Title:

Highly diverse mesophotic reef fish communities in Raja Ampat, West Papua

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Abstract

Mesophotic coral ecosystems (MCEs; reefs 30-150 m depth) are poorly studied, with existing research heavily geographically biased away from the most species-rich reef regions. Yet, MCEs are of high interest because of their unique species and potential to act as refuges from the impacts of fishing. Using baited remote underwater video systems, we surveyed reef fish communities from depths of 2 to 85 m throughout the Raja Ampat archipelago in West Papua, Indonesia – an area considered the heart of the Coral Triangle where coral reef biodiversity is greatest. Here we show—similar to shallow reefs—Raja Ampat MCEs are exceptionally diverse, with 152 fish species recorded at depths greater than 40 m. We found that fish communities were highly depth driven, with declines in fish abundance at increased depth. In contrast to previous studies elsewhere in the world, we found that the proportion of planktivores declined across the shallow reef to MCE depth gradient. While greater human population density correlated with lower reef fish biomass, we did not observe differential impacts based on depth, and so found no evidence that MCEs provide a depth refuge from fishing. Our results expand and contrast some previously established MCE-depth patterns in fish communities, highlighting the need for future MCE studies within the Coral Triangle region.

Introduction

Mesophotic coral ecosystems (MCEs)—reefs from approximately 30-150 m depth—are of increased conservation and research interest because of their unique species assemblages (Rocha et al. 2018; Pinheiro et al. 2019) and potential to act as refuges from shallow reef impacts (Hinderstein et al. 2010; Loya et al. 2016). MCEs are found in tropical and sub-tropical waters globally, and contain a rich array of biodiversity including corals, fishes, sponges, and algae (Kahng et al. 2010; Baker et al. 2016). MCEs have been poorly documented compared to shallower coral reefs because of sampling limitations at greater depths. With advances in survey technology there has been a greater understanding of MCEs, especially in regions such as the Caribbean, Red Sea, Australia, and Hawaii (Turner et al. 2017; Laverick et al. 2018). The Coral Triangle (comprising: Indonesia, Malaysia, Papua New Guinea, the Philippines, Timor Leste, and the Solomon Islands) hosts the greatest shallow reef biodiversity globally (Veron et al. 2009). Yet—despite this diversity—there is comparatively little research effort in the Coral Triangle (Fisher et al. 2011) especially for MCEs (Turner et al. 2017; Laverick et al. 2018). Coral Triangle MCE surveys have been mostly limited to several sites in the Philippines, where highly diverse MCEs have been identified (Cabaitan et al. 2019; Pinheiro et al. 2019).

Based on ecological community composition, MCEs can be divided into upper-MCEs (approximately 30-60 m depth) and lower-MCEs (approximately 60-150 m depth) (Loya et al. 2016). Coral reef fish species richness, abundance, and biomass has broadly been reported to decline across the depth gradient from shallow reefs to MCEs (Kahng et al. 2010; 2014). While reef fish communities are variable between geographical locations, some patterns have begun to emerge. For example, habitat complexity is an important predictor of fish abundance and biomass on MCEs (Boland and Parrish 2005; Brokovich et al. 2008; Bryan et al. 2013). Herbivorous fish—though present in upper-MCEs—often decline in abundance with increased depth and can be near-absent from lower-MCEs (Thresher and Colin 1986; Brokovich et al. 2008; Rocha et al. 2018). While planktivores, in contrast, often increase as a proportion of the fish community on deeper reefs (Thresher and Colin 1986; Brokovich et al. 2008; Rocha et al. 2018).

MCEs may act as fish refuges because shallow reefs maybe more exposed to habitat damage and overfishing, or MCEs may be located at greater distances from shore and so be

subject to fewer human impacts (Bridge et al. 2013). Greater biomass of fisheries target species has been observed on MCEs compared to adjacent shallow reefs in many locations (Bejarano et al. 2014; Lindfield et al. 2016; Andradi-Brown et al. 2017). This supports the idea that some MCEs may be exposed to lower fisheries pressures than adjacent shallow reefs. Many small-scale fisheries gears are highly depth specific, with differential impacts across small depth gradients (Ashworth and Ormond 2005; Tyler et al. 2009; Goetze et al. 2011). Small-scale fisheries gears that reach MCEs require additional cost and effort compared to those used in the shallows (Wood et al. 2006; Lindfield et al. 2014). Yet, in some regions MCEs may support important fisheries – for example, in Papua New Guinea mesophotic species comprise large a proposition of some subsistence fish catches (Longenecker et al. 2017; 2019). Testing potential MCE refuge effects is challenging, however, as fish abundance, biomass, and community composition transitions with depth (Thresher and Colin 1986; Brokovich et al. 2008; Rocha et al. 2018; Pinheiro et al. 2019) and with benthic composition and structural complexity (Boland and Parrish 2005; Gratwicke and Speight 2005; Bridge et al. 2012). Despite some potential protection by virtue of their depth, MCEs are still vulnerable to many human impacts including some fisheries, sedimentation, and global stressors such as coral bleaching and increased tropical storm frequency and intensity (Andradi-Brown et al. 2016a; Rocha et al. 2018). With few—though increasing—MCE studies in the Coral Triangle, human impacts on Coral Triangle MCEs remain poorly understood.

Raja Ampat, located in West Papua, Indonesia, and at the center of the Coral Triangle contains extensive reefs, as well as mangrove forests and seagrass beds (Mangubhai et al. 2012). Raja Ampat reefs contain the greatest richness of scleractinian corals (Veron et al. 2009) and fishes (Allen and Erdmann 2009) recorded in a single region – with over 550 scleractinian coral species and over 1,400 fish species (Mangubhai et al. 2012). Given Raja Ampat's unique diversity, there have been several focused efforts to build regional species lists. For example, Allen and Erdmann (2009) combined detailed field surveys with other records to produce a fish species list for the region. Scleractinian corals have been recorded to 160 m depth within Raja Ampat, though reefs beyond the depths of conventional scuba diving remain poorly characterized (Mangubhai et al. 2012). Unlike many reefs globally, the shallow reefs of Raja Ampat have not faced widespread mortality from bleaching events and

shallow reef scleractinian coral cover remained stable between 2010-2016 at approximately 30% (Ahmadia et al. 2017).

Local people living within Raja Ampat have high marine resource dependence, with approximately two-thirds reliant on marine fish for over half their dietary protein needs, and approximately a quarter reliant on marine capture fisheries as their primary occupation (Ahmadia et al. 2017). Gleaning, hand-lines, and spear guns are the dominant fishing gears used by local communities, though commercial trawlers fish in the region (Mangubhai et al. 2012; Ahmadia et al. 2017). Destructive fishing gears such as dynamite and cyanide, while present, are generally less prevalent in Raja Ampat than elsewhere in Indonesia (Mangubhai et al. 2012). Since the 1990s, several non-governmental organizations (NGOs) have worked in Raja Ampat in partnership with local communities and the district and provincial government to establish a marine protected area (MPA) network. These MPAs are zoned based on periodic harvest closure areas, no-take areas, and large sustainable fisheries areas (Grantham et al. 2013), with the intention of allowing local communities to control their marine resources and reduce the number of commercial vessels from elsewhere in Indonesia fishing within Raja Ampat (Mangubhai et al. 2012; Ahmadia et al. 2017). In addition, the entirety of Raja Ampat regency was declared a shark and ray sanctuary in 2012, banning all shark and ray fisheries within the region[1]. Despite fisheries impacts, Raja Ampat reefs retain high fish biomass including top predators compared to many reefs elsewhere in the world (Ahmadia et al. 2017). These conservation initiatives—while not specifically targeting MCEs—provide benefits to many MCEs. For example, the Raja Ampat MPA network extends protection beyond shallow coral reefs over many MCE and deep-sea areas. While the shark and ray sanctuary is declared based on the boundary of Raja Ampat Regency—representing a political boundary rather than an ecological boundary—and so encompassing all reefs regardless of depth within Raja Ampat.

In this study, we investigate fish communities on MCEs within Raja Ampat and compare them to adjacent shallow reefs. We specifically identify: (i) whether the high fish species richness that is known to occur on the shallow reefs of Raja Ampat extends into the mesophotic zone; (ii) which fish species are indicative of Raja Ampat MCEs; (iii) patterns in fish species richness, abundance, and trophic groups across the depth gradient; and (iv) we

[1]Peraturan Daerah No. 9 Tahun 2012.

consider how human impacts have differentially affected fish biomass on MCEs compared to shallow reefs. Our study represents one of the largest MCE fish community sampling efforts undertaken to date within the Coral Triangle region, and the first within Raja Ampat.

Material and methods

Study sites

Surveys were conducted in January–February 2014 by UPTD Raja Ampat and Conservation International Indonesia staff from the KM Imbekwan research vessel. Two MPAs within the Raja Ampat MPA network were sampled in this study: Suaka Alam Perairan (SAP; Marine Sanctuary) Kepulauan Waigeo Sebelah Barat and Kawasan Konservasi Perairan Daerah (KKPD; Regional Marine Protected Area) Selat Dampier (Fig. 1). SAP Kepulauan Waigeo Sebelah Barat is 271,630 ha in area and was declared in 2009[2], while KKPD Selat Dampier is 336,200 ha and was declared in 2008[3]. At the time of the surveys, provisional zonation plans were being developed and implemented for both MPAs and there was limited MPA enforcement. Sites for SAP Kepulauan Waigeo Sebelah Barat were within the provisionally designated no-take MPA zones and in areas to the south around Kawe Island (henceforth grouped with the MPA sites as Waigeo). Sites in KKPD Selat Dampier were within the provisionally designated no-take and sustainable fisheries zones (henceforth Dampier) and covering both Batanta (on the south side of the Dampier Strait) and Kri (on the north side of the Dampier Strait). As these MPAs were new, and zonation implementation and MPA patrolling and enforcement were still under development, it is likely that any differences between sites inside the MPA and outside, or between different MPA zones reflect pre-MPA differences in reef condition. In this study we therefore do not compare sites inside and outside the MPAs (Waigeo), or between no-take and sustainable fishing zones (Dampier).

Surveys were conducted using baited remote underwater video (BRUV) during daylight hours (07:00-16:00). At each site, surveys were conducted within three depth zones: (i) shallow (2-12 m), (ii) intermediate/mid (15-30 m), and (iii) deep/MCE (40-85 m). A minimum of two BRUV drops were conducted per depth zone at each site - see Electronic

[2]Kepmen-KP No. 64 Tahun 2009.

[3]Peraturan Daerah No. 27 Tahun 2008, Kepmen-KP No. 36 Tahun 2014, and SK Gubernur Papua Barat No. 523/124/7/2019 Tahun 2019 .

Supplementary Material (ESM) Table 1. BRUV replicates within a single site and depth combination were deployed a minimum of 500 m apart. Sites were located a minimum of 1.5 km apart, with 14 sites surveyed within Waigeo, and 10 sites surveyed in Dampier. In total across all sites and depths 160 BRUV drops were completed (see ESM Table 2 for GPS locations). The BRUV consisted of a single GoPro Hero 3 camera, mounted in a frame 0.6 m above the benthos, and recording forward at the BRUV bait arm and seascape. The BRUV bait arm was 1.5 m long and was baited with 0.8-1 kg of crushed skipjack tuna. More details on the survey design and methods are available in Beer (2015). BRUVs were left for 60 min on the benthos before being recovered.

Video analysis and data processing

Video footage from each BRUV drop was analyzed for all fish species using EventMeasure (SeaGIS, Melbourne, Australia). The first 50 min of footage was analyzed from when the BRUV reached the seabed and stabilized, recording the maximum number (MaxN) for each species. MaxN is defined as the largest number of individuals of a species visible in a single video frame and therefore is a relative measure of fish abundance. MaxN is a widely used metric for static video fish analysis, as it avoids problems of counting individual fish multiple times as they leave and then re-enter the camera field of view (Watson et al. 2010). MaxN has been shown to provide reliable fish community data when compared to other conventional reef survey techniques (e.g. Watson et al. 2010; Andradi-Brown et al. 2016c). Fish identification followed Allen and Erdmann (2012), and all fish were identified to species level or the greatest taxonomic resolution possible (e.g. genus or family) if full species identification was not possible.

We categorized each fish species based on trophic group and commercial value. All fish data were filtered to remove records of manta and devil rays (Mobulidae), and eagle rays (Myliobatidae), as these are large-bodied transient species that are unlikely to be accurately recorded in our BRUV sampling. Whitetip, blacktip, and grey reef sharks (Carcharhinidae), nurse sharks (Ginglymostomatidae), bamboo sharks (Hemiscylliidae), wedgefishes (Rhinidae), and whiptail rays (Dasyatidae) were retained in our analysis alongside all other reef fishes. Trophic groups were allocated following the Fishbase ‘Food Items’ table, using the Food I-III hierarchical classification of food items eaten by a species,

189 based on diet composition of >20% of recorded items accessed through rfishbase (Boettiger
190 et al. 2012; Froese and Pauly 2015). Trophic groups were: (i) Herbivore, (ii) Herbivore and
191 Planktivore, (iii) Planktivore, (iv) Planktivore and Mobile Invertebrate Feeder, (v) Omnivore,
192 (vi) Corallivore, (vii) Mobile Invertebrate Feeder, (viii) Piscivore and Mobile Invertebrate
193 Feeder, and (ix) Piscivore. High commercial value fish species were identified based on the
194 Fishbase commercial value listing, with species listed at 'high' or 'very high' commercial
195 value included, and sharks of the families Carcharhinidae, Ginglymostomatidae,
196 Hemiscylliidae, and Rhinidae also included.
197 We explored how broad human and environmental impacts affect reef fish biomass
198 across the depth gradient and region. As our BRUV was single camera, and so only provided
199 MaxN abundance values for each species, we assigned length estimates to each fish to allow
200 estimated total biomass per BRUV to be calculated. Fish lengths were assigned in the
201 following way: Both Waigeo and Dampier have an active shallow reef monitoring program
202 which records visual fish length estimates along transects at 10 m depth (Ahmadia et al.
203 2017). We used these locally sourced fish length records from 2014 visual fish surveys and
204 assigned the median fish species length recorded to each species within each region.
205 Median length was used as it provides a good estimate for missing fish lengths when
206 conducting fish biomass calculations (Wilson et al. 2018). For species that were not
207 recorded in the 2014 shallow reef visual surveys, we instead used the 'Common Length' fish
208 size estimates for each species from Fishbase (Froese and Pauly 2015). We sourced length-
209 weight conversion values following the method outlined in Andradi-Brown et al. (2016b)
210 from Fishbase, enabling us to estimate the biomass of each species at MaxN. The biomass of
211 each species MaxN per BRUV drop was then summed to give an estimate of relative total
212 fish biomass per BRUV that could be compared between depths and across the region. We
213 sourced three additional human/environmental variables from the Marine Socio-
214 Environmental Covariates database (Yeager et al. 2017) for each BRUV drop. These variables
215 were: (i) mean annual wave exposure (kW/m), (ii) 2015 human population within 10 km,
216 and (iii) linear distance to major regional market – in this case Sorong (Fig. 1) on the West
217 Papuan mainland (km). A 10 km human population buffer was used as studies in the Coral
218 Triangle have suggested that fishers using reef gears typically fish at distances <10 km, and
219 fishers generally fish closer to their villages when possible (Soede et al. 2001; Teh et al.
220 2012).

221 Fish communities are highly correlated with benthic habitat cover and complexity on
222 both shallow reefs (Gratwicke and Speight 2005) and MCEs (Brokovich et al. 2008; Bryan et
223 al. 2013). To account for varying habitat complexity at each BRUV drop, we visually assessed
224 from the video the Habitat Assessment Score (HAS) following Gratwicke and Speight (2005).
225 HAS is based on six benthic categories: (i) rugosity of substratum, (ii) variety of benthic
226 organism growth forms, (iii) benthic habitat architecture height, (iv) refuge size categories
227 present in the reef, (v) live cover of benthic organisms, and (vi) % hard substratum present
228 (Gratwicke and Speight 2005). Each benthic category is given a value between 1-5, with 5
229 representing the greatest habitat complexity/structure/cover. All raw data is available from
230 DOI: 10.6084/m9.figshare.8097788. [DOI to be activated upon article publication]
231

232 ## Data analysis

233 We analyzed fish communities based on both abundance and biomass. To visualize
234 changes in benthic habitat and fish communities across the depth gradient we used a
235 Principal Component Analysis (PCA) based on the six benthic categories (each scored
236 between 1-5) and fourth root transformed fish abundance (MaxN). Fourth root
237 transformation was used to down weight the influence of highly abundant species. PCAs
238 based on the correlation matrix were fitted using the 'prcomp' function in R (R Core Team
239 2013). Plots were visualized with 95% confidence ellipses using the ggbiplot package (Vu
240 2011).
241 To identify differences in the fish community based on region (Waigeo or Dampier),
242 site, benthic habitat, and depth we used permutational multivariate analysis of variance
243 (PERMANOVA) based on a fourth root transformed Bray-Curtis dissimilarity matrix of fish
244 abundance where each BRUV drop represented a row in the matrix. PERMANOVA was run
245 for 99999 permutations using the 'adonis' function from vegan (Oksanen et al. 2013). As we
246 had unbalanced data (i.e. differing number of replicates per site and depth combination),
247 and were testing multiple factors, the interaction sums of squares model terms are not
248 independent (Anderson et al. 2008). We therefore used Type 1—sequential—sums of
249 squares, where each term is fitted after taking account of previous fitted terms. While this
250 means that the order in which terms are fitted can affect our results, this is considered
251 appropriate for nested experimental designs where model terms exhibit a natural

hierarchical ordering (Anderson et al. 2008). We fitted PERMANOVAs in the form of Region + Site + Benthic PC1 + Depth. Region represents whether the sites were in the Waigeo or Dampier. Benthic PC1 represents the first principal component axis of a PCA of the benthic data. This was used to combine the six HAS benthic categories into a single explanatory variable, as the six categories exhibited high collinearity.

To identify fish species indicative of different depths, we used Dufrêne and Legendre indicator species analysis (Dufrêne and Legendre 1997) on the fish abundance data across the three depth zones. Dufrêne and Legendre indicator species analysis identifies the association between fish species and a particular depth zone. Dufrêne and Legendre indicator species analysis was conducted and permutational p-values were generated using the 'indval' function from the labdsv package (Roberts 2013).

To identify how fish community trophic structure changed across the depth gradient we summed fish abundance per trophic group per BRUV (sum of MaxN for each individual species within the trophic group) for each depth zone at each site, and then conducted permutational analysis of variance (permutational-ANOVA) to test for differences with depth. Depth was coded as 1 (shallow), 2 (intermediate), 3 (MCE) and treated as a continuous variable to incorporate the gradient of depths. For trophic groups with significant effects of depth on abundance, we identified potential fish species that could be driving depth effects by: Firstly, we constructed a PCA of the untransformed fish abundance data for species belonging to that trophic group. We then tested each species within the trophic group for a correlation between the species abundance and the first and second trophic group principal component axes. Species with a Pearson's correlation coefficient >|0.4| were then tested for depth effects using permutational-ANOVA.

To identify how total and commercially valuable fish biomass across the depth gradient was affected by human and environmental conditions we used linear mixed-effect models. These models used fourth root transformed total fish biomass per BRUV as the response variable and included Site and Region as random factors. Models initially had the form: fish biomass$^{(1/4)}$ ~ Depth * Benthic PC1 * Wave exposure * Human population * Distance to market + (1|Site) + (1|Region). Where '*' means the separate fixed effect and interaction between the variables. Models were fitted using 'lmer' set to optimize the log-likelihood criterion in the package lme4 (Bates et al. 2015). We first fit this full model, but then simplified by using likelihood ratio tests to remove non-significant interactions.

Reported p values were generated by likelihood ratio tests removing the variable/interaction of interest (Bolker et al. 2009). We used partial effects plots to visualize the effects of human population density and distance to market on fish biomass based on the remef package (Hohenstein and Kliegl 2019).

Results

Benthic habitat complexity

Habitat complexity declined as depth increased, from a mean total HAS per BRUV of 26 ± 3 (mean ± SE) and 27 ± 3 on shallow reefs in Dampier and Waigeo respectively, to 11 ± 2 and 13 ± 2 on MCEs (Fig. 2A). All six HAS categories (rugosity, variety of growth forms, height, refuge size category, live cover, and hard substratum) strongly correlate with the first principal component axis (explaining 80% of benthic variation observed), which shows clear depth groupings (ESM Fig. 1A).

Fish species richness and abundance

Overall, we recorded 521 fish species across the two regions and all depth zones, with 328, 307, and 152 fish species recorded on shallow, intermediate, and mesophotic reefs respectively. Our surveys identified 31 species not previously recorded by the Allen and Erdmann (2009) fish species list for Raja Ampat (ESM Table 3). Of these, 13 were potential new records for the region, and 18 had previously been recorded from the adjacent West Papuan reefs of Cenderawasih Bay, Fakfak, or Kaimana. We found 99 fish species at greater depths than their maximum depth listed on Fishbase, of which 76 were extensions onto MCEs in the 40-85 m depth range, and 23 were extensions on shallow or intermediate depth reefs (<40 m maximum depth; ESM Table 4). Species with depth extensions included commercially important families such as emperor (Lethrinidae – nine species with depth extensions) and snapper (Lutjanidae – one species). Some important fisheries species were also exclusively recorded on MCEs (ESM Table 5) – for example four emperor species (*Gymnocranius elongatus*, *Lethrinus laticaudis*, *Lethrinus lentjan*, and *Lethrinus rubrioperculatus*) and one snapper (*Lutjanus argentimaculatus*). We recorded International Union for Conservation of Nature (IUCN) red listed species on MCEs in Raja Ampat, such as the endangered humphead wrasse (*Cheilinus undulatus*) and the vulnerable

green bumphead parrotfish (*Bolbometopon muricatum*). Humphead wrasse were found across all depths at a similar density (ESM Table 5), but bumphead parrotfish were only recorded on intermediate depth reefs and MCEs – where they were observed to 41 m maximum depth (ESM Table 4; ESM Table 5).

Fish species richness declined as depth increased, from a mean number of fish species per BRUV drop of 49 ± 10 and 57 ± 8 on shallow reefs to 22 ± 6 and 19 ± 2 on MCEs in Dampier and Waigeo respectively (Fig. 2B). Fish abundance also declined with increasing depth, however, the magnitude of difference varied between locations (Fig. 2C). For Dampier, fish abundance only slightly declined between shallow (156 ± 41 ind./BRUV) and intermediate reefs (144 ± 30 ind./BRUV) but was much lower on MCEs (73 ± 27 ind./BRUV). For Waigeo, fish abundance declined steadily between shallow reefs and MCEs from 194 ± 26 to 53 ± 7 ind./BRUV.

Differences in fish communities were identified between the two regions, individual sites, benthic habitat structure, and depth (Table 1). Depth was a major driver of fish communities (ESM Fig. 1B), and indicator species analysis identified 74 species associated with the shallows (ESM Table 6), 24 fish species associated with intermediate depths, and 13 species associated with MCEs (Table 2). Of particular note on MCEs were the presence of three Nemipteridae species (*Pentapodus nagasakiensis*, *Pentapodus paradiseus*, and *Scolopsis vosmeri*), which were commonly recorded on MCEs. Purple sand tilefish (*Hoplolatilus purpureus*) were also indicative of MCEs, which given the lower MCE HAS score and that this species associates with sand/rubble areas is unsurprising. Overall, 99 fish species significantly changed in abundance across the depth gradient, with 82 of these fish species at lower abundance on MCEs than shallow reefs, while 17 fish species were at greater abundance on MCEs than shallow reefs (ESM Table 5).

Fish trophic structure

Mobile invertebrate feeders and joint piscivore and mobile invertebrate feeders comprised the largest component of MCE fish communities, together accounting for 65% (Dampier) and 55% (Waigeo) of the community by abundance (Fig. 3A). The majority (83%) of indicator species associated with MCEs were also mobile invertebrate feeders (both exclusively or combined with piscivory) (Table 2). This MCE community contrasts with the

shallows, where herbivorous and planktivorous fishes made up 53% (Dampier) and 57% (Waigeo) of the community abundance (Fig 3A). Shallow reef indicator species were comprised by 14% herbivores, 11% corallivores, and only 19% mobile invertebrate feeders and/or piscivores (ESM Table 6). Removing commercially valuable fish species altered the reef fish community trophic structure considerably (Fig. 3B) by disproportionately removing mobile invertebrate feeders and piscivores. This led to a shallow reef community dominated by herbivores and planktivores, but a more even trophic group distribution on MCEs (Fig 3B).

We tested for differences in overall abundance of each trophic group across the depth gradient, finding that abundance of herbivores, planktivores, omnivores, and corallivores declined at increased depth (Table 3). Herbivores had the greatest abundance decline—with a percentage change of -82% between shallow reefs and MCEs—followed by planktivores at -79% (Table 3). Piscivores and mobile invertebrate feeders showed the opposite pattern – with a 50% increase from shallow reefs to MCEs (Table 3). To identify the species responsible for trophic group abundance change across the depth gradient, we tested each species within the trophic group for correlations with the first two axes of a PCA of the trophic group (Table 4). Two herbivores were found to decline in abundance with depth—the surgeonfish, *Acanthurus maculiceps,* and the damselfish, *Dischistodus melanotus*—and both of these species were absent from the MCE BRUV drops. For planktivores, two species—the fusilier, *Caesio lunaris,* and the triggerfish, *Odonus niger*—correlated with the planktivore PCA and changed abundance across the depth gradient. *Caesio lunaris* declined in abundance at increased depths, while *Odonus niger* increased in abundance from 4.93 ± 1.89 ind./BRUV in the shallows, to 7.29 ± 2.15 ind./BRUV at intermediate depths, but then declined to 1.33 ± 0.59 ind./BRUV on MCEs. Omnivores showed mixed patterns, with five species declining in abundance at increased depths, while three species had greatest abundance at intermediate depths (Table 4). Only one corallivore correlating with the corallivore PCA changed in abundance—the wrasse, *Diproctacanthus xanthurus*—that declined with increased depth (Table 4). Two piscivore and mobile invertebrate feeding species increased in abundance on MCEs, the emperor, *Lethrinus microdon*, and the threadfin bream, *Pentapodus emeryii* (Table 4).

Human impacts on reef fish biomass

Total fish biomass per BRUV declined as the human population within 10 km increased (Table 5; Fig. 4A). Though there was high variation, our partial effects plot indicated approximately 8 kg/BRUV decline in total fish biomass per 100-person population increase within 10 km distance of the reef site after controlling for other factors (Fig. 4A). We found the interaction between human population and depth to be non-significant, suggesting that human population density was not having differential effects on fish biomass dependent on depth, so we removed the interaction from the model. Total fish biomass declined with increased distance from the main fish markets in Sorong (Table 5; Fig 4B) – i.e. more remote sites had lower fish biomass than sites closer to the market. Again, while much variation was present in this relationship, our partial effects plot indicated a decline of approximately 15 kg/BRUV per 25 km increase in distance away from Sorong (Fig. 4B). We found the interaction between depth and distance to market was non-significant, suggesting distance to market effects do not vary based on depth, and so removed the interaction to simplify the model. To identify whether these relationships between human population and distance to market could be confounded by many non-fisheries target species, we also ran the model for only commercially valuable fish biomass (Table 5). Using commercially valuable fish biomass, however, did not detect any effects of human population or distance to Sorong. As expected from our earlier fish abundance analysis (Table 1), we found fish biomass declined as depth increased for both total fish biomass and commercially valuable fish biomass (Table 5). We also identified a significant interaction between depth and benthic habitat structure for total and commercially valuable fish biomass—suggesting more complex reefs have greater fish biomass, but the effect of complexity varies based on depth (Table 5).

Discussion

This study represents one of the largest in situ assessment of coral reef fish community structure across the shallow-mesophotic depth gradient within the Coral Triangle region, based on 160 BRUV drops conducted across the 2-85 m depth gradient. Our results show that fish community structure in Raja Ampat is strongly driven by both depth and benthic habitat complexity, and that diverse mesophotic fish communities exist within

Raja Ampat. We identified commercially valuable and IUCN red listed fish species on MCEs and found 99 fish species at depths greater than their Fishbase recorded depth range. We found evidence of depleted reef fish biomass in areas with higher human population, but that this effect of human population was not mediated by depth. Overall, we recorded 521 fish species across all depth zones, with 152 fish species recorded on MCEs, placing Raja Ampat MCEs amongst the most fish species rich MCEs identified globally.

Changes in benthic habitat complexity with depth

Benthic habitat structure declined with depth, in a similar pattern at both Dampier and Waigeo (Fig. 2A). Unsurprisingly, all six benthic catagories recorded in HAS (rugosity, variety of growth forms, height, refuge size category, live cover, and hard substratum) were highly correlated, with many of the deepest BRUV drops associated with low relief reefs or even recording flat sandy benthos with soft corals. Our results contrast with the only previous shallow-MCE benthic habitat study within Indonesia, which was conducted within the Wakatobi Marine National Park (South East Sulawesi), where reef hard substrate cover was lowest in the shallows and increased down to 80 m depth (Bell et al. 2019). Of the previous MCE studies in the Coral Triangle, changes in benthic communities and complexity in Raja Ampat appear most similar to observations from Apo Island in the Philippines, where the proportion of sand/rubble increased exponentially with depth from 10-80 m depth (Abesamis et al. 2018). Our HAS results suggested a consistent decline in benthic habitat structure with increased depth, with intermediate depth reefs having intermediate habitat structure when compared to shallow reefs and MCEs. Studies in the Philippines have found more variable benthic community composition across the depth gradient, including that shallow benthic communities may not be a good predictor of adjacent MCE benthic communities (Dumalagan et al. 2019). Within the Coral Triangle—and for MCEs more broadly—MCEs are highly variable and influenced by local conditions, for example river outflows can increase MCE sedimentation (Cabaitan et al. 2019) or storms can damage reefs (Abesamis et al. 2018). We used BRUVs to survey benthic communities, unlike most previous MCE benthic studies from Indonesia (Bell et al. 2019) and the Philippines (Cabaitan et al. 2019; Dumalagan et al. 2019; Quimpo et al. 2019), which used diver transects or remote-operated vehicles. BRUVs have to rest on the seabed, preventing our surveys from

incorporating walls or steep slopes. Therefore, the areas we surveyed are likely to have differing benthic complexity to previous studies in the region, as reef slope is an important predictor of MCE benthic communities (Lesser et al. 2018).

Fish species richness and indicator species

The number of fish species recorded on Raja Ampat MCEs—152 species—were amongst the highest recorded to date on MCEs anywhere in the world. For example, in Hawaii 162 fish species were recorded on MCEs by diver surveys spanning 161 sites over 2010-2016 (Fukunaga et al. 2017). In the Philippines a combination of BRUV and technical diving recorded 277 fish species on MCEs (Pinheiro et al. 2019) – though only 92 MCE fish species were recorded by BRUV (Abesamis et al. 2018). These results from the Philippines, however, were based on 29 BRUV drops and so are likely under-sampling fish species richness in comparison to our 160 BRUV drops in Raja Ampat. In Kimbe Bay, Papua New Guinea, 61 species were recorded at 30 m depth by video transects (MacDonald et al. 2016). While focused fish collection surveys detect greater fish species richness than BRUVs on MCEs (Pinheiro et al. 2019), work on Caribbean MCEs suggests that BRUVs detect greater fish species richness than standardized video transects (Andradi-Brown et al. 2016c). Given the wide variation in methods used, it is challenging to directly compare fish species richness between geographical locations. With increased survey effort—including other sampling methods such as targeted fish collection by technical diving—more fish species are likely to be recorded on Raja Ampat MCEs. Therefore, our results should be considered an underestimate of the true fish species richness on Raja Ampat MCEs. Our results, however, confirm that the exceptional fish species richness present on shallow coral reefs within Raja Ampat (Allen and Erdmann 2009) also extends into the mesophotic zone.

Our surveys indicate Raja Ampat MCEs have approximately 40% of the species richness of adjacent shallow reefs. Declines in mean fish species richness at increased depths are recognized across shallow reef and MCE depth gradients at many sites globally (Kahng et al. 2010; 2014). For example, declines have been recorded in the Caribbean (Bejarano et al. 2014; Pinheiro et al. 2016; Andradi-Brown et al. 2016b), Red Sea and Indian Ocean (Brokovich et al. 2008; Andradi-Brown et al. 2019), and Pacific (Thresher and Colin 1986; Lindfield 2015; Pyle et al. 2016; Asher et al. 2017). In the Coral Triangle, previous

comparisons of whole community fish species richness have mostly been limited to smaller depth gradients. In Kimbe Bay, Papua New Guinea, fish species richness declined 15% from 5 to 30 m depth (MacDonald et al. 2016). In the Philippines, fish species richness was lower on MCEs (30-35 m) than shallow reefs (8-20 m), though declines with depth are highly variable – ranging from relatively modest declines to species richness more than halving (Quimpo et al. 2018; 2019).

We identified 12 fish indicator species of MCEs in Raja Ampat, of which ten were piscivores and/or mobile invertebrate feeding species (Table 2). Reef fish species composition across depth gradients are known to be driven by factors such as habitat availability (MacDonald et al. 2018), water temperature (Simon et al. 2016; Gress et al. 2017), fish morphological traits (Bridge et al. 2016), and broader trophic groups (Bejarano et al. 2014; Andradi-Brown et al. 2016b). Many of the MCE indicator species we identified have also been identified as deep species by studies in the Philippines, such as *Hoplolatilus purpureus* and *Parupeneus heptacanthus* (Abesamis et al. 2018). Species identified as characteristic of Raja Ampat MCEs included two species of *Pentapodus* – *Pentapodus nagasakiensis* and *Pentapodus paradiseus*. We also found five *Pentapodus* species correlated with our piscivore and mobile invertebrate feeder PCA (Table 4), and so contributed to the trend of greater piscivore and mobile invertebrate feeder abundance on MCEs. Four *Pentapodus* species increased in abundance on MCEs, though one species declined (ESM Table 5). Several *Pentapodus species* have elongate trailing caudal fin filaments (Allen and Erdmann 2012), which has been associated with reducing hydrodynamic disturbance when swimming (Bridge et al. 2016). This is believed to aid predator avoidance on deeper reefs where water turbulence is less (Bridge et al. 2016). *Pentapodus* species are also known to favor sandy areas immediately adjacent to reefs (Gomelyuk 2009), which are similar to MCE habitats we recorded in Raja Ampat. As several of our analyses have identified MCE *Pentapodus*, this genus could be used as an easy to identify indicator group for MCE fish communities in Raja Ampat.

Whilst there was broad agreement between our indicator species and other studies from the Coral Triangle, several Raja Ampat indicator species were identified at different depths to previous studies. For example, *Sufflamen fraenatum* was found to be a depth generalist between 10-80 m in the Philippines (Abesamis et al. 2018) and *Pentapodus paradiseus* was also found to be common at 30-35 m depth in the Philippines (Quimpo et al.

2018), but our indicator species analysis clustered both as MCE species in Raja Ampat. In even greater contrast, work in the Philippines identified two of our MCE indicator species, *Lethrinus lentjan* and *Pomacentrus nagasakiensis*, as shallow water species (Abesamis et al. 2018). These differences could reflect real differences between the Philippines survey sites and Raja Ampat or they could be the result of methodological differences between surveys that affect detection of species. Surveys using standardized methods across the region are required to directly identify differences in the fish community, but our results imply that depth ranges should not be generalized for species across the Coral Triangle.

Our intermediate depth fish indicator species more broadly aligns with previous studies. For example, *Forcipiger flavissimus* and *Pomacentrus nigromanus*, which we identified as intermediate depth species, are both common at intermediate depths in Papua New Guinea (MacDonald et al. 2016). Studies from Papua New Guinea have highlighted the absence of Acanthuridae from MCEs (Pyle 2000; Longenecker et al. 2019), but their presence at intermediate depths and the transition zone with upper-MCEs (MacDonald et al. 2016; Longenecker et al. 2019). Comparing with our results, we find that *Acanthurus thompsoni* was identified as an intermediate depth indicator species in Raja Ampat. This species is common in coral reef communities at intermediate depths in both Papua New Guinea (MacDonald et al. 2016) and the Philippines (Quimpo et al. 2018).

Fish abundance and community structure across the depth gradient

Raja Ampat fish abundance declined with increased depth in both Dampier and Waigeo (Fig. 2). Globally, differences in fish abundance across shallow reef to MCE depth gradients are highly variable. In many locations abundance declines at increased depths, for example in Honduras (Andradi-Brown et al. 2016b), Curaçao (Pinheiro et al. 2016), Red Sea (Brokovich et al. 2008; 2010), the Chagos Archipelago (Andradi-Brown et al. 2019), and Hawaii (Asher et al. 2017). Whereas, abundance and biomass increases with depth in some locations, for example Bermuda (Pinheiro et al. 2016) and the Mariana Islands (Lindfield et al. 2016), before reducing on lower MCEs (>70 m depth). In the Coral Triangle, fish abundance reflects this variation, with declines at increased depth in Papua New Guinea and the Philippines (MacDonald et al. 2016; Quimpo et al. 2018; 2019) – but some locations where fish abundance increases from the surface to a peak at 30 m depth before declining

(Abesamis et al. 2018; Quimpo et al. 2018). As we only recorded three broad depth groups, it is not possible to identify fine scale changes in fish abundance in Raja Ampat. However, differences in abundance with depth between Waigeo and Dampier could be driven by benthic complexity. Previous BRUV studies in Hawaii have found that benthic structure complexity alters fish patterns across the depth gradient, with unconsolidated substrates having similar overall densities of fish across the depth gradient, while hard bottom habitats show declines (Asher et al. 2017). Given that we detected a significant interaction between depth and habitat complexity when predicting fish biomass (Table 5), it is likely that changes in abundance are also affected by differences in benthic habitats.

We found that MCE fish communities shifted towards increased mobile invertebrate feeders and piscivores at deeper depths, and away from omnivores, corallivores, and planktivores which were more common in the shallows (Fig. 3A). Increases in piscivore abundance on MCEs compared to shallow reefs is consistent with other studies, as are declines in omnivores and corallivores (Abesamis et al. 2018; Quimpo et al. 2019). However, reductions planktivores as a proportion of the fish community at increased depths is unusual. Previously, studies—including some based on BRUV surveys—from the western Atlantic (Bejarano et al. 2014; Pinheiro et al. 2016; Andradi-Brown et al. 2016b), the Marshall Islands (Thresher and Colin 1986), the Red Sea (Brokovich et al. 2008; 2010), and the Philippines (Abesamis et al. 2018; Quimpo et al. 2018; 2019) have characterized MCEs fish communities as planktivore dominated. The decline in planktivores as a proportion of the fish community at increased depths in Raja Ampat could in part be explained by commercially valuable species. Many locations where planktivores are dominant on MCEs have experienced high fishing pressure – removing commercially valuable fish species. Raja Ampat has been exposed to limited fishing pressure in the past and so retains a high abundance of commercially valuable fish species. Filtering our data to remove commercially valuable fish species (Fig. 3B) shifted the MCE fish community towards a greater proportion of planktivores.

Human impacts on MCE reef fishes

Increased human population density in areas where local communities have high marine resource dependence is well-known to be associated with lower reef fish biomass

563 (e.g. Bellwood et al. 2012; Williams et al. 2015). Our results show that locations closer to
564 higher population densities also have lower fish biomass (Table 5; Fig. 4A). MCEs are
565 particularly likely to act as refuges from fisheries when spear-fishing is a dominant fishing
566 method (Lindfield et al. 2014; Andradi-Brown et al. 2017). Community surveys in Dampier
567 region show that people typically use simple hand gears for subsistence fishing, including
568 spear-fishing and single hand lines, but it was not reported which was the most dominant
569 form (Claborn et al. 2017). If MCEs were acting as fisheries refuges, we would have expected
570 to identify a significant interaction between human population density and depth, as spear-
571 fishers would be unable to reach the full depth range of MCEs. The lack of interaction in our
572 results suggests that hand lines are likely to be more dominant in the fishery. Caution is
573 required, however, in interpreting our fish biomass data across depth gradients as we were
574 unable to record individual fish lengths. We allocated average fish lengths to individual fish
575 species, using region-specific length data from shallow reef surveys in Waigeo and Dampier
576 (Ahmadia et al. 2017) supplemented by Fishbase (Froese and Pauly 2015) for species
577 without regional data available. Studies have shown fish length distributions change across
578 shallow reef to MCE depth gradients, with larger individuals often present on deeper reefs
579 (Andradi-Brown et al. 2016b; Gress et al. 2018). Our total fish biomass estimates for each
580 BRUV does not account for biomass differences caused by changes in fish body size with
581 depth for each individual species. Therefore, these values should be considered estimates.
582 Further research is needed to identify whether changes in body size with depth occurs for
583 species in Raja Ampat, and the effect this has on biomass patterns with depth.
584 Remote reefs often have greater fish biomass (Graham and McClanahan 2013;
585 Pinheiro et al. 2016), largely attributed to increased accessibility cost and effort required for
586 fishers (Maire et al. 2016).We found reefs further away from Sorong— the major urban
587 center and fish market within the Raja Ampat region (Ahmadia et al. 2017)—had lower fish
588 biomass. At a global scale, fish biomass is often unchanged within 0-14 km of markets, but
589 then increases exponentially away from the market (Cinner et al. 2013), though some
590 studies have found no effect (e.g. Campbell et al. 2018). While linear distance strongly
591 correlates with market access at a global scale, it can be locally highly variable (Maire et al.
592 2016). For example, travel times for reefs 105-115 km from the nearest market can vary
593 from 2-13 hours (Maire et al. 2016). Reefs in this study varied from 70-183 km from Sorong,
594 with Dampier sites 70-112 km and Waigeo sites 148-183 km. However, while this static view

of market centers may be useful at the global scale, it misses local nuance. In the period up to 2014, Waigeo reefs were visited by large freezer-equipped vessels that purchased fish from villages, effectively creating mobile market centers. In addition, prior to the 2012 shark fishing ban many shark fishers from Indonesian provinces such as Maluku travelled eastwards to fish within Raja Ampat regency (Jaiteh et al. 2016). Therefore, reefs further from Sorong—such as Waigeo—may actually have been more accessible to this historic fishing effort.

Dampier MPA is subject to high and increasing reef tourism (Spalding et al. 2017; Papilaya et al. 2019). During the period 2012-2016 many residents in Dampier shifted primary occupation from wild capture fisheries to wage labor (believed to be tourism related), which was accompanied by a decline in the number of households fishing regularly (Claborn et al. 2017). Despite this decline in fisheries, Dampier residents continue to fish at the highest rate within Raja Ampat (Ahmadia et al. 2017), and demand for fish for tourist consumption is likely to be growing. Tourism brings a range of sustainability and environmental management challenges for the region – including managing coastal development and pollution. Elsewhere in the world, MCEs are known to be damaged by fisheries overexploitation, sedimentation, and pollution (Andradi-Brown et al. 2016a; Rocha et al. 2018). It is therefore important for tourism development in the region to be sustainable managed to ensure that benefits are received by local communities and it does not lead to environmental degradation (Atmodjo et al. 2017; Papilaya et al. 2019).

Our results provide the first overview of fish communities on MCEs in Raja Ampat and represent one of the most extensive MCE fish surveys conducted in the Coral Triangle to date. These results suggest that MCEs in Raja Ampat are likely amongst the most fish species rich globally and retain substantial abundance of higher fish trophic levels. Our findings help increase global understanding of MCE fish ecology and provide the first insight of how human interactions can shape MCEs in the center of coral reef biodiversity.

Conflict of interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

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Figures

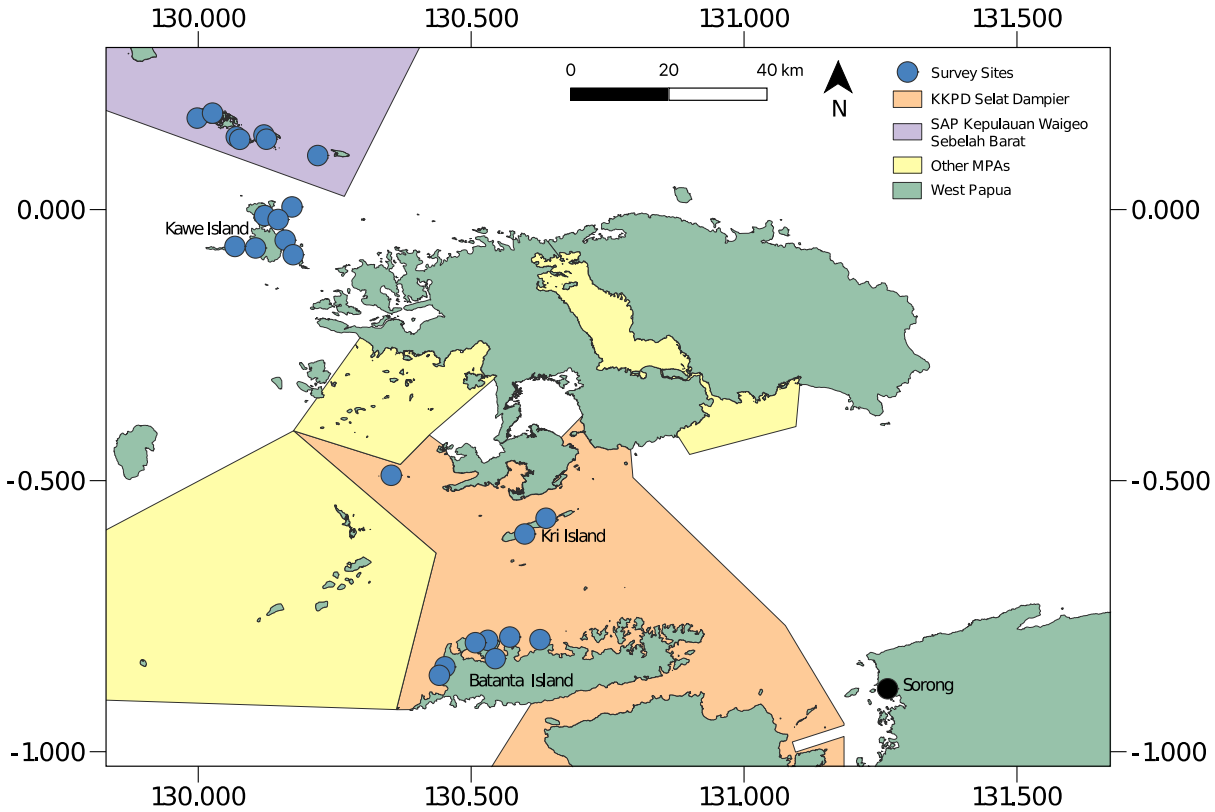

Figure 1. Study sites and marine protected areas within Raja Ampat.

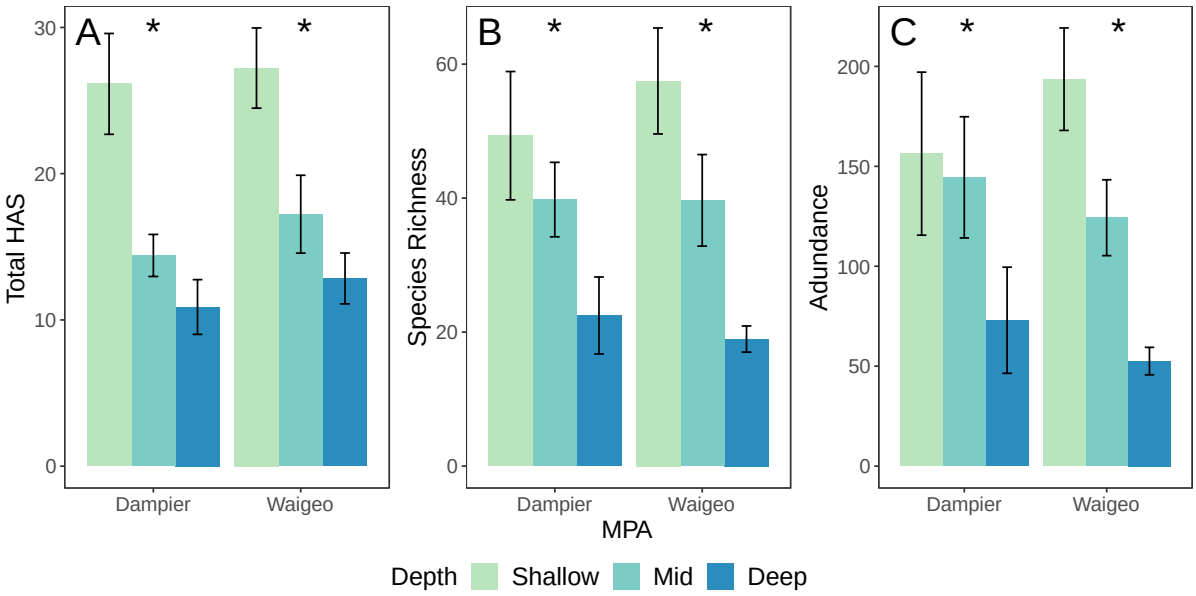

Figure 2. Overall benthic and fish community differences with depth. (A) Habitat assessment score (HAS), (B) fish species richness, and (C) fish abundance. (A) shows the mean total HAS per BRUV drop, with values per BRUV potentially ranging between 6-30 based on scoring a value of 1-5 for each of: rugosity, variety of growth forms, height, refuge size category, live cover, and hard substratum. Abundance represents the mean number of individual fish per BRUV (ind./BRUV), based on summing the MaxN for each species per BRUV. Error bars show 1 standard error above and below the mean. Asterix (*) signified a significant ($p < 0.05$) difference with depth.

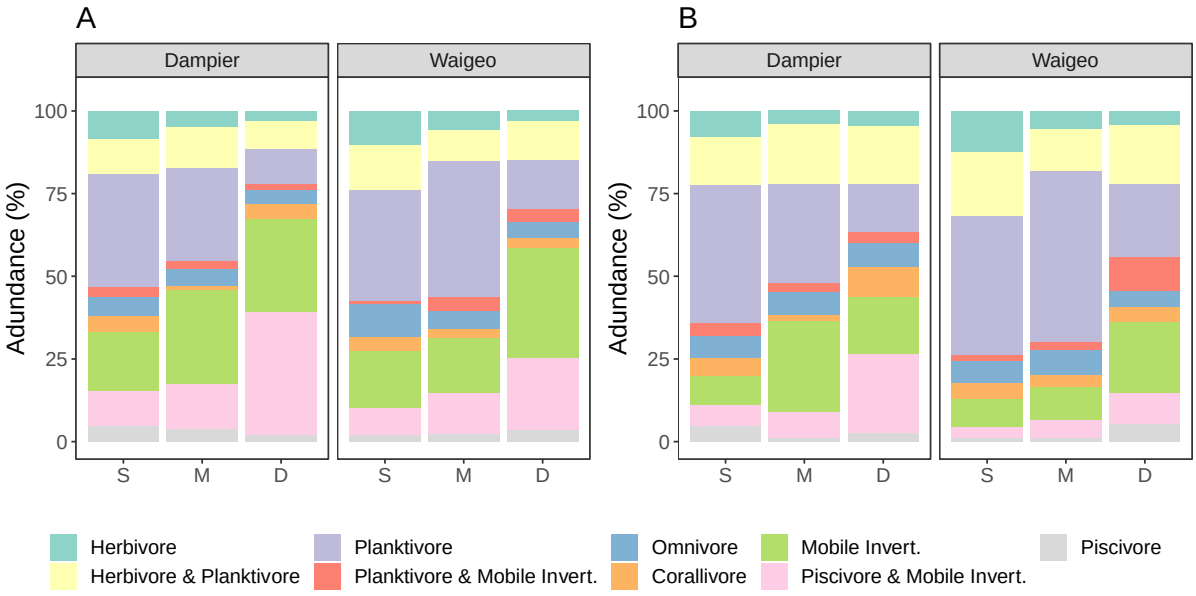

Figure 3. Community composition of each trophic group by depth. (A) abundance of all fish, (B) abundance of all fish excluding high/very high value fish and sharks.

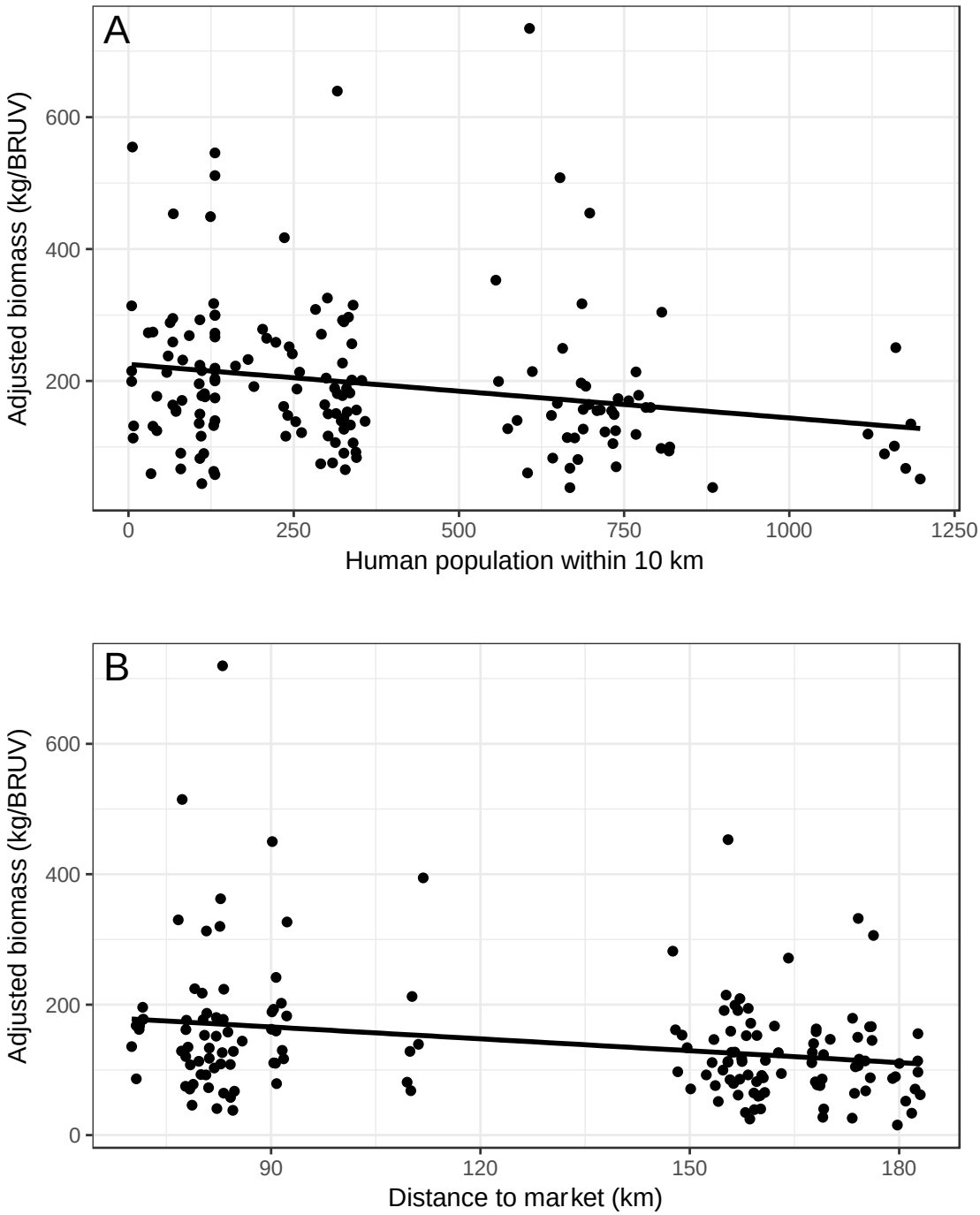

Figure 4. Partial effects plots for (A) human population and (B) distance to market based on total fish biomass per BRUV. Partial effect plots adjust fish biomass for all model fixed effects (Depth, Benthic PC1, Wave exposure, the Depth:Benthic PC1 interaction, and either human population or distance to market) and random effects (Area, Site) with the exception of the plotted fixed effect (human population or distance to market). Adjusted biomass, therefore, allows the relationship between the fixed effect of interest and fish biomass to be examined after controlling for all other fixed and random parts of the model. See Table 5 for full model.

Tables

Table 1. PERMANOVA testing effects of region, site, benthic principal component 1 (PC1), and depth on fish community structure. Fish community structure is calculated as fourth-root transformed abundance (MaxN) per BRUV drop using Bray-Curtis dissimilarities. Degrees of freedom (DF), sum of squares (SS), and mean square (MS) are shown.

	DF	**SS**	**MS**	**Pseudo-F**	**p(perm)**
Region	1	0.92	0.92	2.52	<0.001
Site	22	10.51	0.48	1.31	<0.001
Benthic PC1	1	4.16	4.16	11.40	<0.001
Depth	1	1.38	1.38	3.78	<0.001
Residuals	134	48.92	0.37		
Total	159	65.89			

Table 2. Dufrêne and Legendre indicator species analysis showing fish species indicative of intermediate and MCE depth zones. Analysis is based on fish abundance with results showing the Dufrêne and Legendre indicator value (measuring the association between the fish species and the depth group) and the associated permutational p-value (based on 99999 permutations). Only fish species with a p<0.05 association for the depth band are shown. See ESM Table 6 for an expanded version of this table including fish species indicative of the shallow depth zone.

Depth/Family	**Species**	**Indicator Value**	**p(perm)**	**Trophic Group**
Intermediate				
Acanthuridae	*Acanthurus thompsoni*	0.22	0.008	Planktivore
	Naso thynnoides	0.32	<0.001	Omnivore
Balistidae	*Odonus niger*	0.33	0.032	Planktivore
	Sufflamen bursa	0.39	0.001	Mobile Invert.
Caesionidae	*Pterocaesio digramma*	0.17	0.028	Planktivore
Carcharhinidae	*Triaenodon obesus*	0.18	0.042	Piscivore & Mobile Invert.
Chaetodontidae	*Coradion chrysozonus*	0.22	0.033	Omnivore
	Forcipiger flavissimus	0.17	0.030	Mobile Invert.
	Forcipiger longirostris	0.19	0.015	Mobile Invert.
Labridae	*Bodianus diana*	0.19	0.009	Mobile Invert.
	Bodianus dictynna	0.22	0.010	Mobile Invert.
	Choerodon zosterophorus	0.22	0.012	Mobile Invert.
	Halichoeres chrysus	0.39	<0.001	Mobile Invert.
	Halichoeres prosopeion	0.33	0.002	Mobile Invert.
Lethrinidae	*Monotaxis grandoculis*	0.22	0.020	Mobile Invert.
Lutjanidae	*Macolor macularis*	0.29	0.004	Piscivore & Mobile Invert.
Monacanthidae	*Paraluteres prionurus*	0.17	0.031	Omnivore
Pomacanthidae	*Centropyge bicolor*	0.3	0.002	Mobile Invert.
	Genicanthus lamarck	0.29	0.001	Planktivore
Pomacentridae	*Pomacentrus amboinensis*	0.36	<0.001	Herbivore & Planktivore
	Pomacentrus nigromanus	0.27	0.007	Planktivore
Serranidae	*Plectropomus oligacanthus*	0.19	0.016	Piscivore & Mobile Invert.
	Variola albimarginata	0.19	0.034	Piscivore
Tetraodontidae	*Canthigaster valentini*	0.17	0.031	Omnivore

MCE				
Balistidae	*Abalistes stellatus*	0.41	<0.001	Piscivore & Mobile Invert.
	Sufflamen fraenatum	0.23	0.023	Mobile Invert.
Carangidae	*Carangoides ferdau*	0.35	0.011	Piscivore & Mobile Invert.
Labridae	*Choerodon jordani*	0.25	0.003	Mobile Invert.
Lethrinidae	*Lethrinus amboinensis*	0.25	0.017	Piscivore & Mobile Invert.
	Lethrinus lentjan	0.17	0.031	Piscivore & Mobile Invert.
Malacanthidae	*Hoplolatilus purpureus*	0.25	0.002	Planktivore
Mullidae	*Parupeneus heptacanthus*	0.20	0.027	Piscivore & Mobile Invert.
Nemipteridae	*Pentapodus nagasakiensis*	0.36	0.004	Mobile Invert.
	Pentapodus paradiseus	0.39	<0.001	Piscivore & Mobile Invert.
	Scolopsis vosmeri	0.25	0.003	Mobile Invert.
Pomacentridae	*Pomacentrus nagasakiensis*	0.17	0.031	Herbivore & Planktivore

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Table 3. Fish trophic group species richness and comparison of abundance across the depth gradient. Richness represents the number of unique species recorded for a trophic grouping within a depth zone. Abundance represents the mean total abundance per BRUV drop within a depth zone based on summing species level MaxN for all species within a tropic group per BRUV drop. Changes in abundance across the depth gradient were tested with a permutational-ANOVA of the form Trophic Group Abundance ~ Region + Depth. As permutational-ANOVA uses sequential sums of squares, the biomass depth effects represent the effect of depth on trophic group biomass after controlling for the effect of region. Depth was treated as continuous coded as 1 (shallow), 2 (intermediate), 3 (MCE) to incorporate the gradient of depths. Significant p-values at the p<0.05 level are shown in bold.

Trophic Group	**Shallow**		**Intermediate**		**MCE**		**Abundance depth effect**	
	Richness	**Abundance (ind./BRUV)**	**Richness**	**Abundance (ind./BRUV)**	**Richness**	**Abundance (ind./BRUV)**	**Pseudo-F**	**p(perm)**
Herbivore	50	12.92 ± 1.91	38	7.26 ± 0.84	9	2.35 ± 0.52	8.94	**0.001**
Herbivore & Planktivore	36	17.61 ± 3.65	35	14.56 ± 2.89	10	9.39 ± 4.11	1.25	0.301
Planktivore	56	46.06 ± 7.19	59	46.35 ± 9.38	26	8.62 ± 1.9	8.78	**<0.001**
Planktivore & Mobile Invertebrate	11	2.88 ± 0.62	14	4.77 ± 1.56	7	2.5 ± 0.97	1.02	0.394
Omnivore	43	10.67 ± 3.14	29	7.05 ± 1.24	18	3.41 ± 0.63	2.66	**0.030**
Corallivore	22	6.14 ± 0.53	20	2.98 ± 0.39	7	2.42 ± 0.38	22.77	**<0.001**
Piscivore & Mobile Invertebrate	95	11.83 ± 0.83	95	16.21 ± 1.65	66	17.72 ± 3.04	2.66	**0.071**
Piscivore	16	4.52 ± 1.45	18	3.95 ± 1.05	10	1.75 ± 0.3	1.93	0.134

Table 4. Fish species potentially driving changes in herbivore, planktivore, omnivore, corallivore, and piscivore and mobile invertebrate feeder abundance across the depth gradient. Abundance represents the mean abundance per BRUV drop (MaxN) within a depth zone. Changes in abundance across the depth gradient were tested with a permutational-ANOVA of the form MaxN ~ Region + Depth. Species mean MaxN for each site and depth combination was used in this analysis. As permutational-ANOVA uses sequential sums of squares, the depth effect represent the effect of depth on species abundance after controlling for the effect of region. Depth was treated as continuous coded as 1 (shallow), 2 (intermediate), 3 (MCE) to incorporate the gradient of depths. Significant p-values at the p<0.05 level are shown in bold.

Species	**Biomass (g/BRUV)**			**Biomass depth effect**	
	Shallow	**Intermediate**	**MCE**	**Pseudo-F**	**p(perm)**
Herbivore					
Acanthurus blochii	0.92 ± 0.64	0.69 ± 0.22	0 ± 0	1.50	0.161
Acanthurus maculiceps	2.93 ± 1.45	0.36 ± 0.21	0 ± 0	3.54	**0.003**
Acanthurus nigricans	0.17 ± 0.12	0.06 ± 0.06	0 ± 0	1.20	0.289
Centropyge tibicen	0.14 ± 0.09	0.07 ± 0.05	0 ± 0	1.35	0.304
Centropyge vrolikii	0.06 ± 0.04	0 ± 0	0 ± 0	2.04	0.330
Chlorurus microrhinos	0.11 ± 0.07	0 ± 0	0 ± 0	2.79	0.064
Dischistodus melanotus	0.35 ± 0.23	0.03 ± 0.03	0 ± 0	2.14	**0.015**
Dischistodus pseudochrysopoecilus	0.39 ± 0.3	0.11 ± 0.09	0 ± 0	1.24	0.325
Naso vlamingii	0.36 ± 0.28	0.06 ± 0.04	0.08 ± 0.08	1.00	0.422
Scarus niger	0.03 ± 0.03	0 ± 0	0 ± 0	1.00	1.000
Scarus psittacus	0.11 ± 0.07	0.06 ± 0.06	0 ± 0	1.21	0.371
Toxotes jaculatrix	0.08 ± 0.06	0 ± 0	0 ± 0	1.83	0.327
Planktivore					
Caesio cuning	3.33 ± 1.65	6.15 ± 3.14	0 ± 0	2.25	0.076
Caesio lunaris	7.03 ± 2.79	2.03 ± 1.35	0.31 ± 0.25	3.76	**0.020**
Caesio teres	3.5 ± 2.05	2.58 ± 2.36	0.03 ± 0.03	1.02	0.415
Crenimugil crenilabis	1.22 ± 1.22	0 ± 0	0 ± 0	1.00	1.000
Neopomacentrus azysron	0.11 ± 0.09	0 ± 0	0 ± 0	1.62	0.329
Odonus niger	4.93 ± 1.82	7.29 ± 2.15	1.33 ± 0.59	3.52	**0.030**
Pterocaesio marri	2.58 ± 1.89	3.79 ± 2.32	2.33 ± 1.99	0.14	0.904
Omnivore					
Acanthurus triostegus	0.22 ± 0.2	0 ± 0	0 ± 0	1.29	0.326
Canthigaster amboinensis	0 ± 0	0.06 ± 0.06	0 ± 0	1.00	1.000
Canthigaster valentini	0 ± 0	0.17 ± 0.09	0 ± 0	3.21	**0.008**
Chaetodon citrinellus	0.24 ± 0.1	0 ± 0	0 ± 0	5.29	**0.005**
Chaetodon ephippium	0.36 ± 0.14	0.14 ± 0.08	0 ± 0	3.62	**0.019**
Chaetodon semeion	0.18 ± 0.07	0 ± 0	0 ± 0	6.85	**0.001**
Chaetodon ulietensis	0.14 ± 0.1	0.14 ± 0.08	0.03 ± 0.03	0.77	0.482
Chlorurus bowersi	0.03 ± 0.03	0 ± 0	0 ± 0	1.00	1.000
Kyphosus bigibbus	0.61 ± 0.61	0 ± 0	0 ± 0	1.00	1.000
Kyphosus cinerascens	1.03 ± 0.97	0 ± 0	0 ± 0	1.12	0.106
Kyphosus vaigiensis	1.72 ± 1.59	0 ± 0	0 ± 0	1.18	0.324
Naso thynnoides	0.08 ± 0.08	3.56 ± 1.54	0.03 ± 0.03	5.10	**0.001**

Neoglyphidodon melas	0.36 ± 0.14	0.06 ± 0.06	0 ± 0	4.97	**0.007**
Paraluteres prionurus	0 ± 0	0.19 ± 0.12	0 ± 0	2.67	**0.030**
Pomacanthus navarchus	0.06 ± 0.04	0.03 ± 0.03	0 ± 0	1.03	0.515
Corallivore					
Chaetodon kleinii	0.99 ± 0.26	0.78 ± 0.17	0.61 ± 0.2	0.78	0.480
Chaetodon oxycephalus	0.17 ± 0.09	0.06 ± 0.04	0.06 ± 0.06	0.91	0.455
Diproctacanthus xanthurus	1.04 ± 0.35	0.25 ± 0.15	0.08 ± 0.06	5.31	**0.004**
Piscivore & Mobile Invertebrate					
Grammatorcynus bilineatus	0 ± 0	0.08 ± 0.05	0.11 ± 0.09	1.04	0.425
Gymnocranius grandoculis	0.03 ± 0.03	0.19 ± 0.12	0.25 ± 0.12	1.33	0.270
Lethrinus microdon	0 ± 0	0.25 ± 0.07	0.17 ± 0.08	3.78	**0.023**
Lethrinus nebulosus	0 ± 0	0.18 ± 0.08	0.28 ± 0.17	1.63	0.172
Lethrinus semicinctus	0.12 ± 0.06	1.11 ± 0.63	0.97 ± 0.31	1.71	0.153
Lutjanus argentimaculatus	0 ± 0	0 ± 0	0.03 ± 0.03	1.00	1.000
Parupeneus cyclostomus	0.17 ± 0.06	0.51 ± 0.16	0.35 ± 0.14	1.83	0.168
Pentapodus aureofasciatus	0.08 ± 0.05	1.47 ± 0.47	1.29 ± 0.72	2.27	0.089
Pentapodus caninus	0.03 ± 0.03	1.54 ± 0.92	3.72 ± 1.86	2.38	0.071
Pentapodus emeryii	0.25 ± 0.15	0.68 ± 0.16	1.04 ± 0.31	3.30	**0.037**
Pentapodus numberii	0 ± 0	0.14 ± 0.07	0.46 ± 0.43	0.87	0.611
Pentapodus porosus	0.06 ± 0.04	0.86 ± 0.37	0.31 ± 0.31	2.15	0.095

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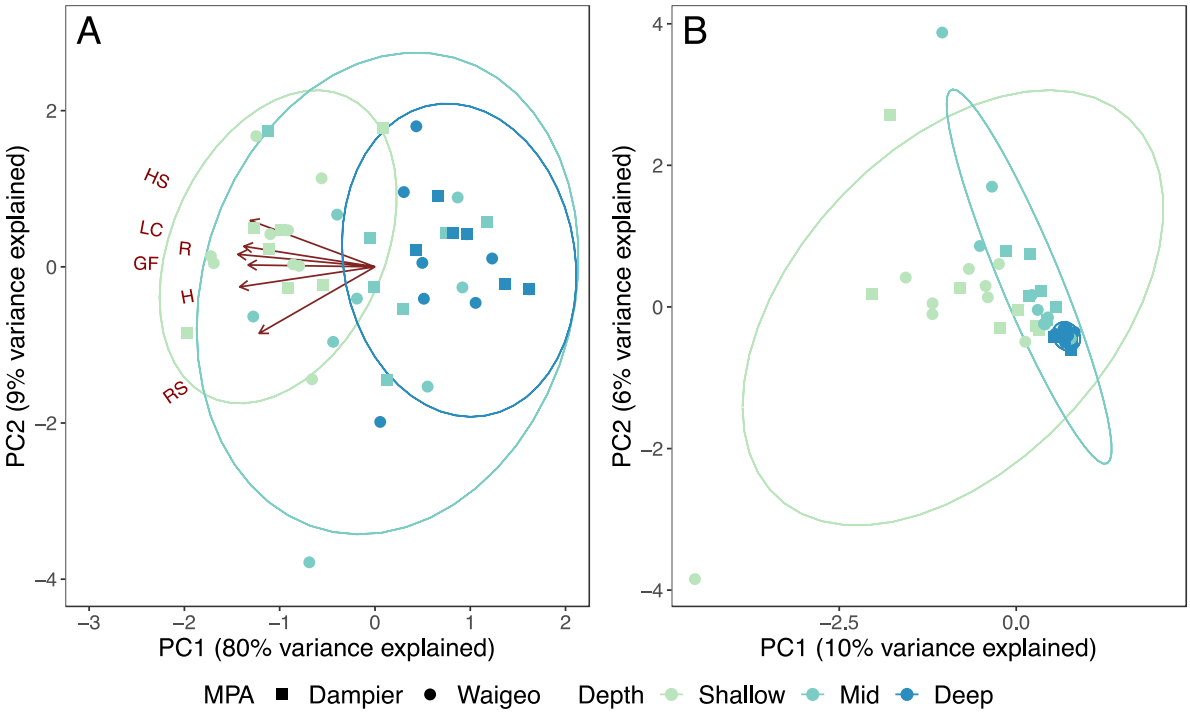
Table 5. Linear mixed-effect model of the effects of depth, benthic cover, wave exposure, human population within 10 km, and the distance to major market on fourth root transformed fish biomass. Results are shown for total fish biomass, and for high/very high value species and sharks. Biomass (g) was fourth root transformed prior to analysis. Sharks included in commercially valuable biomass were all individuals of the families: Carcharhinidae, Ginglymostomatidae, Hemiscylliidae, and Rhinidae. Benthic PC1 indicates the first principal components axis from a PCA of each component of the benthic HAS per BRUV drop.

	Estimate	**SE**	**t-value**	**χ2**	**p**
Total fish biomass					
Intercept	21.354	2.823	7.57		
Depth	-2.884	0.865	-3.33	10.74	**0.001**
Benthic PC1	0.549	0.285	1.92	3.65	0.056
Wave exposure	-0.719	0.580	-1.24	1.47	0.225
Human population	-0.003	0.001	-2.07	4.19	**0.041**
Distance to market	-0.020	0.009	-2.28	4.91	**0.027**
Depth:Benthic PC1	-0.407	0.132	-3.08	9.22	**0.002**
Commercially valuable fish biomass					
Intercept	19.867	3.175	6.26		
Depth	-3.235	0.974	-3.32	10.63	**0.001**
Benthic PC1	0.551	0.227	2.43	5.74	**0.017**
Wave exposure	-0.584	0.652	-0.90	0.79	0.374
Human population	-0.003	0.001	-1.89	3.48	0.062
Distance to market	-0.017	0.010	-1.69	2.81	0.094
Depth:Benthic PC1	-0.372	0.105	-3.54	11.99	**0.001**

Electronic Supplementary Material



ESM Figure 1. PCA of benthic and fish community structure differences based on depth and region. (A) Benthic communities based on mean HAS per depth at each site. (B) Fish communities weighed on abundance. 95% confidence ellipses are shown. Variable labels on (A) are: rugosity (R), variety of growth forms (GF), height (H), refuge size category (RS), live cover (LC), and hard substratum (HS).

ESM Table 1. Number of BRUV drops per site and depth for both regions. A minimum of two BRUV drops were conducted per depth zone at each site with the exception of MCEs at WNTZ site 7 where recorded footage was only analyzable from one BRUV.

Region/Site	Number of replicate BRUV drops per depth		
	Shallow	Intermediate	MCE
Dampier (DNTZ)			
1	3	2	3
2	3	2	2
3	3	2	3
4	2	2	2
5	2	2	2
Dampier (DUZ)			
1	3	3	2
2	3	2	2
3	3	2	2
4	2	2	3
5	2	2	3
Waigeo (WNTZ)			
1	2	2	3
2	2	3	2
3	2	2	2
4	2	2	2
5	2	4	2
6	2	2	2
7	2	2	1
Waigeo (WUZ)			
1	2	2	2
2	2	2	2
3	2	2	2
4	2	2	2
5	2	2	2
6	2	4	2
7	2	2	2

ESM Table 2. GPS coordinates for each BRUV drop. 'Region' indicates both the region and fisheries type as follows: DNTZ – Dampier no-take zone, DUZ – Dampier use zone (sustainable fisheries zone within the MPA), WNTZ – Waigeo no-take zone, and WUZ – Waigeo use area (area open to fisheries outside the MPA). Depth represents depth zone as follows: S – Shallow, M – Mid (intermediate), and D – Deep (MCE). 'Site number' refers to the site number as used in the manuscript. The 'Raw data site number' and 'Replicate numbers' represent the original Conservation International survey site and replicate numbers, which are used in the raw data. Not all sites/replicates surveyed were analyzed in this study, hence the numbers are not continuous. All GPS points are given in WGS84 format decimal degrees.

Region	**Site number**	**Raw data site number**	**Depth**	**Replicate number**	**Longitude**	**Latitude**
DNTZ	1	1	D	1	130.530697	-0.794603
DNTZ	1	1	D	2	130.526488	-0.7905658
DNTZ	1	1	D	3	130.523987	-0.783556
DNTZ	1	1	M	1	130.524713	-0.795062
DNTZ	1	1	M	3	130.52132	-0.7972476
DNTZ	1	1	S	1	130.523	-0.794309
DNTZ	1	1	S	2	130.520595	-0.798318
DNTZ	1	1	S	3	130.532855	-0.7987367
DNTZ	2	2	D	1	130.508027	-0.7989828
DNTZ	2	2	D	2	130.513062	-0.7867608
DNTZ	2	2	M	3	130.509315	-0.7927859
DNTZ	2	2	M	4	130.515608	-0.7952866
DNTZ	2	2	S	1	130.507272	-0.793176
DNTZ	2	2	S	2	130.497068	-0.794196
DNTZ	2	2	S	3	130.511291	-0.8056208
DNTZ	3	3	D	1	130.452206	-0.843469
DNTZ	3	3	D	2	130.454281	-0.851093
DNTZ	3	3	D	3	130.448862	-0.855004
DNTZ	3	3	M	1	130.455182	-0.847037
DNTZ	3	3	M	2	130.449541	-0.839482
DNTZ	3	3	S	1	130.449029	-0.83451
DNTZ	3	3	S	2	130.453843	-0.855849
DNTZ	3	3	S	3	130.452008	-0.859498
DNTZ	4	4	D	2	130.434489	-0.863857
DNTZ	4	4	D	3	130.440475	-0.8744669
DNTZ	4	4	M	1	130.441935	-0.8590817
DNTZ	4	4	M	2	130.449238	-0.8638667
DNTZ	4	4	S	1	130.439157	-0.857953
DNTZ	4	4	S	2	130.434941	-0.860401
DNTZ	5	8	D	1	130.353733	-0.49002
DNTZ	5	8	D	2	130.34567	-0.488285
DNTZ	5	8	M	1	130.357852	-0.487746
DNTZ	5	8	M	3	130.338402	-0.4898128

DNTZ	5	8	S	1	130.362512	-0.486074
DNTZ	5	8	S	3	130.358208	-0.483863
DUZ	1	1	D	2	130.635423	-0.788386
DUZ	1	1	D	3	130.641301	-0.788727
DUZ	1	1	M	1	130.626402	-0.793261
DUZ	1	1	M	2	130.625086	-0.796811
DUZ	1	1	M	4	130.631527	-0.791067
DUZ	1	1	S	1	130.626423	-0.794241
DUZ	1	1	S	2	130.630811	-0.791413
DUZ	1	1	S	3	130.635497	-0.790103
DUZ	2	2	D	1	130.544367	-0.82834
DUZ	2	2	D	3	130.527688	-0.827546
DUZ	2	2	M	1	130.541011	-0.824919
DUZ	2	2	M	2	130.536438	-0.826965
DUZ	2	2	S	1	130.540425	-0.824592
DUZ	2	2	S	2	130.536746	-0.826036
DUZ	2	2	S	3	130.537214	-0.830708
DUZ	3	4	D	1	130.570988	-0.788506
DUZ	3	4	D	2	130.575959	-0.787782
DUZ	3	4	M	1	130.575876	-0.795152
DUZ	3	4	M	3	130.563995	-0.797067
DUZ	3	4	S	1	130.570746	-0.792993
DUZ	3	4	S	2	130.579564	-0.797969
DUZ	3	4	S	3	130.561255	-0.802375
DUZ	4	7	D	1	130.637406	-0.569417
DUZ	4	7	D	2	130.632069	-0.570607
DUZ	4	7	D	3	130.626858	-0.571275
DUZ	4	7	M	2	130.623917	-0.572667
DUZ	4	7	M	3	130.638624	-0.569266
DUZ	4	7	S	2	130.634321	-0.5711356
DUZ	4	7	S	3	130.61781	-0.573148
DUZ	5	9	D	1	130.598434	-0.598411
DUZ	5	9	D	2	130.603696	-0.594229
DUZ	5	9	D	3	130.607279	-0.589442
DUZ	5	9	M	1	130.576687	-0.609784
DUZ	5	9	M	3	130.594597	-0.599805
DUZ	5	9	S	1	130.566139	-0.61247
DUZ	5	9	S	2	130.571207	-0.610765
WNTZ	1	1	D	1	130.069786	0.134305
WNTZ	1	1	D	2	130.06853	0.15673002
WNTZ	1	1	D	3	130.070163	0.14955629
WNTZ	1	1	M	2	130.061787	0.15101625
WNTZ	1	1	M	3	130.065415	0.15681
WNTZ	1	1	S	2	130.060455	0.153615
WNTZ	1	1	S	3	130.065935	0.15262331
WNTZ	2	2	D	2	130.120479	0.137607

WNTZ	2	2	D	3	130.13899	0.133177
WNTZ	2	2	M	2	130.130658	0.134857
WNTZ	2	2	M	3	130.136195	0.13559832
WNTZ	2	2	M	4	130.147438	0.133255
WNTZ	2	2	S	2	130.128722	0.134322
WNTZ	2	2	S	3	130.142698	0.13507001
WNTZ	3	3	D	1	130.223638	0.09694
WNTZ	3	3	D	3	130.210911	0.105589
WNTZ	3	3	M	2	130.216657	0.1027
WNTZ	3	3	M	3	130.212705	0.10462
WNTZ	3	3	S	1	130.219081	0.099818
WNTZ	3	3	S	2	130.228548	0.095535
WNTZ	4	5	D	1	130.125093	0.12996401
WNTZ	4	5	D	3	130.129542	0.120686
WNTZ	4	5	M	2	130.132819	0.12261601
WNTZ	4	5	M	3	130.138764	0.12245701
WNTZ	4	5	S	1	130.123098	0.125012
WNTZ	4	5	S	2	130.133877	0.120297
WNTZ	5	6	D	1	130.076229	0.129769
WNTZ	5	6	D	2	130.067475	0.13330202
WNTZ	5	6	M	1	130.062805	0.13976103
WNTZ	5	6	M	2	130.080999	0.147264
WNTZ	5	6	M	3	130.079717	0.13855998
WNTZ	5	6	M	4	130.078602	0.13337703
WNTZ	5	6	S	1	130.072124	0.13152597
WNTZ	5	6	S	3	130.07027	0.13389001
WNTZ	6	7	D	1	129.998199	0.16885721
WNTZ	6	7	D	2	130.004007	0.163066
WNTZ	6	7	M	1	130.002036	0.17793842
WNTZ	6	7	M	2	130.002848	0.17372911
WNTZ	6	7	S	1	130.006936	0.17944406
WNTZ	6	7	S	2	130.010678	0.178129
WNTZ	7	9	D	3	130.030903	0.17054901
WNTZ	7	9	M	2	130.040895	0.17433504
WNTZ	7	9	M	3	130.030178	0.165611
WNTZ	7	9	S	1	130.02632	0.178
WNTZ	7	9	S	2	130.039838	0.167497
WUZ	1	2	D	1	130.171925	0.004977
WUZ	1	2	D	2	130.177582	0.006271
WUZ	1	2	M	1	130.168195	-0.003426
WUZ	1	2	M	2	130.166462	0.001249
WUZ	1	2	S	2	130.176871	0.00416229
WUZ	1	2	S	3	130.1771	-0.000226
WUZ	2	3	D	2	130.143002	0.004364
WUZ	2	3	D	3	130.118273	0.001968
WUZ	2	3	M	2	130.12406	0.000755

WUZ	2	3	M	3	130.137578	0.00481004
WUZ	2	3	S	1	130.121792	-0.0110666
WUZ	2	3	S	2	130.124705	-0.0037417
WUZ	3	4	D	2	130.123823	-0.026527
WUZ	3	4	D	3	130.128838	-0.025605
WUZ	3	4	M	1	130.146495	-0.018221
WUZ	3	4	M	3	130.141314	-0.021141
WUZ	3	4	S	1	130.134777	-0.025737
WUZ	3	4	S	3	130.126522	-0.036198
WUZ	4	5	D	1	130.159497	-0.056352
WUZ	4	5	D	2	130.160028	-0.05167
WUZ	4	5	M	1	130.165126	-0.061347
WUZ	4	5	M	3	130.157356	-0.045629
WUZ	4	5	S	2	130.154767	-0.0556245
WUZ	4	5	S	3	130.15199	-0.0405267
WUZ	5	6	D	1	130.174079	-0.0831957
WUZ	5	6	D	2	130.188744	-0.091517
WUZ	5	6	M	1	130.178132	-0.085585
WUZ	5	6	M	3	130.184552	-0.102447
WUZ	5	6	S	1	130.191393	-0.098528
WUZ	5	6	S	3	130.179898	-0.094061
WUZ	6	8	D	1	130.10519	-0.0707138
WUZ	6	8	D	3	130.11609	-0.09311
WUZ	6	8	M	1	130.109248	-0.068807
WUZ	6	8	M	2	130.113974	-0.089298
WUZ	6	8	M	3	130.114045	-0.084448
WUZ	6	8	M	4	130.114045	-0.084448
WUZ	6	8	S	1	130.111878	-0.0725609
WUZ	6	8	S	2	130.097381	-0.06316
WUZ	7	9	D	1	130.067343	-0.067851
WUZ	7	9	D	2	130.043359	-0.073457
WUZ	7	9	M	3	130.048681	-0.074707
WUZ	7	9	M	4	130.027712	-0.073842
WUZ	7	9	S	2	130.067135	-0.072522
WUZ	7	9	S	3	130.038239	-0.074227

ESM Table 3. Potential new species records for Raja Ampat. Table contains species we recorded in Raja Ampat absent from Allen and Erdmann (2009) Raja Ampat records. Allen and Erdmann combined field surveys within the Bird's Head Seascape (BHS) including Raja Ampat with literature searching to compile the most comprehensive fish species list for the region. Where Allen and Erdmann (2009) identified a species record from the wider BHS region—but not Raja Ampat—this is noted with the location. Other BHS locations include Cenderawasih Bay (CB) and Fakfak/Kaimana (FK). Species in this table represent absences from Allen and Erdmann (2008), and we believe may represent new records for Raja Ampat.

Species	Species Authority	Notes
Bodianus dictynna	Gomon, 2006	Previous records of *Bodianus diana* (Lacepède, 1801) from the region are likely to be *Bodianus dictynna*.
Carangoides oblongus	Cuvier, 1833	
Carcharhinus obscurus	Lesueur, 1818	
Cheilodipterus parazonatus	Gon, 1993	Previously recorded in CB
Chelmon muelleri	Klunzinger, 1879	Previously recorded in FK
Choerodon monostigma	Ogilby, 1910	
Chromis fumea	Tanaka, 1917	
Chrysiptera flavipinnis	Allen & Robertson, 1974	
Chrysiptera glauca	Cuvier, 1830	Previously recorded in CB
Chrysiptera parasema	Fowler, 1918	
Cirrhilabrus beauperryi	Allen, Drew & Barber, 2008	
Cirrhilabrus cyanopleura	Bleeker, 1851	
Coradion melanopus	Cuvier, 1831	Previously recorded in CB, FK
Gymnocranius elongatus	Senta, 1973	Previously recorded in FK
Hoplolatilus chlupatyi	Klausewitz, McCosker, Randall & Zetzsche, 1978	Previously recorded in FK
Lactoria cornuta	Linnaeus, 1758	Previously recorded in CB
Lagocephalus sceleratus	Gmelin, 1789	
Lethrinus microdon	Valenciennes, 1830	Previously recorded in FK
Lethrinus rubrioperculatus	Sato, 1978	
Lutjanus maxweberi	Popta, 1921	Previously recorded in CB
Myripristis botche	Cuvier, 1829	Previously recorded in CB, FK
Naso caesius	Randall & Bell, 1992	
Parupeneus chrysopleuron	Temminck & Schlegel, 1843	Previously recorded in FK
Pentapodus caninus	Cuvier, 1830	Previously recorded in CB
Pentapodus nagasakiensis	Tanaka, 1915	

Pentapodus porosus	Valenciennes, 1830	Previously recorded in FK
Pseudojuloides splendens	Victor, 2017	Previously recorded in FK as *Pseudojuloides cerasinus*
Rhabdamia spilota	Allen & Kuiter, 1994	Previously recorded in CB, FK
Scomberoides tol	Cuvier, 1832	Previously recorded in CB, FK
Siganus doliatus	Guérin-Méneville, 1829-38	Previously recorded in FK
Valenciennea wardii	Playfair, 1867	Previously recorded in FK

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ESM Table 4. Depth extensions for species. Max fishbase depth represents the maximum depth recorded for the species as stated in fishbase (Froese & Pauly, 2019). Max. Raja Ampat depth represents the maximum BRUV drop depth that the species was recorded on.

FAMILY	Species	Max. Fishbase Depth	Max. Raja Ampat Depth
ACANTHURIDAE	*Ctenochaetus striatus*	35	42
	Naso caeruleacauda	45	50
	Naso thynnoides	40	45
APOGONIDAE	*Ostorhinchus hoevenii*	30	40
BALISTIDAE	*Odonus niger*	40	66
	Rhinecanthus verrucosus	20	47
	Sufflamen chrysopterum	30	52
BLENNIIDAE	*Aspidontus taeniatus*	25	61
	Meiacanthus crinitus	20	51
	Meiacanthus grammistes	20	59
CAESIONIDAE	*Pterocaesio marri*	30	50
	Pterocaesio randalli	30	40
CHAETODONTIDAE	*Chaetodon oxycephalus*	40	43
	Chaetodon ulietensis	30	42
	Chaetodon vagabundus	30	44
	Coradion altivelis	30	60
CIRRHITIDAE	*Cirrhitichthys aprinus*	40	47
EPHIPPIDAE	*Platax batavianus*	40	64
	Platax orbicularis	30	59
GERREIDAE	*Gerres erythrourus*	40	49
HAEMULIDAE	*Plectorhinchus lineatus*	35	59
	Plectorhinchus polytaenia	40	41
LABRIDAE	*Anampses neoguinaicus*	30	52
	Choerodon jordani	30	66
	Choerodon zosterophorus	40	49
	Coris dorsomacula	40	50
	Diproctacanthus xanthurus	25	38
	Halichoeres bicolor	20	42
	Halichoeres chloropterus	10	27
	Halichoeres melanochir	25	55
	Halichoeres nigrescens	10	20
	Halichoeres prosopeion	40	64
	Halichoeres scapularis	20	50
	Iniistius twistii	20	65
	Labroides bicolor	40	60
	Labroides dimidiatus	40	66
	Oxycheilinus celebicus	40	47
	Stethojulis bandanensis	30	35
	Thalassoma amblycephalum	15	59
LETHRINIDAE	*Gnathodentex aureolineatus*	30	52

	Lethrinus atkinsoni	30	60
	Lethrinus amboinensis	30	61
	Lethrinus erythropterus	25	55
	Lethrinus harak	20	65
	Lethrinus laticaudis	35	60
	Lethrinus obsoletus	30	52
	Lethrinus ornatus	30	47
	Lethrinus semicinctus	35	66
LUTJANIDAE	*Lutjanus biguttatus*	36	49
MICRODESMIDAE	*Gunnellichthys pleurotaenia*	15	44
MONACANTHIDAE	*Amanses scopas*	18	55
	Paramonacanthus japonicus	46	61
	Pseudomonacanthus macrurus	10	18
MONODACTYLIDAE	*Monodactylus argenteus*	12	27
	Upeneus tragula	42	60
NEMIPTERIDAE	*Pentapodus aureofasciatus*	35	55
	Pentapodus emeryii	35	61
	Pentapodus trivittatus	30	43
	Scolopsis bilineata	25	47
	Scolopsis ciliata	25	66
	Scolopsis margaritifera	25	50
	Scolopsis temporalis	35	51
	Scolopsis trilineata	20	61
	Scolopsis vosmeri	25	64
PHOLIDICHTHYIDAE	*Pholidichthys leucotaenia*	30	50
PINGUIPEDIDAE	*Parapercis hexophtalma*	25	28
	Parapercis lineopunctata	35	51
	Parapercis snyderi	40	51
	Parapercis tetracantha	25	47
POMACANTHIDAE	*Centropyge bicolor*	25	43
	Chaetodontoplus dimidiatus	35	60
	Chaetodontoplus mesoleucus	20	40
POMACENTRIDAE	*Amblyglyphidodon batunai*	12	30
	Amblypomacentrus clarus	25	46
	Cheiloprion labiatus	3	35
	Chromis margaritifer	20	52
	Chrysiptera bleekeri	35	52
	Chrysiptera cyanea	10	28
	Dischistodus fasciatus	8	27
	Dischistodus melanotus	12	35
	Dischistodus pseudochrysopoecilus	5	27
	Neoglyphidodon crossi	12	18
	Neoglyphidodon oxyodon	4	21
	Neopomacentrus filamentosus	12	27
	Pomacentrus adelus	8	15

	Pomacentrus amboinensis	40	59
	Pomacentrus chrysurus	5	27
	Pomacentrus lepidogenys	12	28
	Pomacentrus littoralis	5	28
	Pomacentrus nagasakiensis	35	47
	Pomacentrus simsiang	10	35
	Pomacentrus tripunctatus	3	35
	Stegastes albifasciatus	4	15
PSEUDOCHROMIDAE	*Pseudochromis perspicillatus*	27	51
SCARIDAE	*Bolbometopon muricatum*	40	41
	Scarus oviceps	20	40
	Scarus tricolor	25	43
TETRAODONTIDAE	*Arothron immaculatus*	30	49
	Arothron mappa	30	45

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ESM Table 5. Change in fish species abundance with depth across all sites. Abundance represents the mean MaxN per BRUV drop within a depth zone. 'Mid' represents intermediate depths. Changes in abundance across the depth gradient were tested with a permutational-ANOVA (9999 permutations) of the form Abundance ~ Depth. Pseudo-F and p(perm) values represent F and p values associated with the depth effect. Depth was treated as continuous coded as 1 (shallow), 2 (intermediate), 3 (MCE) to incorporate the gradient of depths. Abundance data with significant depth effects (p<0.05) are shown in bold.

Family	Species	Shallow	Mid	Deep	Pseudo-F	p(perm)
Acanthuridae	*Acanthurus bariene*	0.03 ± 0.03	0.02 ± 0.02	0 ± 0	0.97	0.441
Acanthuridae	*Acanthurus blochii*	0.8 ± 0.64	0.56 ± 0.22	0 ± 0	2.15	0.150
Acanthuridae	*Acanthurus fowleri*	0.33 ± 0.1	0.56 ± 0.33	0.02 ± 0.02	1.17	0.367
Acanthuridae	*Acanthurus leucocheilus*	**0.15 ± 0.07**	**0.13 ± 0.06**	**0 ± 0**	**4.66**	**0.039**
Acanthuridae	*Acanthurus lineatus*	**0.87 ± 0.31**	**0 ± 0**	**0 ± 0**	**11.63**	**<0.001**
Acanthuridae	*Acanthurus maculiceps*	**2.31 ± 1.07**	**0.24 ± 0.12**	**0 ± 0**	**6.84**	**<0.001**
Acanthuridae	*Acanthurus mata*	0.29 ± 0.27	0.44 ± 0.37	0.06 ± 0.06	0.37	0.614
Acanthuridae	*Acanthurus nigricans*	0.13 ± 0.09	0.03 ± 0.03	0 ± 0	2.59	0.140
Acanthuridae	*Acanthurus nigricauda*	**0.75 ± 0.39**	**0.04 ± 0.03**	**0 ± 0**	**5.35**	**0.011**
Acanthuridae	*Acanthurus nigrofuscus*	0.16 ± 0.09	0.13 ± 0.07	0 ± 0	2.86	0.095
Acanthuridae	*Acanthurus nubilus*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Acanthuridae	*Acanthurus olivaceus*	0.25 ± 0.16	0.15 ± 0.06	0.04 ± 0.04	2.18	0.178
Acanthuridae	*Acanthurus pyroferus*	0.16 ± 0.08	0.23 ± 0.07	0 ± 0	3.20	0.081
Acanthuridae	*Acanthurus thompsoni*	0.04 ± 0.04	0.34 ± 0.15	0 ± 0	0.10	0.785
Acanthuridae	*Acanthurus triostegus*	0.17 ± 0.15	0 ± 0	0 ± 0	1.95	0.223
Acanthuridae	*Acanthurus xanthopterus*	**0.13 ± 0.06**	**0.01 ± 0.01**	**0 ± 0**	**7.75**	**0.004**
Acanthuridae	*Ctenochaetus binotatus*	0 ± 0	0.04 ± 0.03	0 ± 0	0.00	1.000
Acanthuridae	*Ctenochaetus cyanocheilus*	0.08 ± 0.05	0.08 ± 0.06	0 ± 0	1.59	0.256
Acanthuridae	*Ctenochaetus striatus*	**1.14 ± 0.25**	**0.52 ± 0.21**	**0.02 ± 0.02**	**18.14**	**<0.001**
Acanthuridae	*Ctenochaetus tominiensis*	0 ± 0	0.08 ± 0.06	0 ± 0	0.00	1.000
Acanthuridae	*Naso annulatus*	0.3 ± 0.17	0.21 ± 0.15	0.06 ± 0.05	1.57	0.236
Acanthuridae	*Naso brachycentron*	0.35 ± 0.2	0.3 ± 0.27	0 ± 0	1.68	0.215
Acanthuridae	*Naso brevirostris*	**0.63 ± 0.24**	**0.02 ± 0.02**	**0 ± 0**	**9.88**	**<0.001**
Acanthuridae	*Naso caeruleacauda*	0.35 ± 0.27	0.08 ± 0.08	0.1 ± 0.1	0.98	0.395
Acanthuridae	*Naso caesius*	0.46 ± 0.19	0.39 ± 0.22	0.02 ± 0.02	3.40	0.076
Acanthuridae	*Naso hexacanthus*	0.51 ± 0.25	0.43 ± 0.16	0.13 ± 0.11	2.18	0.150
Acanthuridae	*Naso lituratus*	**0.46 ± 0.12**	**0.17 ± 0.06**	**0 ± 0**	**17.59**	**<0.001**
Acanthuridae	*Naso lopezi*	0.03 ± 0.02	0 ± 0	0 ± 0	3.01	0.214
Acanthuridae	*Naso mcdadei*	0.03 ± 0.03	0 ± 0	0 ± 0	1.51	0.680
Acanthuridae	*Naso minor*	0.65 ± 0.62	0.14 ± 0.11	0.2 ± 0.19	0.69	0.544

Acanthuridae	*Naso thynnoides*	0.04 ± 0.04	2.11 ± 0.84	0.02 ± 0.02	0.00	0.982
Acanthuridae	*Naso tonganus*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Acanthuridae	*Naso unicornis*	**0.2 ± 0.1**	**0.03 ± 0.02**	**0 ± 0**	**5.42**	**0.010**
Acanthuridae	*Naso vlamingii*	0.27 ± 0.21	0.06 ± 0.05	0.06 ± 0.06	1.33	0.354
Acanthuridae	*Paracanthurus hepatus*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.675
Acanthuridae	*Zebrasoma scopas*	**0.47 ± 0.08**	**0.13 ± 0.08**	**0.04 ± 0.04**	**18.43**	**<0.001**
Acanthuridae	*Zebrasoma velifer*	0.06 ± 0.05	0.08 ± 0.08	0 ± 0	0.65	0.592
Antennariidae	*Antennatus rosaceus*	0 ± 0	0 ± 0	0.02 ± 0.02	1.51	0.667
Apogonidae	*Cheilodipterus nigrotaeniatus*	0.02 ± 0.02	0.01 ± 0.01	0 ± 0	1.22	0.436
Apogonidae	*Cheilodipterus parazonatus*	0.08 ± 0.05	0.04 ± 0.03	0.13 ± 0.07	0.58	0.490
Apogonidae	*Ostorhinchus cavitensis*	0.1 ± 0.1	0 ± 0	0 ± 0	1.51	0.669
Apogonidae	*Ostorhinchus hoevenii*	0 ± 0	0 ± 0	0.04 ± 0.04	1.51	0.663
Apogonidae	*Pristiapogon exostigma*	0.27 ± 0.27	0 ± 0	0 ± 0	1.51	0.665
Apogonidae	*Rhabdamia spilota*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Apogonidae	*Taeniamia fucata*	0 ± 0	0.08 ± 0.08	0 ± 0	0.00	1.000
Atherinidae	*Atherinomorus lacunosus*	0.19 ± 0.19	0 ± 0	0 ± 0	1.51	0.666
Aulostomidae	*Aulostomus chinensis*	0.1 ± 0.05	0.04 ± 0.04	0 ± 0	3.72	0.086
Balistidae	*Abalistes stellatus*	**0.01 ± 0.01**	**0.08 ± 0.05**	**0.45 ± 0.13**	**14.93**	**<0.001**
Balistidae	*Balistapus undulatus*	**2.24 ± 0.37**	**0.81 ± 0.16**	**0.28 ± 0.07**	**33.84**	**<0.001**
Balistidae	*Balistoides conspicillum*	0.04 ± 0.03	0.08 ± 0.05	0.08 ± 0.04	0.55	0.590
Balistidae	*Balistoides viridescens*	0.03 ± 0.02	0.08 ± 0.04	0.03 ± 0.02	0.00	1.000
Balistidae	*Canthidermis maculata*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Balistidae	*Melichthys niger*	0 ± 0	1.01 ± 1.01	0 ± 0	0.00	1.000
Balistidae	*Melichthys vidua*	**0.31 ± 0.1**	**0.2 ± 0.07**	**0.04 ± 0.03**	**6.70**	**0.011**
Balistidae	*Odonus niger*	3.65 ± 1.3	7.51 ± 2.39	1 ± 0.43	1.27	0.279
Balistidae	*Pseudobalistes flavimarginatus*	0.04 ± 0.03	0.08 ± 0.04	0.06 ± 0.05	0.15	0.851
Balistidae	*Pseudobalistes fuscus*	0.21 ± 0.21	0.48 ± 0.46	0.07 ± 0.04	0.11	0.883
Balistidae	*Rhinecanthus rectangulus*	0.01 ± 0.01	0.08 ± 0.05	0 ± 0	0.11	0.834
Balistidae	*Rhinecanthus verrucosus*	0.08 ± 0.07	0.01 ± 0.01	0.02 ± 0.02	1.23	0.357
Balistidae	*Sufflamen bursa*	0.04 ± 0.03	0.41 ± 0.08	0.25 ± 0.09	3.71	0.058
Balistidae	*Sufflamen chrysopterum*	0.27 ± 0.1	0.28 ± 0.09	0.12 ± 0.09	1.34	0.258
Balistidae	*Sufflamen fraenatum*	**0 ± 0**	**0.14 ± 0.06**	**0.22 ± 0.07**	**9.04**	**0.003**
Balistidae	*Xanthichthys auromarginatus*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.661
Belonidae	*Tylosurus crocodilus*	0.04 ± 0.03	0 ± 0	0 ± 0	3.13	0.218
Blenniidae	*Aspidontus taeniatus*	0.06 ± 0.04	0.02 ± 0.02	0.01 ± 0.01	1.05	0.385
Blenniidae	*Ecsenius midas*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Blenniidae	*Meiacanthus atrodorsalis*	0 ± 0	0.03 ± 0.02	0 ± 0	0.00	1.000
Blenniidae	*Meiacanthus crinitus*	0 ± 0	0.02 ± 0.02	0.08 ± 0.08	1.43	0.440
Blenniidae	*Meiacanthus grammistes*	0.01 ± 0.01	0.12 ± 0.06	0.03 ± 0.02	0.14	0.727

Blenniidae	*Plagiotremus rhinorhynchos*	0 ± 0	0.01 ± 0.01	0 ± 0	0.00	1.000
Caesionidae	*Caesio caerulaurea*	2.83 ± 2.15	0.08 ± 0.06	0 ± 0	2.60	0.061
Caesionidae	*Caesio cuning*	3.89 ± 2.28	5.27 ± 2.4	0 ± 0	2.04	0.174
Caesionidae	*Caesio lunaris*	**4.85 ± 1.92**	**1.52 ± 1.01**	**0.17 ± 0.13**	**7.03**	**0.008**
Caesionidae	*Caesio teres*	2.63 ± 1.51	1.94 ± 1.77	0.01 ± 0.01	1.91	0.186
Caesionidae	*Gymnocaesio gymnoptera*	0.1 ± 0.1	0.04 ± 0.04	0 ± 0	1.29	0.439
Caesionidae	*Pterocaesio digramma*	0.14 ± 0.14	0.68 ± 0.39	0 ± 0	0.16	0.713
Caesionidae	*Pterocaesio marri*	2.36 ± 1.79	3.09 ± 1.82	1.75 ± 1.49	0.06	0.805
Caesionidae	*Pterocaesio pisang*	0.02 ± 0.02	0.97 ± 0.69	0 ± 0	0.00	0.989
Caesionidae	*Pterocaesio randalli*	0 ± 0	0 ± 0	0.04 ± 0.04	1.51	0.665
Caesionidae	*Pterocaesio tile*	**3.11 ± 1.36**	**0.31 ± 0.31**	**0.04 ± 0.04**	**7.19**	**0.004**
Carangidae	*Alectis ciliaris*	0.05 ± 0.03	0 ± 0	0.01 ± 0.01	1.33	0.364
Carangidae	*Alepes kleinii*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Carangidae	*Atule mate*	0.01 ± 0.01	0.08 ± 0.05	0 ± 0	0.11	0.840
Carangidae	*Carangoides bajad*	0.33 ± 0.17	0.42 ± 0.28	0.41 ± 0.35	0.05	0.841
Carangidae	*Carangoides ferdau*	**0.17 ± 0.08**	**0.17 ± 0.07**	**0.81 ± 0.3**	**5.98**	**0.008**
Carangidae	*Carangoides fulvoguttatus*	0.08 ± 0.06	0.04 ± 0.04	0.04 ± 0.03	0.30	0.660
Carangidae	*Carangoides gymnostethus*	0.06 ± 0.03	0.04 ± 0.03	0 ± 0	2.94	0.158
Carangidae	*Carangoides oblongus*	0.05 ± 0.03	0.06 ± 0.05	0.14 ± 0.1	0.90	0.409
Carangidae	*Carangoides plagiotaenia*	0.06 ± 0.04	0.21 ± 0.12	0.02 ± 0.02	0.10	0.794
Carangidae	*Caranx ignobilis*	0.38 ± 0.29	0.1 ± 0.07	0.04 ± 0.04	1.84	0.221
Carangidae	*Caranx melampygus*	1.15 ± 0.4	1.25 ± 0.48	0.29 ± 0.08	2.77	0.101
Carangidae	*Caranx papuensis*	0.1 ± 0.06	0.02 ± 0.02	0.02 ± 0.02	1.92	0.253
Carangidae	*Caranx sexfasciatus*	0.06 ± 0.05	0 ± 0	2.6 ± 2.58	1.46	0.592
Carangidae	*Elagatis bipinnulata*	0 ± 0	0 ± 0	0.06 ± 0.05	2.80	0.212
Carangidae	*Gnathanodon speciosus*	0.03 ± 0.02	0.25 ± 0.23	0.03 ± 0.03	0.00	0.979
Carangidae	*Scomberoides commersonnianus*	0 ± 0	0.13 ± 0.09	0 ± 0	0.00	1.000
Carangidae	*Scomberoides lysan*	**0.12 ± 0.06**	**0 ± 0**	**0 ± 0**	**5.62**	**0.024**
Carangidae	*Scomberoides tol*	0.4 ± 0.4	0 ± 0	0 ± 0	1.51	0.665
Carangidae	*Selar boops*	0 ± 0	0 ± 0	0.23 ± 0.23	1.51	0.668
Carangidae	*Trachinotus blochii*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.663
Carcharhinidae	*Carcharhinus albimarginatus*	0 ± 0	0 ± 0	0.01 ± 0.01	1.51	0.666
Carcharhinidae	*Carcharhinus amblyrhynchos*	0.02 ± 0.02	0.02 ± 0.02	0.02 ± 0.02	0.00	1.000
Carcharhinidae	*Carcharhinus melanopterus*	**0.5 ± 0.1**	**0.28 ± 0.06**	**0.18 ± 0.07**	**8.95**	**0.004**
Carcharhinidae	*Carcharhinus obscurus*	0 ± 0	0.03 ± 0.02	0 ± 0	0.00	1.000
Carcharhinidae	*Triaenodon obesus*	0 ± 0	0.11 ± 0.04	0.04 ± 0.03	0.91	0.385
Chaetodontidae	*Chaetodon auriga*	0.06 ± 0.05	0.08 ± 0.04	0.03 ± 0.03	0.44	0.560
Chaetodontidae	*Chaetodon baronessa*	**0.35 ± 0.1**	**0.01 ± 0.01**	**0 ± 0**	**16.78**	**<0.001**
Chaetodontidae	*Chaetodon bennetti*	0 ± 0	0.01 ± 0.01	0 ± 0	0.00	1.000

Chaetodontidae	*Chaetodon citrinellus*	**0.18 ± 0.08**	**0 ± 0**	**0 ± 0**	**7.33**	**0.005**
Chaetodontidae	*Chaetodon ephippium*	**0.26 ± 0.1**	**0.1 ± 0.06**	**0 ± 0**	**7.38**	**0.004**
Chaetodontidae	*Chaetodon kleinii*	1.03 ± 0.25	0.8 ± 0.17	0.51 ± 0.18	3.29	0.074
Chaetodontidae	*Chaetodon lineolatus*	**0.28 ± 0.09**	**0.07 ± 0.05**	**0 ± 0**	**11.08**	**0.001**
Chaetodontidae	*Chaetodon lunula*	**0.17 ± 0.06**	**0.05 ± 0.03**	**0 ± 0**	**9.42**	**0.003**
Chaetodontidae	*Chaetodon lunulatus*	**0.48 ± 0.11**	**0.02 ± 0.02**	**0 ± 0**	**25.64**	**<0.001**
Chaetodontidae	*Chaetodon melannotus*	0.03 ± 0.03	0.04 ± 0.03	0 ± 0	0.72	0.508
Chaetodontidae	*Chaetodon meyeri*	0.04 ± 0.04	0.04 ± 0.04	0 ± 0	0.76	0.669
Chaetodontidae	*Chaetodon ocellicaudus*	0.01 ± 0.01	0.09 ± 0.08	0 ± 0	0.04	0.811
Chaetodontidae	*Chaetodon octofasciatus*	0.09 ± 0.05	0.03 ± 0.02	0 ± 0	3.82	0.060
Chaetodontidae	*Chaetodon ornatissimus*	0.04 ± 0.04	0.08 ± 0.04	0 ± 0	0.84	0.426
Chaetodontidae	*Chaetodon oxycephalus*	0.11 ± 0.06	0.04 ± 0.03	0.04 ± 0.04	1.13	0.321
Chaetodontidae	*Chaetodon punctatofasciatus*	0.03 ± 0.03	0 ± 0	0 ± 0	1.51	0.664
Chaetodontidae	*Chaetodon rafflesii*	**0.5 ± 0.13**	**0 ± 0**	**0 ± 0**	**19.48**	**<0.001**
Chaetodontidae	*Chaetodon selene*	0 ± 0	0 ± 0	0.04 ± 0.04	1.51	0.665
Chaetodontidae	*Chaetodon semeion*	**0.16 ± 0.07**	**0 ± 0**	**0 ± 0**	**7.52**	**0.002**
Chaetodontidae	*Chaetodon speculum*	**0.22 ± 0.08**	**0.04 ± 0.03**	**0 ± 0**	**10.47**	**0.001**
Chaetodontidae	*Chaetodon trifascialis*	**0.32 ± 0.09**	**0 ± 0**	**0 ± 0**	**18.31**	**<0.001**
Chaetodontidae	*Chaetodon ulietensis*	0.1 ± 0.07	0.1 ± 0.06	0.01 ± 0.01	1.37	0.285
Chaetodontidae	*Chaetodon unimaculatus*	0.04 ± 0.04	0.02 ± 0.02	0 ± 0	1.22	0.434
Chaetodontidae	*Chaetodon vagabundus*	**0.63 ± 0.14**	**0.18 ± 0.09**	**0.1 ± 0.07**	**11.96**	**0.001**
Chaetodontidae	*Chelmon muelleri*	0 ± 0	0 ± 0	0.02 ± 0.02	1.51	0.672
Chaetodontidae	*Chelmon rostratus*	0.04 ± 0.04	0 ± 0	0 ± 0	1.51	0.660
Chaetodontidae	*Coradion altivelis*	0.01 ± 0.01	0.11 ± 0.05	0.08 ± 0.05	1.29	0.293
Chaetodontidae	*Coradion chrysozonus*	0.03 ± 0.02	0.27 ± 0.11	0.1 ± 0.06	0.49	0.538
Chaetodontidae	*Coradion melanopus*	0.02 ± 0.02	0 ± 0	0.02 ± 0.02	0.00	1.000
Chaetodontidae	*Forcipiger flavissimus*	0 ± 0	0.07 ± 0.04	0 ± 0	0.00	1.000
Chaetodontidae	*Forcipiger longirostris*	0.02 ± 0.02	0.17 ± 0.07	0 ± 0	0.10	0.800
Chaetodontidae	*Hemitaurichthys polylepis*	0 ± 0	0.17 ± 0.17	0 ± 0	0.00	1.000
Chaetodontidae	*Heniochus acuminatus*	0 ± 0	0.06 ± 0.06	0.02 ± 0.02	0.15	0.894
Chaetodontidae	*Heniochus chrysostomus*	0.03 ± 0.02	0.03 ± 0.03	0 ± 0	1.33	0.362
Chaetodontidae	*Heniochus monoceros*	0 ± 0	0.06 ± 0.05	0 ± 0	0.00	1.000
Chaetodontidae	*Heniochus singularius*	0.12 ± 0.06	0.04 ± 0.04	0 ± 0	3.92	0.061
Chaetodontidae	*Heniochus varius*	**0.23 ± 0.09**	**0.09 ± 0.06**	**0 ± 0**	**7.47**	**0.009**
Chaetodontidae	*Parachaetodon ocellatus*	0 ± 0	0.06 ± 0.04	0 ± 0	0.00	1.000
Chanidae	*Chanos chanos*	0.1 ± 0.1	0 ± 0	0 ± 0	1.51	0.662
Cirrhitidae	*Cirrhitichthys aprinus*	0 ± 0	0.02 ± 0.02	0.04 ± 0.04	1.22	0.448
Cirrhitidae	*Cirrhitichthys falco*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Cirrhitidae	*Paracirrhites forsteri*	**0.1 ± 0.04**	**0 ± 0**	**0 ± 0**	**8.82**	**0.006**

Dasyatididae	*Pastinachus sephen*	0 ± 0	0 ± 0	0.03 ± 0.02	3.01	0.218
Dasyatididae	*Taeniura lymma*	0 ± 0	0.03 ± 0.02	0 ± 0	0.00	1.000
Diodontidae	*Diodon hystrix*	0.03 ± 0.02	0.02 ± 0.02	0 ± 0	1.77	0.290
Echeneidae	*Echeneis naucrates*	0.11 ± 0.07	0.09 ± 0.04	0.02 ± 0.02	2.00	0.172
Ephippidae	*Platax batavianus*	0 ± 0	0.02 ± 0.02	0.01 ± 0.01	0.46	0.669
Ephippidae	*Platax boersii*	0.03 ± 0.03	0.24 ± 0.12	0.04 ± 0.03	0.02	0.915
Ephippidae	*Platax orbicularis*	0.11 ± 0.11	0.09 ± 0.07	0.43 ± 0.42	0.81	0.542
Ephippidae	*Platax pinnatus*	0.01 ± 0.01	0 ± 0	0 ± 0	1.51	0.663
Fistulariidae	*Fistularia commersonii*	0.1 ± 0.05	0.08 ± 0.04	0.06 ± 0.03	0.58	0.485
Gerreidae	*Gerres erythrourus*	0 ± 0	0 ± 0	0.02 ± 0.02	1.51	0.670
Ginglymostomatidae	*Nebrius ferrugineus*	0.04 ± 0.03	0.02 ± 0.02	0 ± 0	2.09	0.293
Gobiidae	*Amblyeleotris steinitzi*	0 ± 0	0.04 ± 0.04	0 ± 0	0.00	1.000
Gobiidae	*Valenciennea strigata*	0.02 ± 0.02	0.02 ± 0.02	0 ± 0	0.76	0.669
Gobiidae	*Valenciennea wardii*	0 ± 0	0 ± 0	0.02 ± 0.02	1.51	0.660
Haemulidae	*Diagramma pictum*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.659
Haemulidae	*Plectorhinchus albovittatus*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.665
Haemulidae	*Plectorhinchus gibbosus*	0 ± 0	0.04 ± 0.03	0 ± 0	0.00	1.000
Haemulidae	*Plectorhinchus lessonii*	0.04 ± 0.03	0 ± 0	0 ± 0	3.13	0.222
Haemulidae	*Plectorhinchus lineatus*	0.04 ± 0.04	0.08 ± 0.08	0.01 ± 0.01	0.13	0.892
Haemulidae	*Plectorhinchus polytaenia*	0.02 ± 0.02	0.09 ± 0.06	0.02 ± 0.02	0.00	1.000
Haemulidae	*Plectorhinchus schotaf*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Hemiscylliidae	*Chiloscyllium punctatum*	0 ± 0	0.01 ± 0.01	0 ± 0	0.00	1.000
Holocentridae	*Myripristis berndti*	0 ± 0	0.01 ± 0.01	0 ± 0	0.00	1.000
Holocentridae	*Myripristis botche*	0.07 ± 0.05	0.04 ± 0.04	0 ± 0	1.77	0.297
Holocentridae	*Sargocentron caudimaculatum*	0.06 ± 0.05	0.02 ± 0.02	0 ± 0	2.35	0.214
Holocentridae	*Sargocentron violaceum*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.661
Kyphosidae	*Kyphosus bigibbus*	0.46 ± 0.46	0 ± 0	0 ± 0	1.51	0.668
Kyphosidae	*Kyphosus cinerascens*	0.76 ± 0.73	0 ± 0	0 ± 0	1.66	0.070
Kyphosidae	*Kyphosus vaigiensis*	1.26 ± 1.19	0 ± 0	0 ± 0	1.69	0.219
Labridae	*Anampses caeruleopunctatus*	0.02 ± 0.02	0.06 ± 0.03	0 ± 0	0.39	0.761
Labridae	*Anampses geographicus*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.671
Labridae	*Anampses meleagrides*	0.09 ± 0.07	0.08 ± 0.07	0 ± 0	1.41	0.288
Labridae	*Anampses neoguinaicus*	0.06 ± 0.03	0.02 ± 0.02	0.04 ± 0.04	0.09	0.835
Labridae	*Bodianus axillaris*	0.06 ± 0.03	0.02 ± 0.02	0 ± 0	3.66	0.117
Labridae	*Bodianus bilunulatus*	0.02 ± 0.02	0.01 ± 0.01	0 ± 0	1.22	0.439
Labridae	*Bodianus bimaculatus*	0 ± 0	0.01 ± 0.01	0 ± 0	0.00	1.000
Labridae	*Bodianus diana*	0.01 ± 0.01	0.13 ± 0.05	0 ± 0	0.08	0.844
Labridae	*Bodianus dictynna*	0.02 ± 0.02	0.16 ± 0.06	0 ± 0	0.14	0.765
Labridae	*Bodianus mesothorax*	0.08 ± 0.05	0.09 ± 0.04	0 ± 0	2.77	0.107

Labridae	*Cheilinus chlorourus*	0.02 ± 0.02	0.02 ± 0.02	0 ± 0	0.76	0.671
Labridae	*Cheilinus fasciatus*	0.15 ± 0.05	0.21 ± 0.08	0 ± 0	3.88	0.058
Labridae	*Cheilinus trilobatus*	0.05 ± 0.03	0.06 ± 0.03	0 ± 0	2.05	0.190
Labridae	*Cheilinus undulatus*	0.1 ± 0.07	0.04 ± 0.03	0.06 ± 0.03	0.40	0.672
Labridae	*Cheilio inermis*	0.04 ± 0.03	0.09 ± 0.04	0.02 ± 0.02	0.23	0.697
Labridae	*Choerodon anchorago*	**0.17 ± 0.05**	**0.01 ± 0.01**	**0 ± 0**	**12.61**	**0.001**
Labridae	*Choerodon jordani*	**0 ± 0**	**0 ± 0**	**0.24 ± 0.15**	**4.07**	**0.002**
Labridae	*Choerodon monostigma*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Labridae	*Choerodon schoenleinii*	0.03 ± 0.02	0 ± 0	0 ± 0	3.01	0.216
Labridae	*Choerodon zamboangae*	0 ± 0	0.04 ± 0.04	0.11 ± 0.07	2.87	0.117
Labridae	*Choerodon zosterophorus*	0 ± 0	0.31 ± 0.13	0.04 ± 0.03	0.13	0.762
Labridae	*Cirrhilabrus beauperryi*	0 ± 0	0.33 ± 0.31	0 ± 0	0.00	1.000
Labridae	*Cirrhilabrus condei*	0 ± 0	0 ± 0	0.29 ± 0.29	1.51	0.665
Labridae	*Cirrhilabrus cyanopleura*	0.1 ± 0.1	0.29 ± 0.29	0 ± 0	0.17	0.895
Labridae	*Cirrhilabrus exquisitus*	0 ± 0	0.1 ± 0.1	0 ± 0	0.00	1.000
Labridae	*Cirrhilabrus flavidorsalis*	0.96 ± 0.84	0 ± 0	0 ± 0	1.97	0.220
Labridae	*Cirrhilabrus lubbocki*	0.42 ± 0.42	0 ± 0	0 ± 0	1.51	0.666
Labridae	*Cirrhilabrus tonozukai*	0.15 ± 0.15	0 ± 0	0 ± 0	1.51	0.671
Labridae	*Coris batuensis*	0.01 ± 0.01	0.07 ± 0.03	0 ± 0	0.21	0.751
Labridae	*Coris dorsomacula*	0 ± 0	0 ± 0	0.02 ± 0.02	1.51	0.662
Labridae	*Coris gaimard*	0.02 ± 0.02	0.04 ± 0.03	0.01 ± 0.01	0.05	0.864
Labridae	*Coris pictoides*	0.68 ± 0.36	1.18 ± 0.64	0.69 ± 0.29	0.00	0.997
Labridae	*Diproctacanthus xanthurus*	**0.92 ± 0.36**	**0.15 ± 0.08**	**0.05 ± 0.03**	**8.44**	**<0.001**
Labridae	*Epibulus brevis*	0.06 ± 0.05	0.02 ± 0.02	0 ± 0	2.35	0.226
Labridae	*Epibulus insidiator*	0.01 ± 0.01	0 ± 0	0 ± 0	1.51	0.665
Labridae	*Gomphosus varius*	0.2 ± 0.09	0.13 ± 0.09	0 ± 0	4.00	0.050
Labridae	*Halichoeres bicolor*	0.52 ± 0.38	0.1 ± 0.07	0.04 ± 0.03	2.32	0.094
Labridae	*Halichoeres biocellatus*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Labridae	*Halichoeres chloropterus*	0.12 ± 0.05	0.04 ± 0.04	0.01 ± 0.01	3.50	0.075
Labridae	*Halichoeres chrysus*	0.02 ± 0.02	0.74 ± 0.29	0.03 ± 0.03	0.00	0.991
Labridae	*Halichoeres hortulanus*	**0.23 ± 0.06**	**0.09 ± 0.07**	**0 ± 0**	**9.89**	**0.001**
Labridae	*Halichoeres margaritaceus*	0.06 ± 0.06	0 ± 0	0 ± 0	1.51	0.667
Labridae	*Halichoeres marginatus*	0.04 ± 0.03	0 ± 0	0 ± 0	3.13	0.219
Labridae	*Halichoeres melanochir*	0.01 ± 0.01	0.02 ± 0.02	0.02 ± 0.02	0.07	0.885
Labridae	*Halichoeres melanurus*	**0.13 ± 0.05**	**0 ± 0**	**0 ± 0**	**10.56**	**0.002**
Labridae	*Halichoeres melasmapomus*	0.01 ± 0.01	0 ± 0	0 ± 0	1.51	0.669
Labridae	*Halichoeres miniatus*	0.04 ± 0.04	0 ± 0	0 ± 0	1.51	0.661
Labridae	*Halichoeres nigrescens*	0.01 ± 0.01	0.02 ± 0.02	0 ± 0	0.46	0.660
Labridae	*Halichoeres papilionaceus*	0.03 ± 0.02	0 ± 0	0 ± 0	3.01	0.223

Labridae	*Halichoeres podostigma*	**0.12 ± 0.07**	**0 ± 0**	**0 ± 0**	**4.53**	**0.021**
Labridae	*Halichoeres prosopeion*	0.06 ± 0.03	0.38 ± 0.12	0.03 ± 0.02	0.06	0.845
Labridae	*Halichoeres richmondi*	0.06 ± 0.05	0 ± 0	0 ± 0	2.80	0.222
Labridae	*Halichoeres scapularis*	0.16 ± 0.11	0 ± 0	0.08 ± 0.07	0.56	0.526
Labridae	*Halichoeres solorensis*	**0.76 ± 0.68**	**0.03 ± 0.02**	**0 ± 0**	**1.91**	**0.037**
Labridae	*Halichoeres trimaculatus*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.663
Labridae	*Hemigymnus fasciatus*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Labridae	*Hemigymnus melapterus*	**0.46 ± 0.15**	**0.11 ± 0.05**	**0 ± 0**	**12.43**	**<0.001**
Labridae	*Hologymnosus annulatus*	**0.32 ± 0.16**	**0.07 ± 0.05**	**0 ± 0**	**5.77**	**0.003**
Labridae	*Hologymnosus doliatus*	0.02 ± 0.02	0.06 ± 0.05	0 ± 0	0.25	0.821
Labridae	*Iniistius aneitensis*	0.02 ± 0.02	0 ± 0	0.17 ± 0.09	3.79	0.075
Labridae	*Iniistius twistii*	0 ± 0	0 ± 0	0.02 ± 0.02	1.51	0.657
Labridae	*Labrichthys unilineatus*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.660
Labridae	*Labroides bicolor*	0.08 ± 0.04	0.03 ± 0.02	0.02 ± 0.02	2.07	0.171
Labridae	*Labroides dimidiatus*	**1 ± 0.26**	**0.71 ± 0.16**	**0.25 ± 0.09**	**8.57**	**0.002**
Labridae	*Labroides pectoralis*	0.06 ± 0.05	0.01 ± 0.01	0 ± 0	2.59	0.144
Labridae	*Labropsis manabei*	0.04 ± 0.04	0 ± 0	0.02 ± 0.02	0.30	0.895
Labridae	*Leptojulis cyanopleura*	0.18 ± 0.12	0 ± 0	0 ± 0	3.67	0.067
Labridae	*Macropharyngodon negrosensis*	0.02 ± 0.02	0.15 ± 0.11	0 ± 0	0.05	0.911
Labridae	*Novaculichthys taeniourus*	0 ± 0	0.06 ± 0.04	0 ± 0	0.00	1.000
Labridae	*Oxycheilinus arenatus*	0.03 ± 0.02	0 ± 0	0 ± 0	3.01	0.211
Labridae	*Oxycheilinus celebicus*	0.04 ± 0.04	0.15 ± 0.13	0.02 ± 0.02	0.04	0.940
Labridae	*Oxycheilinus digramma*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.673
Labridae	*Oxycheilinus orientalis*	0 ± 0	0.01 ± 0.01	0 ± 0	0.00	1.000
Labridae	*Oxycheilinus unifasciatus*	0.06 ± 0.03	0.17 ± 0.11	0.01 ± 0.01	0.27	0.705
Labridae	*Paracheilinus filamentosus*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Labridae	*Paracheilinus walton*	0.04 ± 0.04	0 ± 0	0 ± 0	1.51	0.671
Labridae	*Pseudocoris heteroptera*	1.03 ± 0.83	0.17 ± 0.08	0.06 ± 0.04	2.07	0.075
Labridae	*Pseudocoris yamashiroi*	0.65 ± 0.48	0.31 ± 0.27	0 ± 0	2.11	0.193
Labridae	*Pseudodax moluccanus*	0.02 ± 0.02	0.04 ± 0.03	0 ± 0	0.51	0.733
Labridae	*Pseudojuloides splendens*	0.02 ± 0.02	0 ± 0	0.01 ± 0.01	0.12	0.891
Labridae	*Stethojulis bandanensis*	0 ± 0	0.22 ± 0.15	0.06 ± 0.06	0.21	0.740
Labridae	*Stethojulis interrupta*	0.06 ± 0.06	0 ± 0	0 ± 0	1.51	0.659
Labridae	*Stethojulis strigiventer*	0.02 ± 0.02	0.26 ± 0.23	0 ± 0	0.01	0.885
Labridae	*Thalassoma amblycephalum*	0.76 ± 0.34	0.22 ± 0.17	0.35 ± 0.31	1.04	0.328
Labridae	*Thalassoma hardwicke*	**1.94 ± 0.36**	**0.01 ± 0.01**	**0 ± 0**	**37.24**	**<0.001**
Labridae	*Thalassoma jansenii*	0.08 ± 0.05	0.04 ± 0.04	0 ± 0	2.55	0.186
Labridae	*Thalassoma lunare*	**2.83 ± 0.6**	**0.32 ± 0.12**	**0 ± 0**	**29.70**	**<0.001**
Lethrinidae	*Gnathodentex aureolineatus*	0.15 ± 0.15	0 ± 0	0.1 ± 0.07	0.12	0.823

Lethrinidae	*Gymnocranius elongatus*	0 ± 0	0 ± 0	0.02 ± 0.02	1.51	0.670
Lethrinidae	*Gymnocranius grandoculis*	0.02 ± 0.02	0.13 ± 0.09	0.17 ± 0.09	2.31	0.138
Lethrinidae	*Lethrinus amboinensis*	**0.01 ± 0.01**	**0.16 ± 0.08**	**0.53 ± 0.2**	**8.54**	**0.003**
Lethrinidae	*Lethrinus atkinsoni*	0.01 ± 0.01	0.05 ± 0.03	0.14 ± 0.11	1.90	0.196
Lethrinidae	*Lethrinus erythracanthus*	0 ± 0	0.01 ± 0.01	0 ± 0	0.00	1.000
Lethrinidae	*Lethrinus erythropterus*	0.02 ± 0.02	0 ± 0	0.02 ± 0.02	0.00	1.000
Lethrinidae	*Lethrinus harak*	0.42 ± 0.14	0.11 ± 0.07	0.47 ± 0.35	0.02	0.913
Lethrinidae	*Lethrinus laticaudis*	0 ± 0	0 ± 0	0.08 ± 0.08	1.51	0.667
Lethrinidae	*Lethrinus lentjan*	**0 ± 0**	**0 ± 0**	**0.15 ± 0.08**	**5.37**	**0.020**
Lethrinidae	*Lethrinus microdon*	0 ± 0	0.18 ± 0.05	0.17 ± 0.09	3.68	0.058
Lethrinidae	*Lethrinus nebulosus*	0 ± 0	0.14 ± 0.06	0.16 ± 0.09	3.47	0.060
Lethrinidae	*Lethrinus obsoletus*	**0.02 ± 0.02**	**0.28 ± 0.12**	**0.35 ± 0.14**	**4.47**	**0.036**
Lethrinidae	*Lethrinus olivaceus*	0.06 ± 0.03	0.17 ± 0.08	0.1 ± 0.05	0.18	0.708
Lethrinidae	*Lethrinus ornatus*	0 ± 0	0.03 ± 0.02	0.17 ± 0.15	1.91	0.162
Lethrinidae	*Lethrinus ravus*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Lethrinidae	*Lethrinus rubrioperculatus*	0 ± 0	0 ± 0	0.11 ± 0.11	1.51	0.657
Lethrinidae	*Lethrinus semicinctus*	0.12 ± 0.07	0.77 ± 0.46	0.88 ± 0.3	2.87	0.091
Lethrinidae	*Lethrinus variegatus*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Lethrinidae	*Monotaxis grandoculis*	0.04 ± 0.03	0.22 ± 0.08	0.05 ± 0.03	0.01	0.953
Lethrinidae	*Monotaxis heterodon*	0.06 ± 0.05	0.09 ± 0.08	0 ± 0	0.65	0.510
Lutjanidae	*Aphareus furca*	0 ± 0	0.02 ± 0.02	0.1 ± 0.1	1.46	0.444
Lutjanidae	*Aprion virescens*	0.03 ± 0.02	0.18 ± 0.06	0.13 ± 0.05	1.96	0.173
Lutjanidae	*Lutjanus argentimaculatus*	0 ± 0	0 ± 0	0.02 ± 0.02	1.51	0.668
Lutjanidae	*Lutjanus biguttatus*	0.43 ± 0.43	0.04 ± 0.03	0.04 ± 0.04	1.22	0.551
Lutjanidae	*Lutjanus bohar*	**0.72 ± 0.18**	**0.27 ± 0.09**	**0.06 ± 0.03**	**15.58**	**<0.001**
Lutjanidae	*Lutjanus carponotatus*	**0.18 ± 0.09**	**0.01 ± 0.01**	**0 ± 0**	**5.97**	**0.002**
Lutjanidae	*Lutjanus decussatus*	**0.34 ± 0.11**	**0.08 ± 0.04**	**0 ± 0**	**13.00**	**<0.001**
Lutjanidae	*Lutjanus ehrenbergii*	0.08 ± 0.05	0 ± 0	0 ± 0	4.29	0.066
Lutjanidae	*Lutjanus fulviflamma*	0.03 ± 0.02	0 ± 0	0 ± 0	3.01	0.220
Lutjanidae	*Lutjanus fulvus*	**0.2 ± 0.08**	**0 ± 0**	**0 ± 0**	**8.30**	**0.001**
Lutjanidae	*Lutjanus gibbus*	0.27 ± 0.27	0.41 ± 0.25	0 ± 0	0.82	0.409
Lutjanidae	*Lutjanus lemniscatus*	0.03 ± 0.02	0.01 ± 0.01	0.02 ± 0.02	0.24	0.733
Lutjanidae	*Lutjanus lunulatus*	0.06 ± 0.06	0 ± 0	0 ± 0	1.51	0.669
Lutjanidae	*Lutjanus lutjanus*	0.03 ± 0.03	0.01 ± 0.01	0 ± 0	1.33	0.446
Lutjanidae	*Lutjanus maxweberi*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.668
Lutjanidae	*Lutjanus monostigma*	0.08 ± 0.04	0.11 ± 0.05	0 ± 0	2.12	0.160
Lutjanidae	*Lutjanus rivulatus*	**0.15 ± 0.07**	**0.04 ± 0.03**	**0 ± 0**	**6.24**	**0.007**
Lutjanidae	*Lutjanus russellii*	0.15 ± 0.06	0 ± 0	0.04 ± 0.04	3.15	0.089
Lutjanidae	*Lutjanus semicinctus*	**0.88 ± 0.16**	**0.2 ± 0.06**	**0 ± 0**	**37.61**	**<0.001**

Lutjanidae	*Lutjanus vitta*	0.03 ± 0.02	0.27 ± 0.19	0.23 ± 0.1	1.19	0.317
Lutjanidae	*Macolor macularis*	0.23 ± 0.13	0.5 ± 0.19	0 ± 0	1.38	0.265
Lutjanidae	*Macolor niger*	0.13 ± 0.06	0.06 ± 0.05	0 ± 0	4.00	0.069
Lutjanidae	*Pinjalo lewisi*	0 ± 0	1 ± 1	0 ± 0	0.00	1.000
Malacanthidae	*Hoplolatilus chlupatyi*	0 ± 0	0.02 ± 0.02	0.01 ± 0.01	0.46	0.672
Malacanthidae	*Hoplolatilus cuniculus*	0 ± 0	0 ± 0	0.06 ± 0.04	2.47	0.218
Malacanthidae	*Hoplolatilus purpureus*	**0 ± 0**	**0 ± 0**	**0.38 ± 0.15**	**9.15**	**0.002**
Malacanthidae	*Malacanthus brevirostris*	**0 ± 0**	**0.01 ± 0.01**	**0.07 ± 0.04**	**3.45**	**0.046**
Malacanthidae	*Malacanthus latovittatus*	0.04 ± 0.04	0.01 ± 0.01	0.03 ± 0.02	0.03	0.964
Microdesmidae	*Gunnellichthys monostigma*	0 ± 0	0.01 ± 0.01	0 ± 0	0.00	1.000
Microdesmidae	*Gunnellichthys pleurotaenia*	0.06 ± 0.03	0 ± 0	0.02 ± 0.02	1.27	0.357
Monacanthidae	*Aluterus scriptus*	0.04 ± 0.03	0 ± 0	0.08 ± 0.05	0.79	0.534
Monacanthidae	*Amanses scopas*	0.06 ± 0.03	0.05 ± 0.03	0.02 ± 0.02	1.15	0.312
Monacanthidae	*Cantherhines dumerilii*	0.15 ± 0.09	0.04 ± 0.03	0.05 ± 0.03	1.52	0.270
Monacanthidae	*Cantherhines fronticinctus*	0.04 ± 0.03	0 ± 0	0 ± 0	3.13	0.212
Monacanthidae	*Cantherhines pardalis*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Monacanthidae	*Paraluteres prionurus*	0 ± 0	0.13 ± 0.09	0 ± 0	0.00	1.000
Monacanthidae	*Paramonacanthus japonicus*	0 ± 0	0 ± 0	0.06 ± 0.04	2.47	0.218
Monacanthidae	*Pervagor janthinosoma*	0.04 ± 0.04	0 ± 0	0 ± 0	1.51	0.674
Monacanthidae	*Pseudomonacanthus macrurus*	0 ± 0	0 ± 0	0.02 ± 0.02	1.51	0.662
Monodactylidae	*Monodactylus argenteus*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Mugilidae	*Crenimugil crenilabis*	0.61 ± 0.61	0 ± 0	0 ± 0	1.51	0.661
Mullidae	*Mulloidichthys flavolineatus*	0.04 ± 0.04	0.02 ± 0.02	0.07 ± 0.05	0.25	0.655
Mullidae	*Mulloidichthys vanicolensis*	0 ± 0	0 ± 0	0.02 ± 0.02	1.51	0.672
Mullidae	*Parupeneus barberinoides*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Mullidae	*Parupeneus barberinus*	0.53 ± 0.11	0.69 ± 0.17	0.26 ± 0.1	2.10	0.161
Mullidae	*Parupeneus chrysopleuron*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Mullidae	*Parupeneus crassilabris*	**0.33 ± 0.08**	**0.06 ± 0.05**	**0 ± 0**	**18.08**	**<0.001**
Mullidae	*Parupeneus cyclostomus*	0.13 ± 0.05	0.47 ± 0.15	0.29 ± 0.12	0.90	0.355
Mullidae	*Parupeneus heptacanthus*	**0 ± 0**	**0.1 ± 0.07**	**0.38 ± 0.19**	**5.31**	**0.013**
Mullidae	*Parupeneus indicus*	0.09 ± 0.05	0.08 ± 0.06	0.17 ± 0.1	0.55	0.501
Mullidae	*Parupeneus multifasciatus*	0.99 ± 0.17	1.14 ± 0.19	0.55 ± 0.2	2.74	0.104
Mullidae	*Parupeneus pleurostigma*	0 ± 0	0.07 ± 0.06	0 ± 0	0.00	1.000
Mullidae	*Upeneus tragula*	0.03 ± 0.02	0.03 ± 0.02	0.17 ± 0.15	1.42	0.347
Muraenidae	*Echidna nebulosa*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.665
Muraenidae	*Gymnothorax chilospilus*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.662
Muraenidae	*Gymnothorax enigmaticus*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.673
Muraenidae	*Gymnothorax flavimarginatus*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.664
Muraenidae	*Gymnothorax javanicus*	**0.13 ± 0.05**	**0.05 ± 0.03**	**0 ± 0**	**6.71**	**0.010**

Muraenidae	*Gymnothorax undulatus*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Muraenidae	*Gymnothorax zonipectis*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Nemipteridae	*Pentapodus aureofasciatus*	0.06 ± 0.03	1.43 ± 0.42	1.39 ± 0.69	4.02	0.050
Nemipteridae	*Pentapodus caninus*	**0.01 ± 0.01**	**1.33 ± 0.73**	**2.55 ± 1.14**	**5.32**	**0.022**
Nemipteridae	*Pentapodus emeryii*	**0.17 ± 0.11**	**0.62 ± 0.14**	**0.97 ± 0.3**	**7.74**	**0.005**
Nemipteridae	*Pentapodus nagasakiensis*	**0 ± 0**	**0.4 ± 0.19**	**2.5 ± 1.28**	**5.59**	**0.002**
Nemipteridae	*Pentapodus numberii*	0 ± 0	0.09 ± 0.05	0.66 ± 0.65	1.58	0.266
Nemipteridae	*Pentapodus paradiseus*	**0.04 ± 0.04**	**0.08 ± 0.08**	**1.62 ± 0.76**	**6.30**	**<0.001**
Nemipteridae	*Pentapodus porosus*	0.03 ± 0.02	0.57 ± 0.25	0.46 ± 0.46	0.99	0.367
Nemipteridae	*Pentapodus trivittatus*	**0.82 ± 0.22**	**0.16 ± 0.09**	**0.06 ± 0.05**	**14.29**	**<0.001**
Nemipteridae	*Scolopsis affinis*	0.56 ± 0.42	0.61 ± 0.25	1.07 ± 0.25	1.34	0.267
Nemipteridae	*Scolopsis bilineata*	**0.53 ± 0.1**	**0.32 ± 0.1**	**0.04 ± 0.04**	**17.04**	**<0.001**
Nemipteridae	*Scolopsis ciliata*	0.15 ± 0.08	0.12 ± 0.07	0.12 ± 0.07	0.11	0.765
Nemipteridae	*Scolopsis lineata*	0.33 ± 0.27	0 ± 0	0 ± 0	2.26	0.065
Nemipteridae	*Scolopsis margaritifera*	0.19 ± 0.07	0.57 ± 0.36	0.19 ± 0.12	0.00	1.000
Nemipteridae	*Scolopsis monogramma*	0.04 ± 0.04	0.44 ± 0.34	0.03 ± 0.02	0.00	0.997
Nemipteridae	*Scolopsis temporalis*	0.21 ± 0.09	0.68 ± 0.43	0.15 ± 0.08	0.02	0.885
Nemipteridae	*Scolopsis trilineata*	0.18 ± 0.11	0.02 ± 0.02	0.04 ± 0.04	2.16	0.162
Nemipteridae	*Scolopsis vosmeri*	**0 ± 0**	**0 ± 0**	**0.4 ± 0.2**	**6.28**	**0.002**
Nemipteridae	*Scolopsis xenochroa*	0.17 ± 0.07	0.1 ± 0.07	0.17 ± 0.11	0.00	1.000
Ophichthidae	*Myrichthys colubrinus*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.671
Ostraciidae	*Lactoria cornuta*	0 ± 0	0.01 ± 0.01	0 ± 0	0.00	1.000
Ostraciidae	*Ostracion cubicus*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Ostraciidae	*Ostracion meleagris*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.674
Pempheridae	*Parapriacanthus ransonneti*	0 ± 0	2.75 ± 2.75	0 ± 0	0.00	1.000
Pholidichthyidae	*Pholidichthys leucotaenia*	0 ± 0	0 ± 0	0.46 ± 0.46	1.51	0.662
Pinguipedidae	*Parapercis clathrata*	0.03 ± 0.02	0 ± 0	0.03 ± 0.03	0.05	0.963
Pinguipedidae	*Parapercis cylindrica*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Pinguipedidae	*Parapercis hexophtalma*	0.07 ± 0.03	0.02 ± 0.02	0.01 ± 0.01	2.70	0.130
Pinguipedidae	*Parapercis lineopunctata*	0.02 ± 0.02	0.04 ± 0.03	0.02 ± 0.02	0.00	1.000
Pinguipedidae	*Parapercis snyderi*	0 ± 0	0 ± 0	0.13 ± 0.11	2.12	0.210
Pinguipedidae	*Parapercis tetracantha*	0.03 ± 0.03	0.1 ± 0.06	0.09 ± 0.05	0.83	0.407
Pinguipedidae	*Parapercis xanthozona*	0 ± 0	0.07 ± 0.04	0.04 ± 0.04	0.86	0.423
Plotosidae	*Plotosus lineatus*	0 ± 0	9.5 ± 9.5	0 ± 0	0.00	1.000
Pomacanthidae	*Apolemichthys trimaculatus*	0.07 ± 0.04	0.08 ± 0.04	0.14 ± 0.06	1.06	0.329
Pomacanthidae	*Centropyge bicolor*	0.06 ± 0.04	0.34 ± 0.11	0.02 ± 0.02	0.17	0.722
Pomacanthidae	*Centropyge bispinosa*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Pomacanthidae	*Centropyge fisheri*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Pomacanthidae	*Centropyge nox*	0.07 ± 0.04	0 ± 0	0 ± 0	4.78	0.070

Pomacanthidae	*Centropyge tibicen*	0.08 ± 0.05	0.08 ± 0.07	0 ± 0	1.58	0.304
Pomacanthidae	*Centropyge vrolikii*	0.03 ± 0.02	0 ± 0	0 ± 0	3.01	0.210
Pomacanthidae	*Chaetodontoplus dimidiatus*	**0 ± 0**	**0.1 ± 0.05**	**0.27 ± 0.12**	**6.45**	**0.008**
Pomacanthidae	*Chaetodontoplus mesoleucus*	0.18 ± 0.08	0.25 ± 0.09	0.02 ± 0.02	2.65	0.119
Pomacanthidae	*Chaetodontoplus poliourus*	0.06 ± 0.05	0 ± 0	0 ± 0	2.80	0.213
Pomacanthidae	*Genicanthus lamarck*	0 ± 0	0.44 ± 0.16	0.06 ± 0.06	0.18	0.740
Pomacanthidae	*Genicanthus melanospilos*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Pomacanthidae	*Paracentropyge multifasciata*	0.02 ± 0.02	0.02 ± 0.02	0.01 ± 0.01	0.07	0.893
Pomacanthidae	*Pomacanthus imperator*	0.12 ± 0.06	0.18 ± 0.06	0.07 ± 0.03	0.43	0.552
Pomacanthidae	*Pomacanthus navarchus*	0.03 ± 0.02	0.01 ± 0.01	0 ± 0	2.58	0.143
Pomacanthidae	*Pomacanthus semicirculatus*	0.01 ± 0.01	0.04 ± 0.04	0 ± 0	0.15	0.891
Pomacanthidae	*Pomacanthus sexstriatus*	0.07 ± 0.05	0.19 ± 0.1	0.07 ± 0.05	0.00	1.000
Pomacanthidae	*Pomacanthus xanthometopon*	0.01 ± 0.01	0.02 ± 0.02	0 ± 0	0.46	0.665
Pomacanthidae	*Pygoplites diacanthus*	**0.18 ± 0.07**	**0.21 ± 0.07**	**0 ± 0**	**5.03**	**0.030**
Pomacentridae	*Abudefduf bengalensis*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.669
Pomacentridae	*Abudefduf sexfasciatus*	0.17 ± 0.17	0 ± 0	0 ± 0	1.51	0.662
Pomacentridae	*Abudefduf vaigiensis*	0.72 ± 0.71	0 ± 0	0 ± 0	1.57	0.223
Pomacentridae	*Acanthochromis polyacanthus*	0.4 ± 0.14	0.76 ± 0.75	0 ± 0	0.42	0.672
Pomacentridae	*Amblyglyphidodon aureus*	0.02 ± 0.02	0.11 ± 0.08	0 ± 0	0.09	0.892
Pomacentridae	*Amblyglyphidodon batunai*	0.1 ± 0.1	0.03 ± 0.02	0 ± 0	1.44	0.371
Pomacentridae	*Amblyglyphidodon curacao*	**0.37 ± 0.18**	**0.02 ± 0.02**	**0 ± 0**	**6.01**	**0.007**
Pomacentridae	*Amblyglyphidodon leucogaster*	0.33 ± 0.16	0.19 ± 0.15	0 ± 0	3.30	0.079
Pomacentridae	*Amblyglyphidodon ternatensis*	**0.35 ± 0.18**	**0 ± 0**	**0 ± 0**	**5.46**	**0.021**
Pomacentridae	*Amblypomacentrus breviceps*	0.04 ± 0.03	0 ± 0	0 ± 0	3.13	0.214
Pomacentridae	*Amblypomacentrus clarus*	1.17 ± 1.15	0.02 ± 0.02	0.02 ± 0.02	1.51	0.409
Pomacentridae	*Cheiloprion labiatus*	0 ± 0	0.04 ± 0.04	0 ± 0	0.00	1.000
Pomacentridae	*Chromis alpha*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Pomacentridae	*Chromis amboinensis*	**1.76 ± 1.38**	**0.08 ± 0.05**	**0 ± 0**	**2.47**	**0.010**
Pomacentridae	*Chromis analis*	0.44 ± 0.26	0 ± 0	0 ± 0	4.08	0.065
Pomacentridae	*Chromis atripectoralis*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.666
Pomacentridae	*Chromis caudalis*	0.1 ± 0.07	0.01 ± 0.01	0.19 ± 0.11	0.71	0.436
Pomacentridae	*Chromis cinerascens*	0.06 ± 0.06	0 ± 0	0 ± 0	1.51	0.664
Pomacentridae	*Chromis fumea*	0.44 ± 0.35	0.13 ± 0.06	0 ± 0	2.25	0.088
Pomacentridae	*Chromis margaritifer*	**0.87 ± 0.25**	**0.08 ± 0.05**	**0.01 ± 0.01**	**16.02**	**<0.001**
Pomacentridae	*Chromis retrofasciata*	0 ± 0	0.06 ± 0.06	0 ± 0	0.00	1.000
Pomacentridae	*Chromis scotochiloptera*	**0.41 ± 0.23**	**0.15 ± 0.1**	**0 ± 0**	**3.96**	**0.039**
Pomacentridae	*Chromis ternatensis*	**3.39 ± 1.87**	**0.05 ± 0.03**	**0 ± 0**	**4.90**	**<0.001**
Pomacentridae	*Chromis viridis*	0.75 ± 0.57	0 ± 0	0 ± 0	2.63	0.069
Pomacentridae	*Chromis weberi*	**0.89 ± 0.41**	**0.22 ± 0.17**	**0 ± 0**	**6.10**	**0.006**

Pomacentridae	*Chromis xanthochira*	0.1 ± 0.05	0.04 ± 0.04	0 ± 0	3.64	0.077
Pomacentridae	*Chromis xanthura*	**0.38 ± 0.2**	**0.06 ± 0.03**	**0 ± 0**	**5.38**	**0.012**
Pomacentridae	*Chrysiptera bleekeri*	0 ± 0	0.33 ± 0.27	0.1 ± 0.07	0.18	0.739
Pomacentridae	*Chrysiptera cyanea*	**1.41 ± 0.77**	**0.01 ± 0.01**	**0 ± 0**	**5.00**	**0.002**
Pomacentridae	*Chrysiptera flavipinnis*	0 ± 0	0.1 ± 0.1	0.06 ± 0.06	0.40	0.669
Pomacentridae	*Chrysiptera glauca*	0.06 ± 0.05	0 ± 0	0 ± 0	2.80	0.221
Pomacentridae	*Chrysiptera hemicyanea*	0.04 ± 0.04	0.13 ± 0.11	0 ± 0	0.20	0.817
Pomacentridae	*Chrysiptera parasema*	0.1 ± 0.09	0.07 ± 0.06	0.02 ± 0.02	0.91	0.390
Pomacentridae	*Chrysiptera pricei*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.674
Pomacentridae	*Chrysiptera rex*	0.14 ± 0.08	0.08 ± 0.08	0 ± 0	2.27	0.183
Pomacentridae	*Chrysiptera rollandi*	0.1 ± 0.07	0.19 ± 0.09	0 ± 0	1.15	0.318
Pomacentridae	*Chrysiptera springeri*	0.06 ± 0.06	0.02 ± 0.02	0 ± 0	1.37	0.436
Pomacentridae	*Chrysiptera talboti*	0.06 ± 0.03	0 ± 0	0 ± 0	4.72	0.067
Pomacentridae	*Dascyllus aruanus*	0.12 ± 0.1	0.04 ± 0.04	0 ± 0	1.85	0.289
Pomacentridae	*Dascyllus melanurus*	0.13 ± 0.11	0 ± 0	0 ± 0	2.12	0.216
Pomacentridae	*Dascyllus reticulatus*	**0.33 ± 0.15**	**0.04 ± 0.04**	**0 ± 0**	**6.47**	**0.010**
Pomacentridae	*Dascyllus trimaculatus*	0.29 ± 0.17	0.04 ± 0.04	0.04 ± 0.04	2.78	0.096
Pomacentridae	*Dischistodus chrysopoecilus*	0.04 ± 0.04	0 ± 0	0 ± 0	1.51	0.664
Pomacentridae	*Dischistodus fasciatus*	0.02 ± 0.02	0.06 ± 0.04	0 ± 0	0.28	0.743
Pomacentridae	*Dischistodus melanotus*	**0.31 ± 0.18**	**0.02 ± 0.02**	**0 ± 0**	**4.38**	**0.010**
Pomacentridae	*Dischistodus perspicillatus*	0.22 ± 0.14	0 ± 0	0 ± 0	3.51	0.073
Pomacentridae	*Dischistodus prosopotaenia*	0.08 ± 0.05	0 ± 0	0 ± 0	3.94	0.071
Pomacentridae	*Dischistodus pseudochrysopoecilus*	0.22 ± 0.16	0.08 ± 0.07	0 ± 0	2.55	0.139
Pomacentridae	*Hemiglyphidodon plagiometopon*	0.1 ± 0.05	0.13 ± 0.13	0 ± 0	0.89	0.465
Pomacentridae	*Lepidozygus tapeinosoma*	0 ± 0	0.04 ± 0.04	0 ± 0	0.00	1.000
Pomacentridae	*Neoglyphidodon crossi*	0.03 ± 0.02	0.02 ± 0.02	0 ± 0	1.46	0.293
Pomacentridae	*Neoglyphidodon melas*	**0.26 ± 0.1**	**0.04 ± 0.04**	**0 ± 0**	**8.96**	**0.002**
Pomacentridae	*Neoglyphidodon nigroris*	0.19 ± 0.09	0.23 ± 0.16	0 ± 0	1.64	0.225
Pomacentridae	*Neoglyphidodon oxyodon*	0.05 ± 0.03	0.1 ± 0.07	0 ± 0	0.53	0.539
Pomacentridae	*Neoglyphidodon thoracotaeniatus*	0 ± 0	0.07 ± 0.05	0 ± 0	0.00	1.000
Pomacentridae	*Neopomacentrus azysron*	0.06 ± 0.05	0 ± 0	0 ± 0	2.80	0.214
Pomacentridae	*Neopomacentrus cyanomos*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Pomacentridae	*Neopomacentrus filamentosus*	0.02 ± 0.02	0.1 ± 0.1	0 ± 0	0.06	0.895
Pomacentridae	*Plectroglyphidodon dickii*	**0.15 ± 0.07**	**0 ± 0**	**0 ± 0**	**6.32**	**0.006**
Pomacentridae	*Plectroglyphidodon lacrymatus*	0.02 ± 0.02	0.02 ± 0.02	0 ± 0	0.76	0.664
Pomacentridae	*Plectroglyphidodon leucozonus*	0.03 ± 0.03	0 ± 0	0 ± 0	1.51	0.671
Pomacentridae	*Pomacentrus adelus*	0 ± 0	0.08 ± 0.08	0 ± 0	0.00	1.000
Pomacentridae	*Pomacentrus amboinensis*	0.02 ± 0.02	0.89 ± 0.45	0.03 ± 0.03	0.00	0.992
Pomacentridae	*Pomacentrus auriventris*	1.96 ± 1.16	1.66 ± 0.89	0.25 ± 0.25	2.01	0.169

Pomacentridae	*Pomacentrus bankanensis*	**0.47 ± 0.16**	**0.04 ± 0.04**	**0 ± 0**	**10.99**	**<0.001**
Pomacentridae	*Pomacentrus brachialis*	**0.24 ± 0.1**	**0.08 ± 0.05**	**0 ± 0**	**6.42**	**0.014**
Pomacentridae	*Pomacentrus chrysurus*	**0.51 ± 0.24**	**0.06 ± 0.06**	**0 ± 0**	**6.46**	**0.009**
Pomacentridae	*Pomacentrus coelestis*	**0.49 ± 0.28**	**0 ± 0**	**0 ± 0**	**4.56**	**0.006**
Pomacentridae	*Pomacentrus cuneatus*	0.01 ± 0.01	0 ± 0	0 ± 0	1.51	0.668
Pomacentridae	*Pomacentrus lepidogenys*	0.08 ± 0.05	0.08 ± 0.08	0 ± 0	0.96	0.405
Pomacentridae	*Pomacentrus littoralis*	0.02 ± 0.02	0.04 ± 0.03	0 ± 0	0.51	0.743
Pomacentridae	*Pomacentrus moluccensis*	**1.94 ± 0.57**	**0 ± 0**	**0 ± 0**	**16.24**	**<0.001**
Pomacentridae	*Pomacentrus nagasakiensis*	**0 ± 0**	**0 ± 0**	**0.16 ± 0.09**	**4.93**	**0.024**
Pomacentridae	*Pomacentrus nigromanus*	0.15 ± 0.09	0.42 ± 0.14	0.02 ± 0.02	0.74	0.419
Pomacentridae	*Pomacentrus nigromarginatus*	0 ± 0	0.06 ± 0.05	0 ± 0	0.00	1.000
Pomacentridae	*Pomacentrus opisthostigma*	0.08 ± 0.05	0 ± 0	0 ± 0	4.29	0.071
Pomacentridae	*Pomacentrus pavo*	0.04 ± 0.03	0 ± 0	0 ± 0	3.13	0.221
Pomacentridae	*Pomacentrus philippinus*	0.06 ± 0.05	0 ± 0	0 ± 0	2.80	0.218
Pomacentridae	*Pomacentrus reidi*	0.2 ± 0.15	0.03 ± 0.02	0 ± 0	2.53	0.113
Pomacentridae	*Pomacentrus simsiang*	**0.14 ± 0.08**	**0.04 ± 0.03**	**0 ± 0**	**4.48**	**0.037**
Pomacentridae	*Pomacentrus taeniometopon*	0 ± 0	0 ± 0	0.04 ± 0.04	1.51	0.664
Pomacentridae	*Pomacentrus tripunctatus*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Pomacentridae	*Pomacentrus vaiuli*	0.02 ± 0.02	0.02 ± 0.02	0 ± 0	0.76	0.672
Pomacentridae	*Stegastes albifasciatus*	0 ± 0	0.01 ± 0.01	0 ± 0	0.00	1.000
Pomacentridae	*Stegastes fasciolatus*	0.01 ± 0.01	0 ± 0	0 ± 0	1.51	0.671
Priacanthidae	*Priacanthus hamrur*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Pseudochromidae	*Pictichromis caitlinae*	0 ± 0	0.04 ± 0.04	0 ± 0	0.00	1.000
Pseudochromidae	*Pseudochromis fuscus*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Pseudochromidae	*Pseudochromis jace*	0 ± 0	0 ± 0	0.02 ± 0.02	1.51	0.668
Pseudochromidae	*Pseudochromis perspicillatus*	0 ± 0	0 ± 0	0.07 ± 0.05	3.01	0.213
Pseudochromidae	*Pseudochromis pylei*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Ptereleotridae	*Ptereleotris evides*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Ptereleotridae	*Ptereleotris hanae*	0.03 ± 0.03	0 ± 0	0 ± 0	1.51	0.669
Ptereleotridae	*Ptereleotris heteroptera*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Rachycentridae	*Rachycentron canadum*	0 ± 0	0.01 ± 0.01	0 ± 0	0.00	1.000
Scaridae	*Bolbometopon muricatum*	0 ± 0	0.03 ± 0.02	0.04 ± 0.03	1.84	0.215
Scaridae	*Cetoscarus ocellatus*	0.02 ± 0.02	0.02 ± 0.02	0 ± 0	0.76	0.673
Scaridae	*Chlorurus bleekeri*	**0.06 ± 0.03**	**0 ± 0**	**0 ± 0**	**6.49**	**0.020**
Scaridae	*Chlorurus bowersi*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.660
Scaridae	*Chlorurus japanensis*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.668
Scaridae	*Chlorurus microrhinos*	0.08 ± 0.05	0 ± 0	0 ± 0	4.29	0.070
Scaridae	*Chlorurus sordidus*	**0.21 ± 0.08**	**0.02 ± 0.02**	**0.01 ± 0.01**	**8.43**	**0.002**
Scaridae	*Hipposcarus longiceps*	0.01 ± 0.01	0 ± 0	0 ± 0	1.51	0.667

Scaridae	*Scarus chameleon*	0.06 ± 0.06	0 ± 0	0 ± 0	1.51	0.669
Scaridae	*Scarus dimidiatus*	**0.13 ± 0.06**	**0 ± 0**	**0 ± 0**	**6.00**	**0.019**
Scaridae	*Scarus flavipectoralis*	0.08 ± 0.03	0.18 ± 0.08	0 ± 0	1.22	0.295
Scaridae	*Scarus forsteni*	0.06 ± 0.05	0 ± 0	0 ± 0	2.80	0.214
Scaridae	*Scarus ghobban*	0.02 ± 0.02	0.02 ± 0.02	0 ± 0	0.76	0.665
Scaridae	*Scarus niger*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.659
Scaridae	*Scarus oviceps*	0.13 ± 0.06	0.1 ± 0.05	0.04 ± 0.04	1.30	0.284
Scaridae	*Scarus prasiognathos*	0.03 ± 0.02	0.02 ± 0.02	0 ± 0	1.77	0.300
Scaridae	*Scarus psittacus*	0.07 ± 0.04	0.04 ± 0.04	0 ± 0	1.96	0.237
Scaridae	*Scarus quoyi*	0.06 ± 0.04	0 ± 0	0 ± 0	4.51	0.065
Scaridae	*Scarus rivulatus*	0.21 ± 0.21	0.02 ± 0.02	0 ± 0	1.50	0.443
Scaridae	*Scarus rubroviolaceus*	0 ± 0	0.04 ± 0.03	0 ± 0	0.00	1.000
Scaridae	*Scarus schlegeli*	0.02 ± 0.02	0 ± 0	0.02 ± 0.02	0.00	1.000
Scaridae	*Scarus spinus*	0.04 ± 0.04	0 ± 0	0 ± 0	1.51	0.666
Scaridae	*Scarus tricolor*	0.02 ± 0.02	0.13 ± 0.07	0.02 ± 0.02	0.00	1.000
Scombridae	*Grammatorcynus bilineatus*	0 ± 0	0.06 ± 0.03	0.08 ± 0.07	1.95	0.250
Scombridae	*Gymnosarda unicolor*	0 ± 0	0.1 ± 0.1	0.06 ± 0.03	0.39	0.659
Scombridae	*Scomberomorus commerson*	0 ± 0	0.08 ± 0.06	0.01 ± 0.01	0.08	0.892
Serranidae	*Aethaloperca rogaa*	**0.19 ± 0.06**	**0.08 ± 0.04**	**0 ± 0**	**9.96**	**0.001**
Serranidae	*Cephalopholis argus*	**0.33 ± 0.09**	**0.16 ± 0.06**	**0 ± 0**	**14.13**	**<0.001**
Serranidae	*Cephalopholis boenak*	**0.25 ± 0.07**	**0.04 ± 0.03**	**0.01 ± 0.01**	**12.67**	**0.001**
Serranidae	*Cephalopholis cyanostigma*	0.01 ± 0.01	0.06 ± 0.05	0 ± 0	0.12	0.817
Serranidae	*Cephalopholis microprion*	0.03 ± 0.02	0.05 ± 0.04	0.01 ± 0.01	0.25	0.677
Serranidae	*Cephalopholis miniata*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Serranidae	*Cephalopholis polleni*	0 ± 0	0.04 ± 0.04	0 ± 0	0.00	1.000
Serranidae	*Cephalopholis sexmaculata*	0 ± 0	0.03 ± 0.02	0.03 ± 0.02	1.62	0.238
Serranidae	*Cephalopholis sonnerati*	0.05 ± 0.03	0 ± 0	0 ± 0	3.07	0.216
Serranidae	*Cephalopholis spiloparaea*	0 ± 0	0.01 ± 0.01	0 ± 0	0.00	1.000
Serranidae	*Cephalopholis urodeta*	0.13 ± 0.05	0.11 ± 0.06	0 ± 0	3.58	0.070
Serranidae	*Diploprion bifasciatum*	0.13 ± 0.06	0.21 ± 0.09	0.17 ± 0.08	0.09	0.778
Serranidae	*Epinephelus areolatus*	0.04 ± 0.04	0 ± 0	0.08 ± 0.07	0.43	0.658
Serranidae	*Epinephelus bontoides*	0.01 ± 0.01	0.01 ± 0.01	0 ± 0	0.97	0.447
Serranidae	*Epinephelus coioides*	0.04 ± 0.03	0.08 ± 0.06	0 ± 0	0.53	0.586
Serranidae	*Epinephelus fasciatus*	0 ± 0	0.04 ± 0.03	0 ± 0	0.00	1.000
Serranidae	*Epinephelus fuscoguttatus*	0.02 ± 0.02	0.04 ± 0.03	0 ± 0	0.51	0.732
Serranidae	*Epinephelus macrospilos*	0.02 ± 0.02	0 ± 0	0 ± 0	1.51	0.669
Serranidae	*Epinephelus malabaricus*	0.02 ± 0.02	0.02 ± 0.02	0 ± 0	0.76	0.662
Serranidae	*Epinephelus merra*	0.04 ± 0.03	0 ± 0	0 ± 0	2.80	0.222
Serranidae	*Epinephelus polyphekadion*	0 ± 0	0.02 ± 0.01	0 ± 0	0.00	1.000

Serranidae	*Epinephelus spilotoceps*	0 ± 0	0.01 ± 0.01	0 ± 0	0.00	1.000
Serranidae	*Gracila albomarginata*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Serranidae	*Plectropomus areolatus*	0.02 ± 0.02	0.08 ± 0.05	0 ± 0	0.24	0.710
Serranidae	*Plectropomus laevis*	0.01 ± 0.01	0 ± 0	0 ± 0	1.51	0.660
Serranidae	*Plectropomus leopardus*	0.02 ± 0.02	0.02 ± 0.02	0 ± 0	0.76	0.669
Serranidae	*Plectropomus maculatus*	0.01 ± 0.01	0.04 ± 0.04	0 ± 0	0.15	0.891
Serranidae	*Plectropomus oligacanthus*	0.01 ± 0.01	0.14 ± 0.07	0 ± 0	0.05	0.863
Serranidae	*Pseudanthias dispar*	0.71 ± 0.71	0 ± 0	0 ± 0	1.51	0.658
Serranidae	*Pseudanthias huchtii*	0.02 ± 0.02	0.04 ± 0.04	0 ± 0	0.30	0.889
Serranidae	*Pseudanthias pleurotaenia*	0 ± 0	0.11 ± 0.11	0 ± 0	0.00	1.000
Serranidae	*Variola albimarginata*	0.02 ± 0.02	0.18 ± 0.08	0.04 ± 0.03	0.09	0.819
Serranidae	*Variola louti*	0.16 ± 0.06	0.16 ± 0.07	0.1 ± 0.07	0.50	0.505
Siganidae	*Siganus argenteus*	**0.44 ± 0.33**	**0.04 ± 0.04**	**0 ± 0**	**2.57**	**0.023**
Siganidae	*Siganus canaliculatus*	0.01 ± 0.01	0 ± 0	0 ± 0	1.51	0.666
Siganidae	*Siganus corallinus*	**0.16 ± 0.07**	**0.13 ± 0.06**	**0 ± 0**	**4.37**	**0.045**
Siganidae	*Siganus doliatus*	**0.15 ± 0.08**	**0 ± 0**	**0 ± 0**	**5.29**	**0.021**
Siganidae	*Siganus guttatus*	0 ± 0	0.01 ± 0.01	0 ± 0	0.00	1.000
Siganidae	*Siganus puellus*	**0.26 ± 0.1**	**0.06 ± 0.04**	**0 ± 0**	**9.23**	**0.002**
Siganidae	*Siganus punctatissimus*	0.08 ± 0.05	0.12 ± 0.09	0 ± 0	0.92	0.411
Siganidae	*Siganus punctatus*	0.17 ± 0.08	0.13 ± 0.09	0 ± 0	2.92	0.138
Siganidae	*Siganus vulpinus*	**0.24 ± 0.07**	**0.06 ± 0.04**	**0 ± 0**	**12.96**	**0.001**
Sphyraenidae	*Sphyraena barracuda*	0 ± 0	0 ± 0	0.03 ± 0.03	1.51	0.660
Syngnathidae	*Choeroichthys brachysoma*	0 ± 0	0.01 ± 0.01	0 ± 0	0.00	1.000
Syngnathidae	*Dunckerocampus pessuliferus*	0 ± 0	0.01 ± 0.01	0 ± 0	0.00	1.000
Synodontidae	*Synodus variegatus*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Tetraodontidae	*Arothron caeruleopunctatus*	0.02 ± 0.02	0.05 ± 0.03	0.02 ± 0.02	0.00	1.000
Tetraodontidae	*Arothron hispidus*	0.04 ± 0.03	0 ± 0	0 ± 0	3.13	0.221
Tetraodontidae	*Arothron immaculatus*	0 ± 0	0 ± 0	0.01 ± 0.01	1.51	0.662
Tetraodontidae	*Arothron mappa*	0.02 ± 0.02	0 ± 0	0.04 ± 0.03	0.51	0.732
Tetraodontidae	*Arothron nigropunctatus*	0.02 ± 0.02	0.08 ± 0.05	0 ± 0	0.22	0.834
Tetraodontidae	*Arothron stellatus*	0 ± 0	0 ± 0	0.02 ± 0.02	1.51	0.662
Tetraodontidae	*Canthigaster amboinensis*	0 ± 0	0.03 ± 0.03	0 ± 0	0.00	1.000
Tetraodontidae	*Canthigaster valentini*	0 ± 0	0.11 ± 0.07	0 ± 0	0.00	1.000
Tetraodontidae	*Lagocephalus sceleratus*	0 ± 0	0.02 ± 0.02	0 ± 0	0.00	1.000
Toxotidae	*Toxotes jaculatrix*	0.05 ± 0.03	0 ± 0	0 ± 0	3.07	0.225
Zanclidae	*Zanclus cornutus*	**0.82 ± 0.16**	**0.77 ± 0.16**	**0.26 ± 0.12**	**6.91**	**0.011**

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ESM Table 6. Dufrêne and Legendre indicator species analysis showing fish species indicative of shallow, intermediate, and MCE depth zones. Analysis is based on fish abundance with results showing the Dufrêne and Legendre indicator value (measuring the association between the fish species and the depth group) and the associated permutational p-value (based on 99999 permutations). Only fish species with a p<0.05 association for the depth band are shown.

Family / Depth group	**Species**	**Indicator value**	**P(perm)**	**Trophic Group**
Shallow				
Acanthuridae	*Acanthurus lineatus*	0.38	<0.001	Herbivore
Acanthuridae	*Acanthurus maculiceps*	0.53	<0.001	Herbivore
Acanthuridae	*Acanthurus nigricauda*	0.16	0.044	Omnivore
Acanthuridae	*Acanthurus xanthopterus*	0.19	0.009	Planktivore
Acanthuridae	*Ctenochaetus striatus*	0.54	<0.001	Planktivore
Acanthuridae	*Naso brevirostris*	0.32	0.001	Herbivore
Acanthuridae	*Naso lituratus*	0.33	0.002	Herbivore_Planktivore
Acanthuridae	*Naso unicornis*	0.18	0.044	Herbivore
Acanthuridae	*Zebrasoma scopas*	0.49	<0.001	Herbivore
Balistidae	*Balistapus undulatus*	0.59	<0.001	Mobile.Invert
Caesionidae	*Caesio lunaris*	0.28	0.017	Planktivore
Caesionidae	*Pterocaesio tile*	0.26	0.004	Planktivore
Carangidae	*Scomberoides lysan*	0.17	0.031	Piscivore_Mobile.Invert
Carcharhinidae	*Carcharhinus melanopterus*	0.37	0.011	Piscivore_Mobile.Invert
Chaetodontidae	*Chaetodon baronessa*	0.44	<0.001	Corallivore
Chaetodontidae	*Chaetodon citrinellus*	0.21	0.009	Omnivore
Chaetodontidae	*Chaetodon ephippium*	0.21	0.021	Omnivore
Chaetodontidae	*Chaetodon lineolatus*	0.26	0.004	Corallivore
Chaetodontidae	*Chaetodon lunula*	0.23	0.011	Mobile.Invert
Chaetodontidae	*Chaetodon lunulatus*	0.48	<0.001	Corallivore
Chaetodontidae	*Chaetodon rafflesii*	0.46	<0.001	Corallivore
Chaetodontidae	*Chaetodon semeion*	0.25	0.003	Omnivore

Chaetodontidae	*Chaetodon speculum*	0.25	0.005	Corallivore
Chaetodontidae	*Chaetodon trifascialis*	0.46	<0.001	Corallivore
Chaetodontidae	*Chaetodon vagabundus*	0.4	<0.001	Corallivore
Chaetodontidae	*Heniochus varius*	0.21	0.022	Mobile.Invert
Cirrhitidae	*Paracirrhites forsteri*	0.21	0.009	Piscivore
Labridae	*Choerodon anchorago*	0.31	0.001	Mobile.Invert
Labridae	*Diproctacanthus xanthurus*	0.44	<0.001	Corallivore
Labridae	*Halichoeres hortulanus*	0.3	0.002	Mobile.Invert
Labridae	*Halichoeres melanurus*	0.25	0.003	Mobile.Invert
Labridae	*Halichoeres podostigma*	0.17	0.031	Mobile.Invert
Labridae	*Hemigymnus melapterus*	0.37	<0.001	Mobile.Invert
Labridae	*Hologymnosus annulatus*	0.24	0.014	Piscivore
Labridae	*Labroides dimidiatus*	0.38	0.013	Piscivore_Mobile.Invert
Labridae	*Thalassoma hardwicke*	0.87	<0.001	Mobile.Invert
Labridae	*Thalassoma lunare*	0.75	<0.001	Mobile.Invert
Lutjanidae	*Lutjanus bohar*	0.4	0.002	Mobile.Invert
Lutjanidae	*Lutjanus carponotatus*	0.23	0.006	Piscivore_Mobile.Invert
Lutjanidae	*Lutjanus decussatus*	0.33	0.001	Piscivore_Mobile.Invert
Lutjanidae	*Lutjanus fulvus*	0.25	0.003	Piscivore_Mobile.Invert
Lutjanidae	*Lutjanus rivulatus*	0.2	0.033	Piscivore_Mobile.Invert
Lutjanidae	*Lutjanus russellii*	0.19	0.014	Piscivore_Mobile.Invert
Lutjanidae	*Lutjanus semicinctus*	0.61	<0.001	Piscivore_Mobile.Invert
Mullidae	*Parupeneus crassilabris*	0.42	<0.001	Mobile.Invert
Muraenidae	*Gymnothorax javanicus*	0.18	0.048	Piscivore_Mobile.Invert
Nemipteridae	*Pentapodus trivittatus*	0.36	0.001	Piscivore_Mobile.Invert
Nemipteridae	*Scolopsis bilineata*	0.45	<0.001	Mobile.Invert
Nemipteridae	*Scolopsis trilineata*	0.19	0.033	Piscivore_Mobile.Invert

Pomacentridae	*Amblyglyphidodon curacao*	0.2	0.015	Herbivore_Planktivore
Pomacentridae	*Amblyglyphidodon ternatensis*	0.17	0.031	Herbivore_Planktivore
Pomacentridae	*Chromis margaritifer*	0.45	<0.001	Herbivore_Planktivore
Pomacentridae	*Chromis ternatensis*	0.29	0.003	Planktivore
Pomacentridae	*Chromis weberi*	0.27	0.006	Planktivore
Pomacentridae	*Chrysiptera cyanea*	0.25	0.004	Herbivore_Planktivore
Pomacentridae	*Dascyllus reticulatus*	0.18	0.022	Planktivore
Pomacentridae	*Dischistodus melanotus*	0.2	0.023	Herbivore
Pomacentridae	*Neoglyphidodon melas*	0.25	0.003	Omnivore
Pomacentridae	*Plectroglyphidodon dickii*	0.21	0.009	Piscivore
Pomacentridae	*Pomacentrus bankanensis*	0.34	<0.001	Herbivore_Planktivore
Pomacentridae	*Pomacentrus chrysurus*	0.22	0.008	Omnivore
Pomacentridae	*Pomacentrus coelestis*	0.21	0.009	Mobile.Invert_Planktivore
Pomacentridae	*Pomacentrus moluccensis*	0.58	<0.001	Omnivore
Scaridae	*Chlorurus bleekeri*	0.17	0.030	Herbivore
Scaridae	*Chlorurus sordidus*	0.29	0.002	Herbivore
Scaridae	*Scarus dimidiatus*	0.17	0.031	Herbivore
Serranidae	*Aethaloperca rogaa*	0.24	0.016	Piscivore_Mobile.Invert
Serranidae	*Cephalopholis argus*	0.31	0.004	Piscivore
Serranidae	*Cephalopholis boenak*	0.31	0.001	Piscivore_Mobile.Invert
Siganidae	*Siganus argenteus*	0.19	0.035	Omnivore
Siganidae	*Siganus doliatus*	0.17	0.032	Herbivore
Siganidae	*Siganus puellus*	0.21	0.008	Omnivore
Siganidae	*Siganus vulpinus*	0.31	0.001	Herbivore_Planktivore
Zanclidae	*Zanclus cornutus*	0.37	0.023	Omnivore
Intermediate				
Acanthuridae	*Acanthurus thompsoni*	0.22	0.008	Planktivore
Acanthuridae	*Naso thynnoides*	0.32	<0.001	Omnivore
Balistidae	*Odonus niger*	0.33	0.032	Planktivore
Balistidae	*Sufflamen bursa*	0.39	0.001	Mobile.Invert

Caesionidae	*Pterocaesio digramma*	0.17	0.028	Planktivore
Carcharhinidae	*Triaenodon obesus*	0.18	0.042	Piscivore_Mobile.Invert
Chaetodontidae	*Coradion chrysozonus*	0.22	0.033	Omnivore
Chaetodontidae	*Forcipiger flavissimus*	0.17	0.030	Mobile.Invert
Chaetodontidae	*Forcipiger longirostris*	0.19	0.015	Mobile.Invert
Labridae	*Bodianus diana*	0.19	0.009	Mobile.Invert
Labridae	*Bodianus dictynna*	0.22	0.010	Mobile.Invert
Labridae	*Choerodon zosterophorus*	0.22	0.012	Mobile.Invert
Labridae	*Halichoeres chrysus*	0.39	<0.001	Mobile.Invert
Labridae	*Halichoeres prosopeion*	0.33	0.002	Mobile.Invert
Lethrinidae	*Monotaxis grandoculis*	0.22	0.020	Mobile.Invert
Lutjanidae	*Macolor macularis*	0.29	0.004	Piscivore_Mobile.Invert
Monacanthidae	*Paraluteres prionurus*	0.17	0.031	Omnivore
Pomacanthidae	*Centropyge bicolor*	0.3	0.002	Mobile.Invert
Pomacanthidae	*Genicanthus lamarck*	0.29	0.001	Planktivore
Pomacentridae	*Pomacentrus amboinensis*	0.36	<0.001	Herbivore_Planktivore
Pomacentridae	*Pomacentrus nigromanus*	0.27	0.007	Planktivore
Serranidae	*Plectropomus oligacanthus*	0.19	0.016	Piscivore_Mobile.Invert
Serranidae	*Variola albimarginata*	0.19	0.034	Piscivore
Tetraodontidae	*Canthigaster valentini*	0.17	0.031	Omnivore
MCE				
Balistidae	*Abalistes stellatus*	0.41	<0.001	Piscivore_Mobile.Invert
Balistidae	*Sufflamen fraenatum*	0.23	0.023	Mobile.Invert
Carangidae	*Carangoides ferdau*	0.35	0.011	Piscivore_Mobile.Invert
Labridae	*Choerodon jordani*	0.25	0.003	Mobile.Invert
Lethrinidae	*Lethrinus amboinensis*	0.25	0.017	Piscivore_Mobile.Invert
Lethrinidae	*Lethrinus lentjan*	0.17	0.031	Piscivore_Mobile.Invert

Malacanthidae	*Hoplolatilus purpureus*	0.25	0.002	Planktivore
Mullidae	*Parupeneus heptacanthus*	0.2	0.027	Piscivore_Mobile.Invert
Nemipteridae	*Pentapodus nagasakiensis*	0.36	0.004	Mobile.Invert
Nemipteridae	*Pentapodus paradiseus*	0.39	<0.001	Piscivore_Mobile.Invert
Nemipteridae	*Scolopsis vosmeri*	0.25	0.003	Mobile.Invert
Pomacentridae	*Pomacentrus nagasakiensis*	0.17	0.031	Herbivore_Planktivore

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