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High diversity, but low abundance of cryptobenthic fishes on soft sediment habitats in Southeast Asia

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Abstract

Cryptobenthic fishes play a crucial role in marine ecosystems as trophic links between the base of the food chain and higher-level consumers. Infralittoral soft sediments are the largest marine habitat, yet little is known about fish assemblages in these ecosystems. This study investigates the cryptobenthic fish abundance and diversity on soft sediment habitats in the centre of tropical marine biodiversity. We surveyed 20 sites across three regions in Indonesia (Bali, Lembeh Strait) and the Philippines (Dauin) using Underwater Visual Surveys (UVC) and roving diver surveys. We tested the effects of depth (6m, 16m), benthic cover and sediment grain size characteristics on fish assemblages. Our results showed a high diversity (112 species), but low abundances (mean: 93 individuals/500m^2 ± SE: 28 ind.). Benthic cover on surveyed sites consisted for 90.1% (± SE: 0.7%) of unconsolidated sediments, which were predominantly poorly sorted ($\sigma = 0.975\ \phi$), gravelly sand. PERMANOVA analyses showed that fish assemblages and fish diversity was significantly different between regions ($p<0.001$) and depth ($p = 0.002$). Distance based linear Models (DistLM) explained respectively 25% and 33.5% of the variation in fish assemblages and fish diversity. The high cryptobenthic fish diversity found in this study exceeds that of many coral reefs and contradicts the current view of soft sediment fish communities as depauparate ones. Our results provide valuable insights in a poorly studied marine ecosystem and call for more research in these valuable habitats.

Highlights

First study of cryptobenthic fishes on soft sediment in Southeast Asia
Soft sediment showed high fish species diversity, but low abundance
Grain size and benthic cover were important drivers of fish assemblages
Results challenge current views of fish communities on soft sediment habitats

Keywords

Indonesia; Philippines; sediment characteristics; Underwater Visual Census; ecology; benthic cover

1. Introduction

One of the foremost challenges in marine ecology is explaining existing patterns in biodiversity. Species-rich habitats such as coral and temperate reefs have received considerable research effort attempting to explain these patterns for fish assemblages. This has led to a good understanding of ecological concepts such as species distribution or abundance, yet questions remain on the drivers of small-scale, community-level processes (Sale 2013). Large scale patterns in distribution and dispersion are strongly affected by biogeographical history (Cowman et al. 2013; Bowen et al. 2016), but also by genetic diversity and ecological plasticity (DiBattista et al. 2015). While, on a smaller scale, species composition is more affected by environmental variables such as microhabitat (Messmer et al. 2011), depth (Bridge et al. 2016), and reef zonation (Depczynski and Bellwood 2005). On an even finer scale, interactions between species and differing trophic roles are central in structuring fish communities (Griffin et al. 2008; Levine and HilleRisLambers 2009). At this level, cryptobenthic fishes play an important role in shaping the trophodynamics of coral reef systems (Depczynski and Bellwood 2003; Ackerman et al. 2004). These small-sized species provide a crucial link in the base of the food chain through high abundances and rapid generational turnover rates (Depczynski and Bellwood 2006). Therefore, understanding what drives patterns in the composition and distribution of cryptobenthic fish assemblages can help us understand what drives patterns in the entire fish assemblage (Coker et al. 2018).

Cryptobenthic fish are small fishes (typically less than 50 mm Total Length (TL)) that are associated with the seabed, and which are visually or behaviourally cryptic (Goatley and Brandl 2017). On coral reefs they are the most abundant guild of reef fishes and have short life cycles with quick generational turnover rates (Lefèvre et al. 2016). Most species have small home ranges, resulting in a high diversity and big differences in community composition on small spatial scales, as seen in the Red Sea (Coker et al. 2018). Many cryptobenthic species are habitat specialists associated with a preferred microhabitat (Depczynski and Bellwood 2004; Ahmadia et al. 2012). This dependence on microhabitats drives many cryptobenthic assemblages, and habitat associations are phylogenetically conserved over large timescales (Ahmadia et al. 2018). Cryptobenthic fish assemblages are often strongly depth structured (Dalben and Floeter 2012). As a result, cryptobenthic fish assemblages can vary greatly between different reef zones. On the Great Barrier Reef for example, sandy and rubbly habitats had a higher abundance and diversity than open coral reefs (Depczynski and Bellwood 2005). On a biogeographical scale, cryptobenthic fishes show distinct regional assemblages that increase in diversity with decreasing latitude (Brandl et al. 2017).

Biogeographical history affects taxonomic composition of fishes, but the functional composition of fish assemblages is more strongly defined by the habitat they live in (Hemingson and Bellwood 2017). Hemingson and Bellwood (2017) studied three dominant shallow-water marine habitats in the tropics; coral reefs, mangroves, and seagrass beds. Many other studies have investigated species assemblages in these “dominant” habitats, but very few have included one of the most extensive marine habitats in shallow waters: soft sediment (e.g., Travers et al. 2010; Schultz et al. 2012). Because of their close association with the seabed, the composition of cryptobenthic species assemblages are highly dependent on available habitat (Munday 2004; Depczynski and Bellwood 2005; Ahmadia et al. 2012). Therefore, it is expected that cryptobenthic fish assemblages on soft sediment habitats will differ markedly from other, better studied, habitats such as mangroves, seagrass beds, or coral reefs.

Soft sediment habitats (muds, sand, and gravel) make up to 55% of the shallow coastal areas in the coral triangle (Hayes 1967). Faunal assemblages on these habitats have received limited research attention. Research on coral rubble habitats exists; while these resemble gravel habitats, they are typically associated with degraded reefs (e.g., Bellwood and Fulton 2008; Enochs and Manzello 2012; Bailey-Brock et al. 2007). However, not all soft sediment habitats are degraded reefs or seagrass sites (Nyström et al. 2012). The absence of complex biological structures indicates that environmental factors prevent the development of more complex habitats, rather than the disappearance of these habitats by anthropogenic impacts (Gray and Elliott 2009). As such, some soft sediment sites could be considered to be as 'pristine' as untouched coral reefs. The lack of physical complexity typical to soft sediment habitats make them challenging environments for fish to thrive in. In terms of fish fauna, soft sediment habitats have been considered to be 'depauparate' habitats (e.g. Depczynski and Bellwood (2004)), yet they are important as nursery grounds for commercially important species (Hatcher et al. 1989). Since soft sediment habitats differ so strongly from other systems, it has been argued that different paradigms are needed to understand drivers of species assemblages (Wilson 1990).

To date, research on soft sediment habitats has predominantly focused on infaunal invertebrate assemblages (Alongi 1990; Gray 2002; Gray and Elliott 2009). Grain size and related variables such as sorting have been shown to be important environmental factors driving infaunal communities (Gray 2002; Gray and Elliott 2009). Variations in benthic cover or grain size can offer refuge or suitable habitat and has been shown to affect fish assemblages (Langlois et al. 2006; van Denderen et al. 2014; Schultz et al. 2015). Cryptobenthic fish fauna on coral reefs and sub-tropical reefs depends on specific microhabitats for shelter or food (Munday 2004; Ahmadia et al. 2018). Despite extensive work done on invertebrate communities on soft sediment, and cryptobenthic fishes on coral reefs, there is a paucity of data on cryptobenthic fish communities on soft sediment habitats, particularly in the tropics (Alongi 1989, Gray 2002; Schultz et al. 2012).

Our limited knowledge about the most common coastal habitat is a critical knowledge gap, as soft sediment habitats play a vital role in supporting livelihoods of coastal communities. Southeast Asia has the highest marine biodiversity in the world (Hoeksema 2007; Allen 2008), yet less than 25% of the fishery production in Southeast Asia depends on coral reef fishes, instead focusing on pelagic or soft sediment associated species such as scad (*Selar* spp.) and sardines (*Clupeidae*) (Clifton and Foale 2017). Scuba dive tourism on soft sediment habitat is worth more than USD $150 million year^{-1} and employs over 2000 people in Indonesia and Philippines (De Brauwer et al. 2017). The ecology of species driving tourism is poorly understood and their conservation status is often unknown (De Brauwer and Burton 2018).

This study aims to investigate cryptobenthic fish assemblages and diversity on soft sediment habitats in the centre of tropical marine biodiversity, Southeast Asia. This study focusses on sites where local coastal communities are dependent on soft sediment habitats for their livelihoods. In particular we investigated 1) regional differences in fish assemblages and species diversity; and 2) the role of benthic cover, sediment grain size characteristics, and depth in driving differences in fish assemblages.

2. *Methods*

2.1 Cryptobenthic fishes

Cryptobenthic fishes on coral reefs have been defined as species that "closely resemble a part of a substratum, a plant, or a sedentary animal such as a sponge or soft coral" (Randall 2005), or species that are "typically less than 5 cm long that are visually or behaviourally cryptic, and live near to or within the seabed" (Goatley and Brandl 2017). Recent work further emphasised the importance of small adult size when defining cryptobenthic reef fishes, rather than their benthic position (Brandl et al. 2018). Due to the unique characteristics of soft sediment habitats compared to reefs, we extended this definition to also including larger cryptic species that live in close association with the benthos (e.g. stargazers (*Uranoscopidae*) and frogfishes (*Antennariidae*)), as they form an important part of the cryptobenthic fish communities in these ecosystems.

The two most commonly found cryptobenthic fish families (*Gobiidae*, *Blenniidae*) on coral reefs were not included in surveys despite their abundance on soft sediment habitats. The decision not to include this important group was taken due to the logistical constraints of sampling these families. Soft sediment *Gobiidae* and *Blenniidae* exhibit rapid predator avoidance responses in which they retreat into burrows in the sediment, making reliable species identification during visual surveys nearly impossible. These families are best sampled with ichthyocides (such as rotenone or clove oil), which is prohibited in the majority of the locations surveyed for this research.

2.2 Study sites

Surveys were conducted in three regions across Southeast Asia where soft sediment sites are important in supporting local livelihoods through tourism or sustenance fishing; Dauin (Philippines), Lembeh Strait (Indonesia), Bali (Indonesia). Five sites were surveyed in Dauin, seven sites in Lembeh, eight in Bali (Figure 1). All sites were slopes (slope angle approximately 40 - 50 degrees), consisting mainly of black or dark brown volcanic sand. Sites were in locations where "muck dive" tourism was present, although three surveyed sites (sites 4, 15, and 16) were not considered to be dive sites by tourism operators, and thus receive limited numbers of divers.

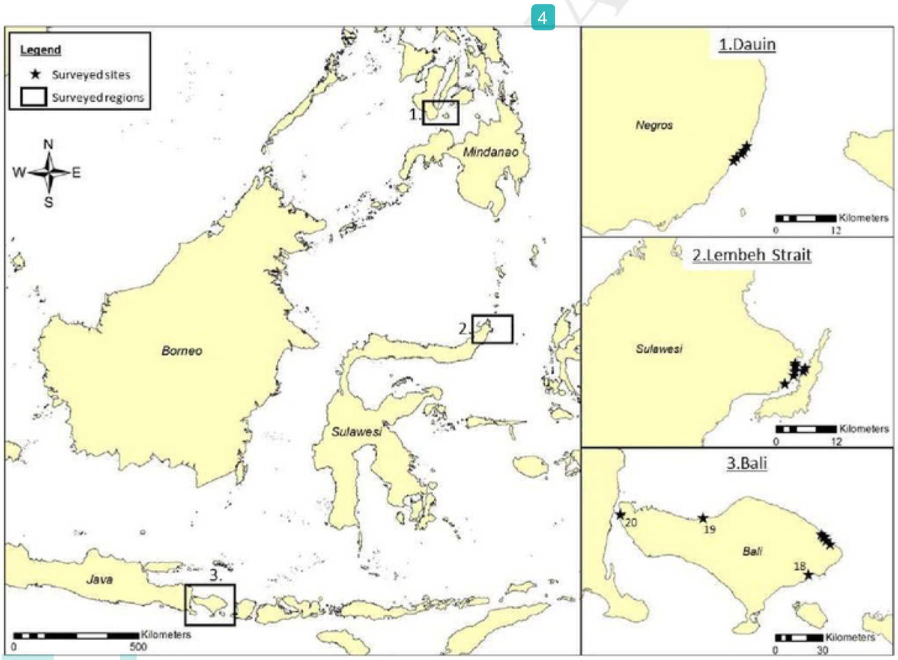

Figure 1. Map of survey sites

2.2.1 *Dauin*

Dauin (9° 11' 22'' N, 123° 16' 56'' E) is a coastal town in southern Negros, Philippines with a growing dive tourism industry (De Brauwer et al. 2017). The underwater seascape consists mainly of volcanic sand slopes, with occasional widely interspersed small coral reef patch reefs and seagrass growth in some of the shallow areas. Five sites were surveyed in Dauin in May 2015 (Supplementary Table S1).

2.2.2 Lembeh Strait

Lembeh Strait (1° 28' 22'' N, 125° 14' 26'' E) in North-Sulawesi (Indonesia) is one of the world's most popular muck dive destinations (De Brauwer et al. 2017). The area is a narrow strait between Lembeh Island and the North-Sulawesi mainland, subjected to strong daily tidal currents. The strait consists of multiple bays with black sand slopes, alternated with small coral reefs on the current-swept capes. A large industrial port city (Bitung) on the mainland is situated in the centre of the strait. Seven sites were surveyed in Lembeh strait in July 2015 (Supplementary Table S1).

2.2.3 Bali

Bali (8° 19' 51'' S, 115° 38' 54'' E) is Indonesia's most popular tourist destination, with most tourism occurring in the south and centre of the island (Sanders and Willson 2017). Surveys in Bali were done on sites on the northeast coast, one site on the east coast and two sites on the northwest coast. Sites were slopes predominantly consisting of black volcanic sand. One site (site 20) was a protected sandy lagoon, one site (site 18) had a large jetty running through the middle of the surveyed area. Eight sites were surveyed in Bali between August and September 2015 (Supplementary Table S1).

2.3 Surveys

2.3.1 Fish assemblages

Underwater Visual Census (UVC) surveys were conducted by two SCUBA divers using 25 m x 2 m belt transects parallel to the shoreline. The width of belt transects was reduced compared to standard 5 m wide UVC belt transects, to more efficiently detect cryptic species (McCormick and Choat 1987;

Bozec et al. 2011). At each site, five transects were conducted at 16 m water depth, and five transects at 6 m depth, unless this was not possible due to site topography or weather conditions. The same observer (MDB) surveyed fish fauna for all transects by passing over the transect line twice, recording species and abundance. The initial pass was done while laying out the transect line and detected mobile species with the tendency to flee divers (e.g. *Trichonotidae*, *Callionymidae*). The second pass was at a slower speed and aimed to detect less mobile and smaller species (e.g. *Antennaridae*, *Syngnathidae*).

2.3.2 Diversity roving diver surveys

Additional roving diver surveys were conducted on each site to account for rare species that would remain undetected during UVCs (Schmitt et al. 2002). Roving surveys were conducted as a separate third dive after completing the UVC transects at both depths. The entire site, including the area surveyed during UVC transects, was surveyed by descending to 20m deep and then slowly ascending the site in a zigzag-pattern. A maximum total dive time of 70 minutes was set as a limit for roving surveys. During the roving diversity surveys species not yet detected during the initial UVC transects were recorded. Presence data only was recorded, no abundance data was recorded during these surveys.

To allow for comparison with other studies, abundance and diversity data was compiled from recently published literature on cryptobenthic fishes. Abundance was standardised to 100m^2, but diversity was kept for the entire study area as described in each paper.

2.4 Environmental variables

2.4.1 Benthic cover

To measure benthic cover, a photo was taken of the substrate at every meter of the transect (26 photos per transect) after finishing each UVC transect swim, ensuring the tape measure was visible in each photo. Photos of the substrate were analysed using Coral Point Count (CPCe 4.1) software

(Kohler and Gill 2006). Based on the tape measure visible in the photos, 30 cm x 30 cm quadrats were transposed over each photo. Twenty points were randomly placed inside the quadrat and classified into different categories (Description of categories in Supplementary Table S2). This approach allowed for a benthic cover resolution of 520 points per 50m^2 transect (5200 per site).

2.4.2 *Sediment grain size characteristics*

For each transect 100 g of sediment was collected from the top layer (5 cm) of the substrate. Sediment samples were air-dried and organic material removed prior to sediment analyses in Australia (to comply with Australian customs requirements). Dry sediment samples from Dauin were weighed, and then divided into 6 size classes using wet sieving (Syvitski 2007). Each size class was oven dried for 48 hours, after which each size class was weighed again. Dry sediment samples from Lembeh Strait and Bali were weighed and then dry sieved to remove the coarse fraction (>2000μm). The remaining fraction was then analysed using laser diffraction with a Malvern Mastersizer 2000. Both methods have been shown to yield similar results and can be used and compared for the type of sediment in the survey sites (Singer et al. 1988; Loizeau et al. 1994). A full list of all grainsize characteristics that were quantified can be found in appendices (Supplementary Table S3).

2.5 Data analysis

2.5.1 *Environmental variables*

Benthic cover was calculated using CPCe analysis (Kohler and Gill 2006). Grain size characteristics were analysed using Excel GRADISTAT 4.0 (Blott and Pye 2001). Environmental data was averaged for each depth per site, normalised, and a Euclidean distance resemblance matrix was constructed in PRIMER. Differences between environmental variables were tested using PERMANOVA in Primer, based on a two factor design (Region (Fixed), Depth (Fixed)), with a permutation of data under a reduced model, running 9999 permutations. Pairwise PERMANOVA tests were conducted when the main test showed significant differences.

2.5.2 Fish assemblages

Analyses of soft sediment cryptobenthic were conducted with the PRIMER 7 package (Clarke and Gorley 2015). Fish assemblage analyses used UVC data only, as roving diver surveys did not measure abundance. Data for each site were pooled for deep and shallow transects, making site the replication unit for each region. Abundance data met assumptions of homogeneity of variance, so untransformed abundance data was used to construct a zero-adjusted Bray-Curtis resemblance matrix. We tested the differences between assemblages using PERMANOVA based on a two factor design (Region (Fixed), Depth (Fixed)), with a permutation of data under a reduced model, running 9999 permutations. Subsequent pairwise PERMANOVA tests were conducted to compare Regions, and Depth differences between and within regions.

Patterns in the data were visualised using Principal Coordinate Analysis (PCO), followed by a constrained Canonical Analysis of Principal Coordinates (CAP) (Anderson and Robinson 2003; Anderson and Willis 2003). PCO is an unconstrained analysis, visualising the largest differences between sites without applying a priori hypotheses, and thus showing broad patterns in abundance data. CAP is a constrained analysis which tests for a specific hypothesis, i.e. differences between regions in this study (Anderson and Willis 2003). Leave-one-out allocation success tests gave an estimate of how samples were allocated to distinct regions. This gave an estimate of how distinct assemblages were at each region (Anderson and Willis 2003). The CAP plots were then overlayed with vectors illustrating the species that were most strongly correlated to the observed difference (Pearson's correlation value > ±0.5).

Distance based linear models (DistLM) were calculated to test the role of environmental variables in assemblage patterns, using the "best" selection procedure and the Akiake Information Criterion (AIC). Predictor environmental variables were first averaged per site and depth, then normalised. We tested correlations between environmental variables by constructing a draftsman plot. Variables which were strongly correlated (> ±0.8) were excluded, in this case we excluded the predictor variables Skewness, Kurtosis, Median Grainsize, and percent cover of Gravel from analysis. The assemblage was plotted using a distance based Redundancy Analysis (dbRDA) and overlayed with dominant predictor variables (Pearson's correlation > ±0.4).

2.5.3 Fish species diversity

Presence / absence data for species diversity used species lists collated from the combined UVC and roving diver surveys. Using the PRIMER 7 software package (Clarke and Gorley 2015), a Jaccard resemblance matrix was constructed on the presence / absence data. General differences in fish diversity between regions were tested using PERMANOVA (one factor: Region (Fixed)), with a permutation of data under a reduced model, running 9999 permutations. Further pairwise PERMANOVA tests were then conducted to compare the different regions. Data were visualised using PCO and CAP following the same procedure as for the fish assemblages (Anderson and Willis 2003). The CAP plots were then overlayed with species that were most strongly correlated to the observed difference (Pearson's correlation value > ±0.7)

Distance based linear models (DistLM) were calculated to test the role of environmental variables in driving diversity patterns, using the same procedure as described above. For this analysis, the strongly correlated (> ±0.8) variables excluded were Skewness, Kurtosis, and Percent cover of gravel. The results were plotted using a distance based Redundancy Analysis (dbRDA) and overlayed with dominant predictor variables (Pearson's correlation > ±0.4).

3. Results

3.1 Summary statistics

A total of 187 transects were conducted across 20 sites (Dauin: 5, Lembeh: 7, Bali: 8). In Bali there were two sites where it was only possible to collect data at one depth for two sites (site 20: 6m, site 18: 16m). At one site in Bali (site 17) only two transects were possible in the shallow area as the habitat beyond these transects consisted of dense coral reefs and was therefore beyond the scope of this research project (Supplementary Table S1). During the surveys, a total of 112 different cryptobenthic fish species were observed (Dauin: 48 species, Lembeh: 73 species, Bali: 71 species). The average fish abundance was 93 individuals (± SE: 28) per site (500m^2) (Dauin: 235 ± SE: 74, Lembeh: 33 ± SE: 6, Bali: 57 ± SE: 27). The most common species in all regions was *Trichonotus elegans* (Full species list in Supplementary Table S4).

Comparisons with published research showed that cryptobenthic species richness recorded in this study was higher than most surveys on tropical coral reefs, except for one study on the Great Barrier Reef (Table 1). Other studies in subtropical or temperate regions similarly reported lower species numbers than this study (Table 1). Abundance, however, was up to three orders of magnitude smaller than in previous studies (Table 1).

Table 1. Comparison of cryptobenthic fish diversity and abundance in different habitats and locations based on published literature. Studies are ranked from highest to lowest diversity (= species richness). Abundance has been standardised to 100m^2 when data was available in the original study.

Country	Location	Habitat	Method	Diversity	Abundance (100m^2)	Reference
Australia	Great Barrier Reef	Coral reef	Clove oil	79	3070	Goatley et al. 2016
Indonesia	Lembeh Strait	Soft sediment	UVC	73	7	This study
Indonesia	Bali	Soft sediment	UVC	71	10	This study
Indonesia	Hoga Island	Coral reef	Clove oil	50	833	Ahmadia et al. 2012
Philippines	Dauin	Soft sediment	UVC	48	47	This study
Australia	Great Barrier Reef	Coral reef	Clove oil	48	N/A	Depczynski and Bellwood 2003
Indonesia	Hoga Island	Coral reef	Clove oil	47	1111	Ahmadia et al. 2018
Micronesia	Pohnpei	Coral reef	Clove oil	46	1389	Ahmadia et al. 2018
Australia	Great Barrier Reef	Coral reef	Clove oil	42	N/A	Depczynski and Bellwood 2004
Mexico	Baja California	Rocky reef	UVC	40	2560	Galland et al. 2017
Croatia	Cape Silo	Rocky reef	Quinaldine	27	600	Kovačić et al. 2012
French Polynesia	Moorea	Coral reef	Clove oil	22	1667	Ahmadia et al. 2018
Belize	Belizean Barrier Reef	Dock pilings	Clove oil	21	N/A	Brandl et al. 2017
USA	4 locations	Dock pilings	Clove oil	19	N/A	Brandl et al. 2017
Panama	Bocas, Punta Caracol	Dock pilings	Clove oil	14	N/A	Brandl et al. 2017

Benthic cover consisted mostly of unconsolidated sediments (sand, gravel, pebbles, coral rubble), with a mean cover of 90.1% (± SE: 0.7%) across all sites. Marine plants and natural debris were the other principal components of the benthic cover at 5.6% (± SE: 0.5%) and 3.5% (± SE: 0.3%) respectively. Mean coral cover was very low across sites (0.3% ± SE: 0.05%), with little difference between regions (Supplementary Materials: Figure SF1 + Table S3).

The sediment was predominantly poorly sorted (σ = 0.975 ϕ), gravelly sand (Fig. 2). Grain size distribution was ~~fine~~ skewed, coarse sand and was platykurtic with a bimodal distribution. The mean grain size was 817.4μm, and distribution of particles (D10 – D90) ranged from 269.6μm to 2148.6μm.

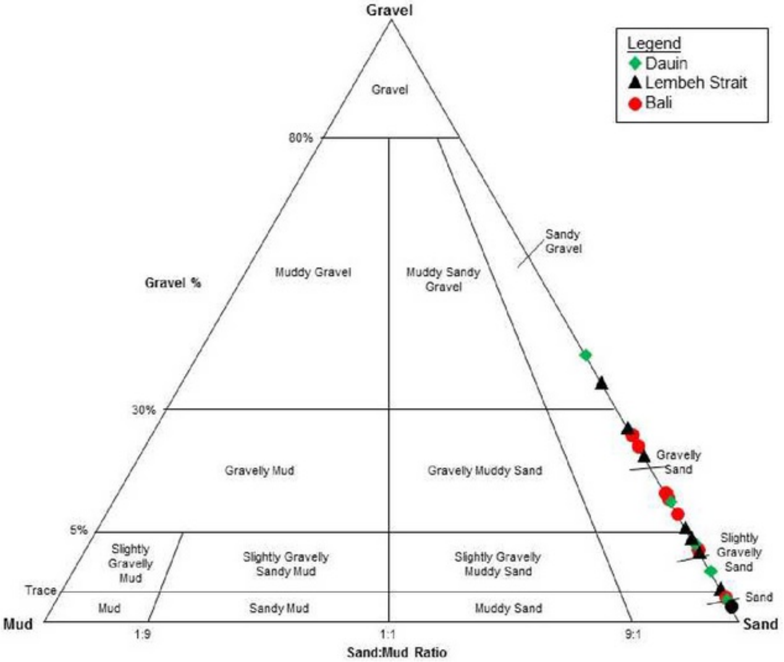

Figure 2. Folk sediment classification for 20 soft sediment sites surveyed in Southeast Asia.

Multivariate PERMANOVA analyses indicated statistical differences between environmental variables on the level of region, but not between different depths, nor was there a Region x Depth interaction (Table 2). Pairwise analyses for region indicated differences between Lembeh and Dauin ($p = 0.05$, t: 1.5), and Lembeh and Bali ($p = 0.02$, t: 1.6), but not between Dauin and Bali ($p = 0.40$, t: 1.0).

3.2 Fish assemblages

PERMANOVA tests of species assemblages and abundance indicated significant differences between the regions, depth, and a region x depth interaction (Table 2). Differences in depth were driven by site x depth interactions in Dauin ($p = 0.02$, t: 1.6) and Bali ($p = 0.02$, t: 1.4), there was no effect of depth in Lembeh ($p = 0.19$, t: 1.2). Pairwise analyses between regions showed that the species assemblages of all regions were significantly different from each other (Dauin – Lembeh: $p < 0.001$, t: 2.2, Dauin – Bali: $p < 0.001$, t: 2.2; Lembeh – Bali: $p < 0.001$, t: 1.7).

Table 2. Results of multivariate PERMANOVA analyses of environmental variables, fish assemblages and fish diversity on soft sediment habitats in Southeast Asia. Values in bold show significance at $P < 0.05$

Factor	*df*	*MS*	*Pseudo-F*	*P*
Environmental variables				
Region	2	19.3	1.8	0.04
Depth	1	11.9	1.1	0.32
Region x Depth	2	8.0	0.7	0.72
Fish assemblage				
Region	2	13208	4.0	<0.001
Depth	1	6869	2.1	0.002
Region x Depth	2	5944.1	1.8	0.002
Fish diversity				
Region	2	7251	2.7	<0.001

The principal coordinate analysis illustrated clear patterns in the fish assemblages (Fig. 3A). The different regions separated out with minor overlap. Shallow sites in Bali and Dauin were different from deep ones, which was not the case in Lembeh. A hypothesis-driven constrained ordination (CAP) was then applied since the PERMANOVA analyses indicated significant differences in regions (Fig. 3B). The CAP plot indicated a clear separation between regions and a separation between depths in Dauin (Fig. 3B). Differences seen between sites were mainly driven by *Antennarius pictus*, *Cymolutes torquatus* and *Callionymus superbus* in Dauin (Fig. 3B). The allocation success for each region was very high, Dauin (100%), Lembeh (85.7%), Bali (71.4%) (Trace statistic: 1.70; $p < 0.001$) which confirms that the fish assemblage at each location is distinct (Anderson and Willis 2003).

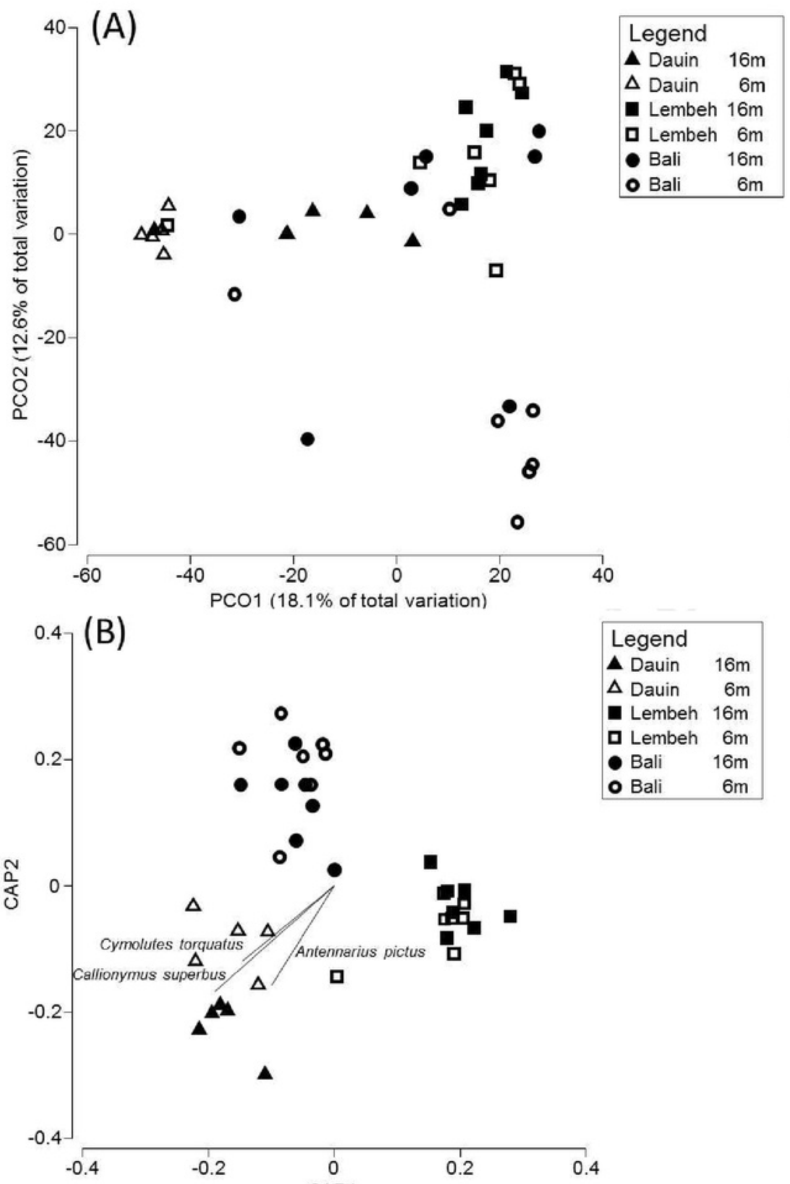

Figure 3. A) 15cipal Component Ordination of fish assemblages at different depths in three regions in Southeast Asia. B) constrained Canonical Analysis of Principal Coordinates (CAP) of these same fish assemblages for the interactions between regions, species overlayed with Pearson R correlation to either axis of value > ±0.5.

The DistLM procedure to test the contributions of different habitat variables resulted in a final model which explained 25% of the variation seen in the assemblage and included five variables. These variables included two components of benthic cover (Sand: 4.9%, Plants: 7.0%) and three sediment grain characteristics (mean grain size: 5.3%, D10: 4.1%, and D90: 4.2%) (AIC = 315.8, R^2 =

0.250) (Table 3). D10 and D90 are both measures of the distribution of sediment particle size, indicating that respectively 10% and 90% of the volume of measured sediment is contained below that grainsize. The dbRDA illustrates limited separation of crypto-benthic fish assemblages explained by these environmental variables, indicated by the limited separation between the different depths and regions (25% explained; Fig. 4).

Table 3. Contribution of different habitat variables to cryptobenthic fish assemblages (abundance + diversity) on soft sediment sites in Southeast Asia: results of Distance based Linear model in Primer. Variables in bold were those included in final model.

Variable	SS (trace)	Pseudo-F	P	Proportion explained
AIC = 315.8, R^2 = 0.250, No. of variables = 5				
% Sand	**7322.2**	**1.85**	**0.02**	**0.049**
% Pebbles	6619.2	1.66	0.03	0.044
% Plants	**10510**	**2.71**	**<0.001**	**0.070**
% Artificial objects	2814.5	0.69	0.86	0.019
% Natural Debris	6512.3	1.63	0.01	0.043
% Coral	5231.9	1.30	0.11	0.035
% Sponges	6661.8	1.67	0.03	0.044
Mean grain size	**7931.7**	**2.01**	**0.01**	**0.053**
D10	**6208.3**	**1.55**	**0.05**	**0.041**
D90	**6249.9**	**1.56**	**0.05**	**0.042**
Sorting	3765	0.93	0.53	0.025

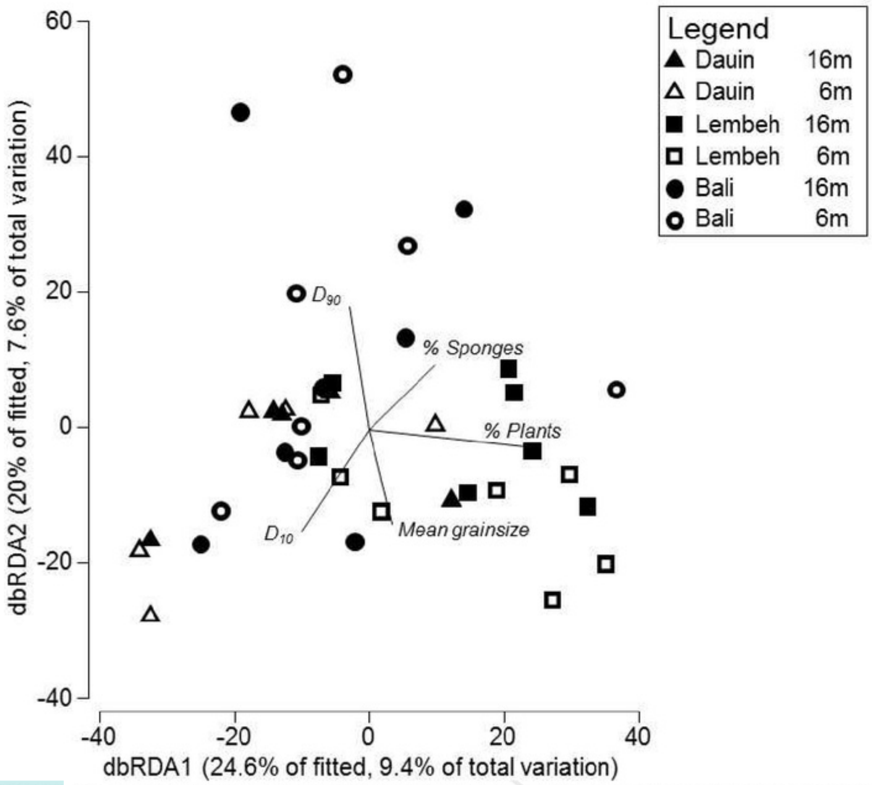

Figure 4. Distance based Redundancy Analysis plot of soft sediment fish assemblages (abundance + diversity) in three regions in Southeast Asia, overlayed with environmental variables responsible for changes in the assemblage.

3.3 Species diversity

The roving diver surveys detected 34 species that were not observed during the UVC surveys (30.4% increase). The PERMANOVA tests of combined species diversity of UVC transects and roving diver surveys showed significant differences between each of the three regions (Table 2). The PCO showed clear differentiation between the different regions, however, two sites in Bali (18 and 20) clustered closer to the Lembeh region than to Bali (Fig. 5A). The hypothesis driven CAP analysis confirmed a strong regional separation in diversity (Trace statistic: 1.78, p < 0.001; Fig. 5B). There was a very high regional allocation success (Lembeh: 100%, Dauin: 100%, Bali: 75%), reconfirming the regional distinctness of species richness.

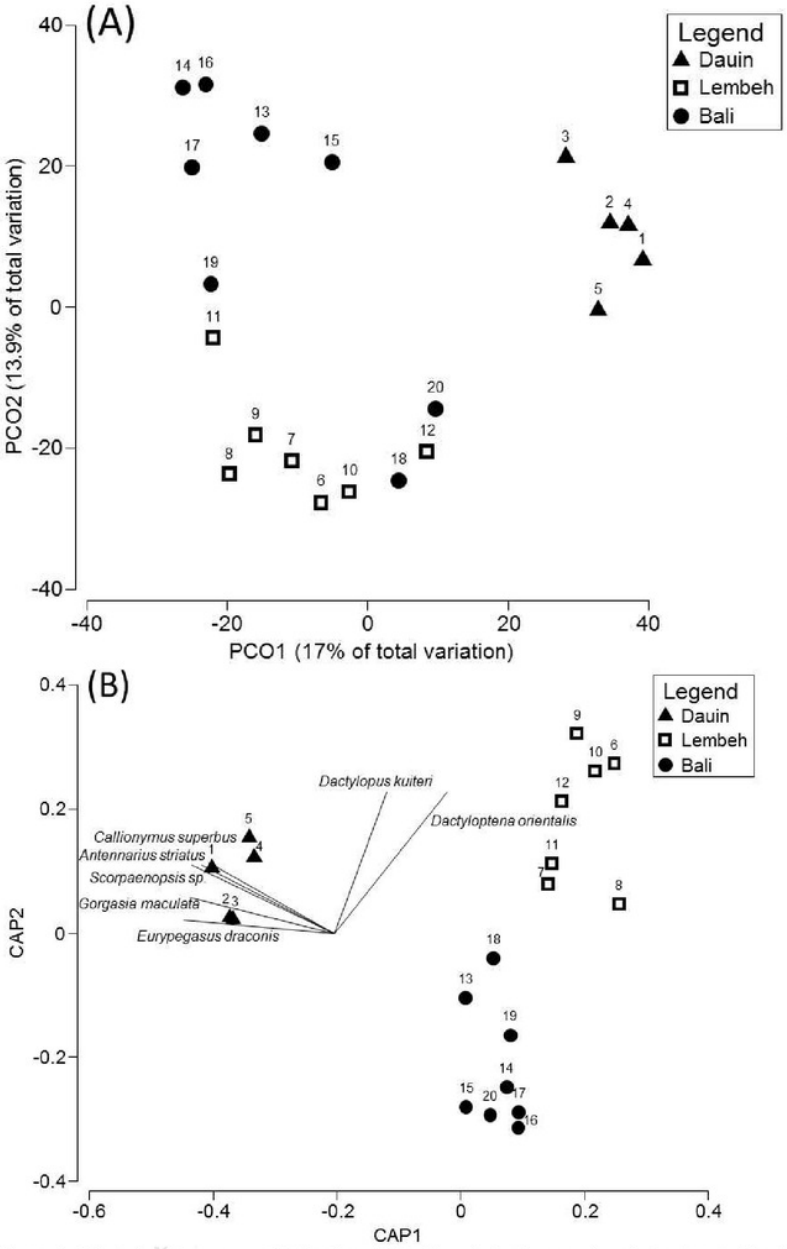

Figure 5. A) Principal Component Ordination of fish diversity in three regions in Southeast Asia. B) constrained Canonical Analysis of Principal Coordinates (CAP) of these same fish assemblages for the interactions between regions, species overlayed with Pearson R value > ±0.7.

The best model identified using Distlm explained 33.5% (R^2 = 0.335, AIC = 163.7) of species diversity (Table 4). The final model included five variables: percent cover of sand (5% variation explained) and plants (9%), mean grainsize (4%), D10 (4%), and D90 (4%) (Table 4). The dbRDA plot showed a clear differentiation between the three different regions (Fig. 6).

Table 4. Contribution of different habitat variables to cryptobenthic fish diversity on soft sediment sites in Southeast Asia: Results of Distance based Linear model in Primer. Variables in bold were included in final model.

Variable	SS (trace)	Pseudo-F	P	Proportion explained
AIC = 163.7, R^2 = 0.335, No. of variables = 5				
% Sand	**3022.8**	**0.968**	**0.49**	**0.05**
% Pebbles	3847.8	1.250	0.15	0.06
% Plants	**5147.5**	**1.712**	**0.01**	**0.09**
% Artificial objects	2826.9	0.902	0.60	0.05
% Natural Debris	3225.8	1.04	0.42	0.05
% Coral	3118.8	0.999	0.46	0.05
% Sponges	3110.7	0.998	0.46	0.05
Mean grain size	**2571.4**	**0.817**	**0.76**	**0.04**
D10	**2489.2**	**0.789**	**0.81**	**0.04**
Median grain size	2538.6	0.806	0.78	0.04
D90	**3783.2**	**1.227**	**0.17**	**0.06**

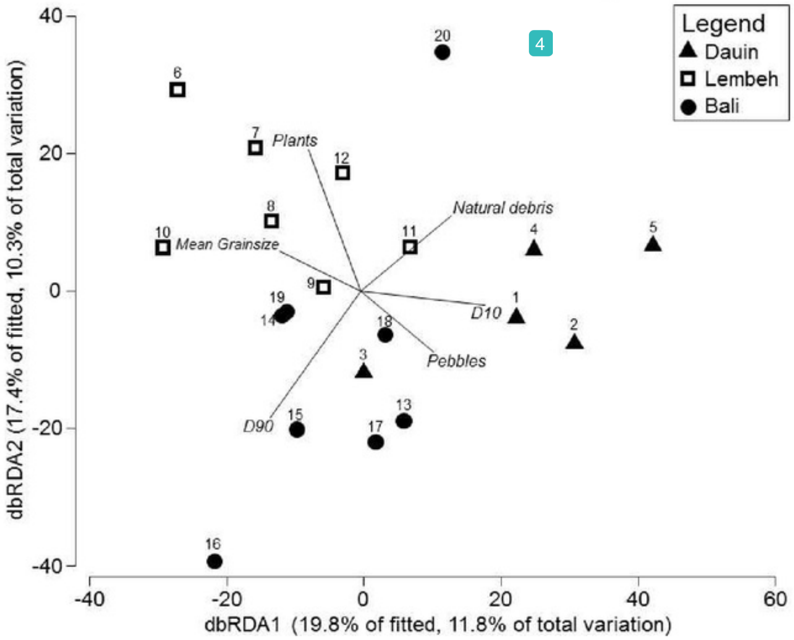

Figure 6. Distance based Redundancy Analysis plot of soft sediment fish diversity in three regions in Southeast Asia, overlayed with environmental variables responsible for changes in the assemblage.

4. *Discussion*

Cryptobenthic fishes are highly abundant and play an important role in the trophodynamics of coral reefs, but their assemblage composition on coastal soft sediment habitats is poorly understood. To our knowledge, this study is the first to extensively survey cryptobenthic fish assemblages on tropical infralittoral soft sediments. Our results showed that cryptobenthic fish diversity is considerably higher than what is currently assumed in the literature. Fish abundance, however, was much lower than on coral reefs. Strong regional differences existed in fish assemblages and species diversity, but the environmental variables tested had limited power to explain the observed patterns in fish assemblages. This is likely because similar habitat types were sampled at all of the sites, and there was little variation in sediment characteristics. Overall, these findings suggest that soft sediment habitats in Southeast Asia are far richer in fish diversity than previously assumed, which has important implications for future management.

Despite the current view of soft sediment habitats as depauparate communities, we found strikingly high fish diversity compared to other habitats. Cryptobenthic fish diversity on the sites surveyed in this study was higher than on many coral reefs. Studies on the Great Barrier Reef and Indonesian reefs found either similar or lower diversities (Depczynski and Bellwood 2003; Depczynski and Bellwood 2004; Ahmadia et al. 2012; Goatley et al. 2016). Research across a latitudinal gradient on dock pilings along America found the highest diversity in the tropics, yet the highest recorded number of species was a third lower than this study (Brandl et al. 2017). Studies in subtropical or temperate regions reported lower diversities than this study (Kovačić et al. 2012; Galland et al. 2017). The highest diversity in this study was found in North Sulawesi, the region closest to the centre of the coral triangle, and known to have the highest global fish diversity on coral reefs (Allen 2008). This study suggests that the high fish diversity extends beyond coral reefs and includes different habitats, indicating regional biogeographical drivers of high diversity rather than small-scale local processes (Ahmadia et al. 2018).

While the diversity was higher than most other cryptobenthic fish assemblages across the world, fish abundance much smaller than 21 in previous studies on more complex habitats (e.g. Kovačić et al. 2012; Goatley et al. 2016; Ahmadia et al. 2018). Abundances differed across regions and the region with lowest diversity showing the highest fish abundance. Low abundances were expected as surveyed sites showed very limited physical complexity, making them a fundamentally more hostile environment (Hemingson and Bellwood 2017). Lack of available microhabitat increases predatory pressure by decreasing shelter, thus increasing predation mortality (Depczynski and Bellwood 2004). Furthermore, variations in structural complexity can influence invertebrate prey diversity and abundance, which is in turn likely to affect fish abundance (38 Kramer et al. 2013; Kramer et al. 2014).

The environmental factors tested to investigate the effect of variations in microhabitat did not 37 explain a large proportion of the variation in assemblages. Grainsize characteristics can directly influence habitat or food availability by increasing complexity and interstitial space (Gray and Elliott 2009), but they can also reflect hydrodynamic energy (e.g. waves, currents) in the water (Trenhaile 13 et al. 1996). Relative to the spectrum of soft sediment habitats (which ranges from mud to sand and gravel), the surveyed locations had little variation in sediment grain characteristics. Despite the small scale of these differences, measurements of particle size did explain variation in the assemblage. D10 and D90 are both measures of the distribution of sediment particle size, indicating that respectively 10% and 90% of the volume of measured sediment is contained below that grainsize, or whether sand is distributed more towards the fine or the coarse end of the spectrum. Their importance in the models highlights the influence of grain size. Larger differences in grainsize, for example on muddy sediments, would be expected to drive a much more significant change in fish assemblage.

Benthic cover on all sites consisted predominantly of sand or gravel. Non-sediment cover was dominated by plant matter (algae or seagrasses in this study) or natural debris (leaves, wood, etc.). Models indicated that plant and sand cover had the strongest effect on fish assemblages. Besides influencing the amount of available shelter, plant growth might be linked to primary productivity and available light level or nutrients (Gray and Elliott 2009). The availability of complex habitat may have both positive and negative influences on soft sediment associated cryptobenthic fishes, depending on the species. Differences in the physical complexity on soft sediment appear limited compared to coral reefs, but can be high enough to make a difference for the small fish species found in these habitats. For sand associated specialist species such as *Trichonotus* spp. or *Callionymus* spp., high sand cover might mean a decrease in competition with species less adapted to sandy bottoms (Sogard 1984; Clark and Pohle 1996).

It is likely that other factors drive fish assemblages on soft sediment. Previous studies of cryptobenthic fish on dock pilings showed low predictive power from habitat, but strong regional differentiation (Brandl et al. 2017). Besides biogeographical history, another factor that might play a role is the distance to nearby reefs, or "halo effect" (Langlois et al. 2005). The halo effect predicts that interactions between reefs and soft sediment can cause changes in faunal abundance depending on the distance from reefs. This effect has been observed in temperate regions, but remains to be comprehensively tested for tropical soft sediment fish assemblages (Schultz et al. 2012). The presence of such a halo effect in soft sediment fish fauna might indicate how strongly some coral reef predators rely on soft sediments for prey.

Due to legislations restricting the use of ichthyocides, this study did not use rotenone or other destructive sampling methods which are typically used when assessing cryptobenthic fish fauna (Ackerman and Bellwood 2002; Kovačić et al. 2012; Brandl et al. 2017; Coker et al. 2018). As a result, the species that dominate cryptobenthic fish assemblages on coral or rocky reefs (e.g. Gobiidae) were excluded from this study. The real diversity on soft sediment is therefore higher than described in this study, this is supported by the strong increase in number of species detected during roving diver surveys. Abundances might likewise be higher, though it remains unlikely to approach abundance levels of sites with higher complexity. Non-destructive sampling of cryptobenthic fauna remains a challenge, although alternatives methods have been proposed. Absence/presence surveys with increased detection probabilities can be beneficial for conservation planning for rare or cryptic species such as seahorses (Aylesworth et al. 2017). Environmental DNA (eDNA) surveys allow for cost-effective sampling of the entire fish community, yet require more fine-tuning to increase reliability for cryptobenthic species (DiBattista et al. 2017). Alternatively, fluorescence in cryptic fishes has been used to successfully survey triplefins and pygmy seahorses on coral reefs (De Brauwer et al. 2018). It remains to be tested which of the above methods would be most suitable for soft sediment cryptobenthic fish communities, but combining multiple methods might be the most practical option.

This study contributes to the existing literature on cryptobenthic fish fauna, yet it creates many more questions. The locations used for this project were known to have high diversity, and as such were important for dive tourism, it is yet unclear if these sites are anomalies with extreme high diversity, or whether they are representative of soft sediment sites in Indonesia and the Philippines. Similarly, surveyed sites represent a specific sediment type (volcanic, gravelly sand), but the assemblages on different types of sediment might differ strongly from the present study. On coral reefs, more complexity leads to higher diversity and abundance (Graham and Nash 2013). If this paradigm holds for soft sediment, a gradient of increasing diversity and abundance would be expected with increasing grain size. The high diversity found in this study begs the question of how limited structural complexity can support high diversity. In a terrestrial, but comparable system, the high diversity of lizards in Australian deserts can be explained by an abundant food source (termites), combined with lack of competition and predation of species less adapted to arid environments (Morton and James 1988). Similar processes are possible on soft sediment, with high availability of invertebrate prey (e.g. amphipods, caprellid shrimp), and decrease in large predators with distance from reef. Several unanswered questions remain about interactions between soft sediment habitats and other biomes, this is particularly relevant since soft sediment environments are the most extensive infralittoral habitat.

The results from this study provide insights into cryptobenthic fish diversity on tropical infralittoral soft sediments, but considerable work needs to be done to deepen our understanding of ecosystem processes in these valuable habitats. We agree with previous suggestions that new paradigms are needed to study these biomes (Wilson 1990). To improve understanding of soft sediment habitats, we suggest three focal points for future research. First, due to the extensive nature of the habitat, it might be more relevant to investigate species diversity on a larger scale by investigating regional diversity rather than small-scale (site level) diversity (Gray 2002). Second, the lack of clear boundaries, higher uniformity, and typical sediment characteristics might allow for different migration and settlement dynamics compared to better studied habitats such as coral reef (Watzin 1986; Butman 1987). Therefore, defining appropriate boundaries of what makes up an ecoregion for fish fauna on soft sediment is an important challenge for future work. Third, low abundances coupled to high species diversity call for different survey approaches than those currently used. Presence/absence surveys and emerging technologies such as eDNA have been shown to be more efficient for rare species (Aylesworth et al. 2017; DiBattista et al. 2017). The high importance, but limited understanding of these habitats represent a glaring knowledge gap in our understanding of marine ecosystems, which should be addressed in the future.

5. *Conclusion*

This study set out to investigate cryptobenthic fish assemblages and diversity on soft sediment habitats in the centre of tropical marine biodiversity. We found a high species diversity comparable or richer than on coral reefs, coupled with very low abundances. Differences in cryptobenthic fish assemblages seem to be principally driven by large-scale regional factors, with smaller site-specific effects of grain size characteristics and benthic cover. The high economic value of soft sediment habitats coupled with the present limited understanding of their ecology calls for more research. This study lays the groundwork for future research into fish assemblages on infralittoral soft sediment habitats and highlights the need for a paradigm-shift when studying fish assemblages on these habitats.

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