own species)	Holothuriidae, Phyllophoridae, Stichopodidae (further identified; excluding Synaptic Sea Cucumbers)	Holothuriidae, Phyllophoridae, Stichopodidae	Echinodermata	Generalist	Reef health indicator (cleaner organism); commercially important (food); local consumption
Other Shell	Gastropoda > 5cm (excluding any species monitored separately)	Gastropoda (Class)	Mollusca	Generalist	Reef health indicator (>10cm used as bait for commercial fish); local consumption
Other Shrimp	Penaeidae >5cm (excluding Other Cleaner Shrimp and any species monitored separately)	Penaeidae	Arthropoda	Generalist	Commercially important (food)
Other Topshell	<i>Tectus pyramis</i> , <i>Tectus spp.</i> , <i>Trochus hanleyanus</i> , <i>Trochus maculatus</i> , <i>Trochus rota</i> , <i>Trochus sacellum</i> , <i>Trochus stellatus</i> , <i>Trochus spp.</i> (excluding <i>niloticus</i>)	Tegulidae	Mollusca	Reef Specialist	Reef health indicator (herbivore; >10cm used as bait for commercial fish); commercially important (shell trade); local consumption
Pearl Oyster	<i>Pinctada margaritifera</i> , <i>Pinctada spp.</i>	Pteriidae	Mollusca	Reef Specialist	Commercially important (food; shell trade; permit required)
Pen Oyster	<i>Atrina vexillum</i>	Pinnidae	Mollusca	Seagrass Specialist	Commercially important (food; shell trade; permit required)
Pineapple Sea Cucumber	<i>Thelenota ananas</i>	Stichopodidae	Echinodermata	Generalist	Reef health indicator (cleaner organism); commercially important (food); local consumption
Pinkfish Sea Cucumber	<i>Holothuria edulis</i>	Holothuriidae	Echinodermata	Generalist	Reef health indicator (cleaner organism); commercially important (food); local consumption
Pleurobranch	<i>Pleurobranchus spp.</i> , Pleurobranchidae	Pleurobranchidae	Mollusca	Generalist	High touristic value
Rock Boring Urchin	<i>Echinometra mathaei</i> , <i>Echinostrephus aciculatus</i>	Echinometridae	Echinodermata	Reef Specialist	Reef health indicator (herbivore; diet of commercial fish)

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

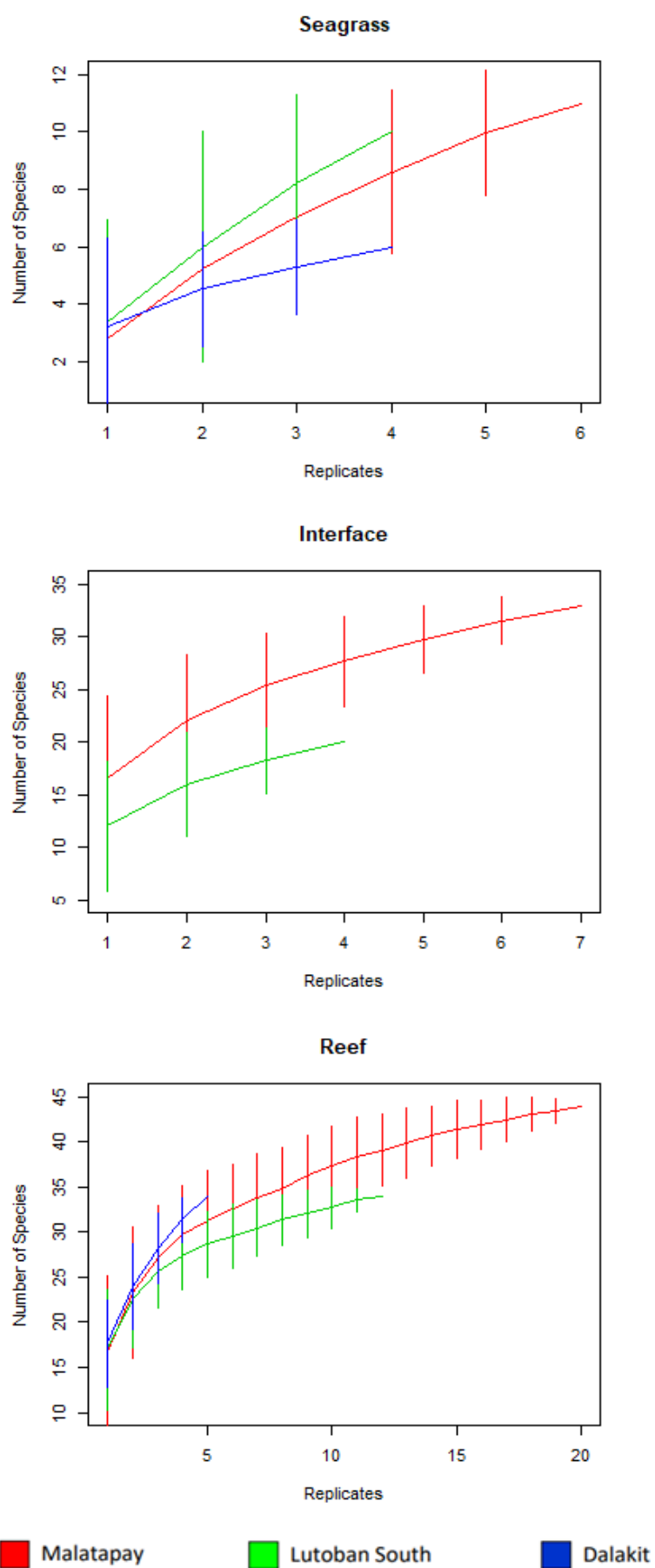
Rock Murex	<i>Chicoreus banksii</i> , <i>Chicoreus microphyllus</i> , <i>Chicoreus palmarosae</i> , <i>Chicoreus ramosus</i> , <i>Chicoreus territus</i> , <i>Chicoreus spp.</i>	Muricidae	Mollusca	Reef Specialist	Commercially important (shell trade)
Rocky Turban	<i>Turbo argyrostomus</i>	Turbinidae	Mollusca	Reef Specialist	Reef health indicator (herbivore); commercially important (shell trade); local consumption
Sand Murex	<i>Haustellum spp.</i> , <i>Murex pecten</i> , <i>Murex tribulus</i> , <i>Murex spp.</i>	Muricidae	Mollusca	Seagrass Specialist	Commercially important (shell trade; permit required)
Sap-Sucking Slugs	Costasiellidae, Hermaeidae, Limapontiidae, Plakobranchidae, Platyhedylidae	Costasiellidae, Hermaeidae, Limapontiidae, Plakobranchidae, Platyhedylidae	Echinodermata	Generalist (occasionally Seagrass Specialist)	Reef health indicator (herbivore)
Scallop	<i>Anadara spp.</i> , Pectinidae	Arcidae, Pectinidae	Mollusca	Seagrass Specialist	Commercially important (food; permit required)
Scorpion Spider Conch	<i>Harpago chiragra</i> , <i>Lambis lambis</i> , <i>Lambis millepeda</i> , <i>Lambis scorpius</i> , <i>Lambis truncata</i> , <i>Lambis wheelrighti</i> , <i>Lambis spp.</i>	Strombidae	Mollusca	Generalist	Reef health indicator (herbivore); commercially important (food; shell trade; permit required); local consumption
Sea Hare	<i>Aplysia spp.</i>	Aplysiidae	Mollusca	Seagrass Specialist	Reef health indicator (herbivore); commercially important (eggs only); local consumption (eggs only)
Sea Star	Echinasteridae	Echinasteridae	Echinodermata	Generalist	Reef health indicator (diet of commercial fish)
Small Conch	<i>Canarium microurceus</i> , <i>Canarium mutabile</i> , <i>Dolomena variabilis</i>	Strombidae	Mollusca	Generalist	Reef health indicator (herbivore); commercially important (food); local consumption
Smooth Turban	<i>Turbo petholatus</i> , <i>Turbo reevii</i>	Turbinidae	Mollusca	Reef Specialist	Reef health indicator (herbivore); commercially important (shell trade); local consumption
Squid	Idiosepiidae, Loliginidae	Idiosepiidae, Loliginidae	Mollusca	Generalist	Reef health indicator; commercially important (food)
Starry Night Octopus	<i>Callistoctopus luteus</i>	Octopodidae	Mollusca	Generalist	Local consumption
Swimming Crab	Portunidae	Portunidae	Arthropoda	Generalist	Reef health indicator (diet of commercial fish); commercially important (food)
Thorny Oyster	<i>Spondylus spp.</i>	Spondylidae	Mollusca	Reef Specialist	Commercially important (food; shell trade)
Tiger Cowrie	<i>Cypraea tigris</i>	Cypraeidae	Mollusca	Reef Specialist	Commercially important (shell trade; permit required)

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Triton Shell	<i>Charonia tritonis</i>	Ranellidae	Mollusca	Reef Specialist	Reef health indicator (Crown of Thorns predator); commercially important (shell trade; protected status); local consumption
Tun Shell	<i>Malea pomum</i> , <i>Tonna allium</i> , <i>Tonna canaliculata</i> , <i>Tonna cumingii</i> , <i>Tonna galea</i> , <i>Tonna perdix</i> , <i>Tonna sulcosa</i> , <i>Tonna spp.</i>	Tonnidae	Mollusca	Seagrass Specialist	Commercially important (shell trade); local consumption
Volcano Sea Cucumber	<i>Stichopus herrmanni</i>	Stichopodidae	Echinodermata	Generalist	Reef health indicator (cleaner organism); commercially important (food); local consumption
Volute Shell	<i>Cymbiola vespertilio</i>	Volutidae	Mollusca	Seagrass Specialist	Commercially important (shell trade); local consumption
White Teatfish Sea Cucumber	<i>Holothuria fuscogilva</i>	Holothuriidae	Echinodermata	Generalist	Reef health indicator (cleaner organism); commercially important (food); local consumption
Wonderpus Octopus	<i>Wunderpus photogenicus</i>	Octopodidae	Mollusca	Generalist	Local consumption; high touristic value

SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Appendix E: Fish Species Accumulation Curves



SEAGRASS-REEF CONNECTIVITY IN THE PHILIPPINES

Appendix F: Invertebrate Species Accumulation Curves

